Bulletin of Entomological Research (2002) **92**, 177–184 DOI: 10.1079/BER2001147

The influence of plant age on tolerance of rice to injury by the rice water weevil, *Lissorhoptrus oryzophilus* (Coleoptera: Curculionidae)

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Abstract

For most plant species, tolerance to many types of herbivory increases as plants age, but the applicability of this pattern to root herbivory has not been tested. Injury to roots of rice plants by larvae of the rice water weevil, *Lissorhoptrus oryzophilus* Kuschel, causes severe reductions in yields in the United States. It is generally thought that young rice plants, because their root systems are smaller, are less tolerant than older plants of root feeding by *L. oryzophilus*. Field experiments were conducted to test this hypothesis. Plots of rice (4.7 to 6.5 m^2) were established and subjected to natural infestations of *L. oryzophilus* larvae. A soil insecticide was applied to plots at different times during the tillering phase of rice in order to manipulate the timing of weevil infestation. The impact of these treatments (timings of insecticide applications) was assessed by comparing relationships between yield loss and larval pressure for each treatment using analysis of covariance. Yield losses ranged from 13% to over 40% in plots not treated with insecticide. Patterns of yield losses from plots treated with insecticide at different times were best explained by the hypothesis that yield loss is determined both by the age of plants infested and by the size of larvae infesting plants. Young plants appear to be less tolerant than older plants, and feeding by large larvae appears to be more deleterious than feeding by smaller larvae. Management practices that delay infestation of rice by *L. oryzophilus* until plants are older may be an important component of management programmes for this pest.

Introduction

The resistance of plants to arthropod herbivores changes as plants age. Age-related changes in the suitability of plant tissues for herbivores and in the susceptibility of plants to infestation have been frequently documented (Smith, 1989; Koch & Mew, 1991; Diawara *et al*. 1994). For example, survival, growth, and feeding of green leafhopper, *Nephotettix virescens* Distant (Hemiptera: Cicadellidae), adults were greater on 10- to 20-day-old rice plants than on older rice plants (Rapusas & Heinrichs, 1987). Plant tolerance, defined here as the ability of a plant to grow or reproduce following injury such that reductions in growth or yield experienced by tolerant plants are lower than those experienced by susceptible plants, is also influenced by plant age (Bardner & Fletcher, 1974; Trumble *et al.*, 1993; Rosenthal & Kotanen, 1994; Strauss & Agrawal, 1999). The nature of the

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https://doi.org/10.1079/BER2001147 Published online by Cambridge University Press

relationship between plant age and plant tolerance varies with, at the least, plant species and type of injury (Strauss & Agrawal, 1999; Peterson & Higley, 2001). For many plant species, tolerance to defoliation increases once the seedling phase is passed and as vegetative growth proceeds (Bardner & Fletcher, 1974). However, the applicability of this generality to other types of natural injury is a largely unexplored topic (Strauss & Agrawal, 1999).

The rice water weevil, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae), is the most destructive insect pest of rice, *Oryza sativa* L. (Poaceae), in the United States. This insect is native to North America but has been accidentally introduced into some of the major rice-producing regions of Asia and therefore poses a global threat to rice production (Heinrichs & Quisenberry, 1999). Although both larvae and adults of this insect feed on rice, it is primarily the larval stage that causes economic losses (Way, 1990). Adult weevils feed on the foliage of rice plants, leaving longitudinal slit-like scars. Oviposition commences when rice fields are flooded (Rice *et al.*, 1999), and larvae feed externally on the roots of flooded rice plants. Chronic injury caused by root pruning results in reductions in plant growth, tillering and grain yields (Grigarick, 1984; Way, 1990). This insect is a particularly severe pest in southwestern Louisiana, where two or three generations may occur annually. Yield losses in Louisiana typically approach 10% and can exceed 25% under heavy weevil pressure (Stout *et al.*, 2000).

Oviposition by female rice water weevils is strongly dependent on the presence of water (Rice *et al.*, 1999). For this reason, initial infestation of rice roots by weevil larvae is effectively synchronous with the time at which permanent flood is applied to fields. The plant stage at which permanent flood is applied to rice fields can vary considerably. In some fields, rice is flooded within two weeks of planting; in others, flooding is delayed until plants are at the 5–6 leaf stage or older. Thus, an understanding of the relationship between rice plant age and tolerance of weevil feeding is critical to an understanding of the determination of yield loss from this insect and is an important consideration in the development of a weevil management programme.

It is generally thought that young rice plants, because their root systems are smaller and less developed, are less tolerant than older plants of root injury caused by feeding of *L. oryzophilus* larvae. However, this hypothesis has never been directly tested. In the experiments reported here, the timing of infestation by *L. oryzophilus* larvae was manipulated by varying the timing of insecticide applications to plots. Grain yields from plots of the different treatments were then compared. If young rice plants are less tolerant of root injury by larvae than older plants, then the yield benefit derived from protecting young plants from infestation should be greater than the yield benefit derived from protecting older plants. Alternatively, if tolerance does not vary with plant age, then the yield benefit of insecticide applications should not vary with timing of application.

Materials and methods

General cultural practices

Four experiments were conducted, one in 1999 and three in 2000, at the Louisiana State University Rice Research Station, Crowley, Acadia Parish, Louisiana. The soil type was a silt loam (fine, montmorillonitic, thermic Typic Albaqualf). The rice cultivar used in 1999 was 'Cypress', and the cultivar used in 2000 was 'Cocodrie'. 'Cypress' and 'Cocodrie' are semi-dwarf, early-maturing long grain cultivars with similar pedigrees, both developed and released in Louisiana within the past ten years (Linscombe *et al.*, 2000). The date of planting in 1999 was 12 April. In 2000, planting dates were spaced throughout the growing season, with the earliest planting date in April and the latest planting date in June. Rice was drill-seeded at a rate of 112 kg ha^{-1} (1999) or 100 kg ha^{-1} (2000). Total nitrogen fertilization rate was roughly 135 kg ha^{-1} in all experiments, with most of the fertilizer supplied before flooding. Other agronomic practices used were typical of those used in rice in southwest Louisiana.

Experimental approach and treatments

Timings of insecticide applications were varied in order to manipulate the timing of infestation of rice roots by *L. oryzophilus* larvae. Insecticide was applied on a total of three dates in all experiments, although not all plots received insecticide on all three dates. The insecticide used in all experiments was Furadan® 3G (carbofuran, 30 g kg^{-1} active ingredient; FMC Corporation, Philadelphia) at 0.7 kg ha^{-1}. Furadan 3G is a granular carbamate insecticide that was used as a soil insecticide for control of *L. oryzophilus* larvae for over 30 years until its recent removal from the market. Carbofuran was used in these experiments despite the fact that it is no longer used commercially because it was the only product available that controls larvae after they have established on rice roots. The direct effects of carbofuran on crop plant physiology are probably minimal (Haile *et al.*, 1999). Carbofuran was shaken out evenly over plots from glass jars with perforated metal lids.

The treatments employed were as follows: (i) an untreated control ('no exclusion'), in which no insecticide was applied to plots; (ii) 'early' exclusion, in which plants were protected at an 'early' phase of tillering, but not at 'mid' or 'late' phases; (iii) 'mid' exclusion, in which plants were protected at a 'mid' phase of tillering, but not at 'early' or 'late' phases; (iv) 'late' exclusion, in which plants were protected at a 'late' phase, but not at 'early' or 'mid' phases; or (v) 'total exclusion', in which plants were protected at 'early', 'mid', and 'late' phases of tillering. For experiments in 2000, a sixth treatment ('early + mid') was employed in which insecticide was applied at 'early' and 'mid' time points but not the 'late' time point. Thus, no carbofuran applications were made to 'no exclusion' plots; one carbofuran application was made to plots in treatments 'early', 'mid', and 'late'; two applications were made to treatment 'early + mid', and three applications were made to the 'total exclusion' treatment.

The schedule for planting, flooding, applying insecticide, sampling weevils, and harvesting for each experiment is shown in table 1. Dates of flooding and carbofuran application were adjusted somewhat in later plantings to compensate for the more rapid growth of plants and insects later in the season. However, in all experiments, rice was flooded before plants began to tiller, when they possessed two to four true leaves (stages V2–V4 in the system of Counce *et al.*, 2000). Applications of carbofuran were made to appropriate plots somewhat earlier in 2000 than in 1999

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Table 1. Schedule of cultural and management practices for the four rice plant age / tolerance experiments conducted during the 1999 and 2000 field seasons at the Louisiana State University Rice Research Station.

	1999	2000		
	Experiment 1	Experiment 1	Experiment 2	Experiment 3
Date of seeding	12 April 1999	11 April 2000	11 May 2000	1 June 2000
Date of flooding	23 DAS	17 DAS	19 DAS	22 DAS
First carbofuran application (E, E+M, and TE plots)	9 DAF	6 DAF	6 DAF	5 DAF
First larval core sampling	19 DAF	18 DAF	13 DAF	13 DAF
Second carbofuran application (M, E+M, and TE plots)	23 DAF	19 DAF	16 DAF	13 DAF
Second larval core sampling	30 DAF	27 DAF	22 DAF	19 DAF
Third carbofuran application (L and TE plots)	37 DAF	32 DAF	27 DAF	21 DAF
Third larval core sampling	51 DAF	39 DAF	30 DAF	28 DAF
Field drain	94 DAF	91 DAF	85 DAF	81 DAF
Harvest date	112 DAF	110 DAF	99 DAF	101 DAF

DAF, days after flooding; DAS, days after seeding; E, exclusion during early tillering phase; M, exclusion during mid tillering phase; E + M, exclusion during both early and mid tillering phases; L, exclusion during late tillering phse, TE, exclusion during early, mid, and late tillering; NE, no exclusion.

(table 1). In all experiments, the first application of carbofuran was always made just prior to tillering or at the very early tillering stage. The second application of carbofuran was made to appropriate plots during the period of rice growth when rice was actively tillering. The third application was made later in the tillering stage, but before panicle initiation in all experiments.

The impact of timing and frequency of carbofuran applications on rice was assessed by taking grain yields. Whole plots were harvested with a mechanical harvester. Grain moistures were determined and grain yields were adjusted to 12% moisture. Yields are expressed as kg ha^{-1}.

The experimental design used for all experiments was a randomized complete block design with six replications (1999, 12 April planting), eight replications (2000, 11 April and 11 May plantings), or five replications (2000, 1 June planting). Plot sizes were 6.5 m^2 (1999 experiment and June 1, 2000 planting) and 4.7 m^2 (April and May, 2000 plantings).

Insect sampling

Densities of immature *L. oryzophilus* in plots of the different treatments were assessed at three time points during the growing season, usually about a week after an insecticide application (table 1). Densities of weevil immatures in plots were determined using a soil / root core sampler with a diameter of 9.2 cm and a depth of 7.6 cm. Two or, on some sampling dates, three, core samples were taken from each plot; each core sample contained from one to ten rice plants. Core samples were processed by placing them in a 40-mesh screen sieve bucket and washing soil from roots. Buckets were then placed into basins of salt water, and immature weevils were counted as they floated to the surface of the salt solution (Stout *et al.*, 2000). Immature weevils were categorized as small, medium, or large larvae or as pupae. Counts of immatures from the two or three core samples for each plot were averaged to give a mean density (expressed as immature weevils per core).

Statistical analyses

Insect density data from each core sampling date for each of the four experiments were analysed separately. In addition, a total weevil count for each plot in each experiment was obtained by summing mean immature densities from the three core sampling dates for each plot. Data were analysed by mixed model ANOVA using PROC MIXED in SAS with treatment as a fixed effect and block (replicate) as a random effect (Littell *et al.*, 1996). Means were separated using an LSD test.

Yield data from the 1999 and 2000 experiments were pooled and analysed using PROC MIXED in SAS with treatment as a fixed effect and planting date, block and planting date × treatment as random effects (Littell *et al.*, 1996). A pooled analysis was justified because preliminary analyses of yields showed very similar patterns of yield loss among treatments in the four experiments. Planting date is known to affect rice yield; in particular, rice yields are reduced when fields are planted after mid-May in southwest Louisiana. However, planting date was treated as a random effect because the planting dates used were essentially chosen randomly from the range of possible planting dates. Means were separated using an LSD test.

Analyses of total weevil counts showed significant differences among treatments (see below). These differences in weevil pressure may have had effects on yields independent of the effects of treatment. To account for this possibility, and to account for differences in absolute yields between experiments, pooled data from all four experiments were re-analysed using a mixed-model, analysis of covariance approach (Littell *et al.*, 1996) in which the relationships between treatment, adjusted total weevil counts (the covariate for the analyses), and standardized yield losses were assessed (Reese *et al.*, 1994). A standardized yield loss (Smith *et al.*, 1994) for each plot was calculated using the formula

$$\text{Yield loss}_{j,k} = (\text{Yield}_{j,k} - \text{Yield}_{TE,k}) / \text{Yield}_{TE,k}$$

in which $\text{Yield}_{j,k}$ represents the yield in kg ha^{-1} from a plot of treatment *j* and block *k* and $\text{Yield}_{TE,k}$ represents the yield from the total exclusion plot in the same block. An adjusted total weevil count for each plot was obtained using the formula,

$$\text{Adjusted total weevils}_{j,k} = \text{Total weevils}_{j,k} - \text{Total weevils}_{TE,k}$$

in which $\text{Total weevils}_{j,k}$ is the total weevil count from a plot of treatment *j* and block *k* and $\text{Total weevils}_{TE,k}$ represents the total weevil count from the total exclusion plot in the

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same block. Using the PROC MIXED module in SAS, a series of regression models were then used to test specific hypotheses about the relationship between total weevil counts (covariate) and standardized yield loss for the different treatments. The ESTIMATE statement in PROC MIXED was used to compare slopes. The LSMEANS procedure with an LSD was used to compare treatment means at the mean value of the covariate (24.75 total weevils per plot), in essence adjusting yield losses for differences in weevil counts (Steel & Torrie, 1980)

Results

Densities of immature weevils

In the 1999 experiment, densities of larvae and pupae in untreated ('no exclusion') plots were low at the 'early' sampling point, quickly rose to their highest point at the 'mid' sampling point, and declined thereafter (table 2). Densities at the 'early' and 'late' sampling points were similar. In 2000, overall weevil densities were similar in the three experiments (table 2) and higher than the densities found in 1999. Larval densities in untreated plots in all three experiments increased as the growing season progressed such that weevil densities on the third core sampling date were at least twice as high as weevil densities on the first core sampling date.

Because *L. oryzophilus* females generally do not oviposit until fields are flooded, larvae in 'early' core samplings were less than 19 days old (the maximum time from flooding until the first core sampling). In the experiments planted in April and May, 80–90% of the larvae found in the first core sampling were classified as small (first or second instars), and no pupae were found (data not shown). In the late-planted experiment in 2000, approximately 45% of larvae found in the first core sampling point were classified as small. In all four experiments, weevils in later core samplings were a mixture of small, medium, and large larvae and a few pupae, with approximately 20–45% of larvae classified as small. This mixture of age classes in 'mid' and 'late' core samplings resulted from the development of larvae infesting rice early after flooding and continued re-infestation of rice by later-arriving females. Hence, 'early' carbofuran applications eliminated predominantly small (first or second instar) larvae, whereas later carbofuran applications eliminated a mixture of small, medium, and large larvae and pupae.

Use of the insecticide carbofuran had the desired effect of temporarily reducing densities of *L. oryzophilus* in those plots to which carbofuran was applied (table 2). Generally speaking, densities of weevils were reduced on the sampling date subsequent to carbofuran application, but rose again as the season progressed, with an apparent larvicidal activity of two to three weeks. As a result, plots of the different treatments were subject to different temporal patterns of infestation. In 'early'-treated plots, approximately 10% of the total weevils found in plots were found on the first core sampling date, 40% were found on the 'mid' core sampling date, and 50% on the 'late' core sample. The majority of immature weevils found in 'mid' treated plots were found in 'early' and 'late' core samplings: 42% of total weevils found in plots were found at the 'early' core sampling point, 23% at the 'mid' sampling point, and 35% at the 'late' sampling point. The corresponding figures for 'late' treated plots were 23%, 57% and 20% of total weevils found at the 'early', 'mid' and 'late' sampling points, respectively.

Table 2. Densities of immature *Lissorphopturs oryzophilus* (larvae + pupae per core sampling ± S.E.) on three sampling dates in plots subjected to different insecticide exclusion regimes.

Sampling date (days after flooding)	Larval densities (larvae per core ± S.E.)					
	No exclusion (no applications)	Early	Mid	Late	Early + mid	Total exclusion (3 applications)
1999 Planting date 1: April 12						
19 DAF	6.2 ± 1.9 b	1.9 ± 0.6 a	6.2 ± 1.2 b	6.8 ± 1.6 b	–	2.3 ± 1.2 a
30 DAF	16.1 ± 1.8 c	6.4 ± 0.5 b	3.3 ± 0.5 b	16.8 ± 1.3 c	–	1.8 ± 0.4 a
51 DAF	7.6 ± 1.9 c	6.3 ± 0.9 bc	4.4 ± 0.6 ab	2.4 ± 0.6 a	–	2.7 ± 0.8 a
Total	29.9 ± 4.2 c	14.7 ± 1.3 b	13.9 ± 1.6 b	25.9 ± 2.4 c	–	6.8 ± 1.2 a
2000 Planting date 1: April 11						
18 DAF	8.7 ± 0.9 b	3.1 ± 0.5 a	8.9 ± 1.9 b	10.1 ± 1.7 b	6.9 ± 1.7 ab	6.9 ± 1.6 ab
27 DAF	21.9 ± 4.1 b	15.8 ± 2.0 b	3.3 ± 0.3 a	19.9 ± 3.0 b	2.6 ± 0.9 a	2.8 ± 0.7 a
39 DAF	25.1 ± 1.9 d	23.4 ± 1.2 d	5.6 ± 1.0 b	10.5 ± 1.8 c	7.2 ± 1.2 bc	1.1 ± 0.5 a
Total	55.7 ± 5.0 c	42.3 ± 2.3 c	17.8 ± 2.7 b	40.4 ± 3.6 c	16.6 ± 1.8 b	10.8 ± 2.0 a
2000 Planting date 2: May 11						
13 DAF	7.8 ± 1.4 b	1.3 ± 0.4 a	8.5 ± 1.3 b	5.9 ± 0.8 b	1.0 ± 0.2 a	1.6 ± 0.5 a
22 DAF	28.1 ± 4.0 c	17.5 ± 2.8 b	10.9 ± 1.8 b	41.6 ± 1.9 c	4.9 ± 1.2 a	4.4 ± 0.9 a
30 DAF	28.1 ± 3.4 c	18.3 ± 2.5 bc	7.6 ± 1.4 a	18.1 ± 3.4 b	6.6 ± 1.1 a	6.3 ± 1.1 a
Total	64 ± 6.4 c	37.1 ± 4.9 b	27.0 ± 2.8 b	65.6 ± 3.7 c	12.4 ± 1.9 a	12.3± 1.4 a
2000 Planting date 3: June 1						
13 DAF	11.5 ± 1.3 b	5.2 ± 1.6 a	12.6 ± 1.7 b	13.7 ± 1.4 b	7.7 ± 1.6 ab	4.3 ± 1.5 a
19 DAF	18.1 ± 2.7 c	12.6 ± 2.9 c	2.5 ± 1.0 a	20.3 ± 3.5 c	7.8 ± 2.6 c	4.5 ± 0.9 b
28 DAF	24.8 ± 8.9 c	19.7 ± 3.0 bc	13.6 ± 4.1 b	7.8 ± 2.3 ab	16.9 ± 6.2 bc	3.6 ± 2.6 a
Total	54.4 ± 9.3 c	37.5 ± 4.7 bc	28.7 ± 5.3 b	41.8 ± 3.4 bc	32.4 ± 5.4 b	12.4 ± 2.1 a

Data shown from four experiments conducted during the 1999 and 2000 field seasons at the Louisiana State University Rice Research Station. Means in the same row followed by the same letter are not significantly different based on an LSD test. DAF, days after flooding.

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The total number of immature weevils found in plots over the three core sampling dates differed among treatments (table 2). Total weevil counts were highest in 'no exclusion' plots and lowest in 'total exclusion' and 'early + mid' plots. Of those plots receiving one application of carbofuran, weevil counts were lower in 'mid'-treated plots than in 'early' or 'late' treated plots. In three of the four experiments, total weevil counts were higher in 'late' plots than in 'early' plots, but differences were significant in only one experiment.

Grain yields

Yield losses in untreated plots averaged 13% in 1999 and exceeded 40% in 2000. Patterns of yield loss in the four experiments were similar. The pooled analysis of grain yield data from 1999 and 2000 (fig. 1) shows that grain yields from plots increased as the number of carbofuran applications to plots increased. Grain yields were highest from plots treated three times with carbofuran ('total exclusion'). Plots receiving two applications of carbofuran ('early + mid') yielded more grain than plots receiving only one application of carbofuran (2000 experiments only), regardless of the timing of application. Yields were lowest from plots receiving no insecticide. Of the plots receiving only one application of carbofuran, plots treated at the 'mid' point had significantly higher yields than plots treated at the 'early' time point. Yields from plots treated 'late' were intermediate and did not differ significantly from yields obtained from either 'early' or 'mid' plots.

Analysis of covariance results

The relationships between treatment, adjusted total number of weevils, and standardized yield loss were explored using a series of covariance models. Linear regression models were used because incorporation of quadratic and higher-order terms did not improve the fit or significance of the models. The initial model, in which a significant overall relationship between adjusted total weevil count and standardized yield loss was found (fig. 2; $F_{5,103} = 7.43$, $P < 0.0001$), confirmed that *L. oryzophilus* reduced yields in these experiments. Results of a subsequent model gave evidence that the slopes of relationships between weevil counts and yield losses differed among treatments (significant treatment by covariate interaction: $F_{4,101} = 2.44$, $P = 0.05$). This result indicated that the yield benefit derived from application of insecticide was influenced by timing of the application. The relationships between adjusted total weevil count, treatment, and standardized yield loss were then described by five separate regression models. The parameters for these models are shown in table 3, and the regression lines for treatments 'no exclusion', 'early', 'mid', and 'late' are shown on fig. 2.

Of the regression models generated by the ANCOVA, the model describing yield loss from 'early + mid' plots was most distinct. Both the slope of this model (essentially, 0) and the estimated yield loss at the mean of the covariate (0.3% yield loss at a total weevil count of 24.8 larvae) indicate no loss of yield from weevil feeding for the 'early + mid' treatment. In contrast, weevil feeding reduced yields from plots of the remaining treatments. The slopes of the regression models for the 'late' and 'no exclusion' treatments were significantly lower than the slope for the 'early + mid' model; the slopes of the models for the 'mid' and 'early' treatments were intermediate.

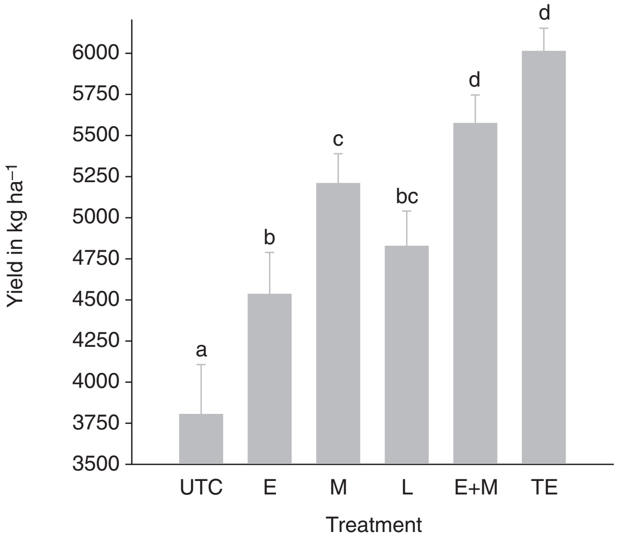

Fig. 1. Grain yields (kg ha^{-1} + S.E.) from rice plots subjected to different frequencies and timings of insecticide (carbofuran at 0.7 kg ha^{-1}) application. Data are pooled from four experiments conducted in 1999 and 2000. For description of treatments, see table 1. Bars accompanied by the same letter are not significantly different (LSD).

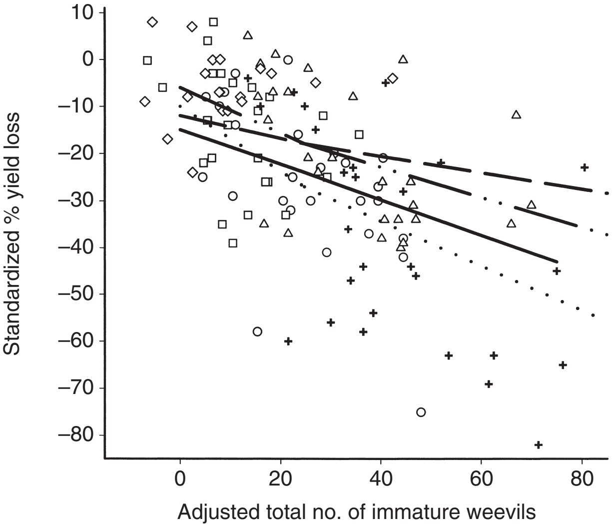

Fig. 2. Relationship between standardized yield loss and adjusted total counts of *Lissorhoptrus oryzophilus* in plots of rice subjected to different timings and frequencies of insecticide application. Each point represents standardized yield from one plot of rice from one of four experiments conducted in 1999 and 2000. Regression lines for four of the treatments are shown. ○, Early exclusion (solid line); □, mid exclusion (dashed line); △, late exclusion (dashed-dotted line); +, no exclusion (dotted line); ◇, early + mid exclusion.

When yield losses were compared at the mean of the covariate (24.8 total weevils per plot), in essence adjusting yield losses for differences in weevil counts (Steel & Torrie, 1980), significant differences were found between

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treatments. Yield losses at the mean of the covariate were highest in the 'no exclusion' treatment, lowest in the 'early + mid' treatment, and intermediate in the plots treated once with carbofuran (table 3). Importantly, yield losses were slightly greater from 'early'-treated plots than from 'mid'- or 'late'-treated plots. This latter result suggests that yields from plots to which insecticide was applied early but not late were not higher than yields from plots to which insecticide was applied late but not early.

Discussion

Feeding by *L. oryzophilus* larvae on the roots of rice plants can be an important constraint on rice yields in the United States. For example, in the experiments reported here, chronic injury from *L. oryzophilus* in 'no exclusion' plots caused yield losses of approximately 1% per larva. Plant age is a potentially important determinant of yield loss from this insect; moreover, the age at which plants are infested by larvae can vary considerably depending on water management practices. Thus, the influence of plant age on tolerance of weevil feeding is an important consideration in the development of a management programme for *L. oryzophilus*. The objective of these experiments was to quantify the relative tolerance of rice plants at different stages of tillering.

Quantifying plant tolerance is more difficult than quantifying other aspects of plant resistance, particularly when differences in herbivory levels must be taken into account (Reese *et al.*, 1994; Smith *et al.*, 1994). In these experiments, the tolerance of rice plants of different ages to root injury was investigated by protecting, via applications of the insecticide carbofuran, rice plants of different ages from injury by weevil larvae, then characterizing yield benefits relative to a total exclusion treatment. Carbofuran applications were made during the tillering period of rice growth (Counce *et al.*, 2000), with the earliest application made very early in the tillering stage and the third application made before panicle initiation (beginning of the reproductive stage). Interpretation of the results of these experiments was complicated by changes in weevil populations during the tillering phase and by differences among treatments in total insect pressure. To adjust for these factors, data were analysed by an ANCOVA using total weevil counts as a covariate. Differences in the tolerance of rice plants of different ages were inferred by comparing regression models. If a phase of development in rice is particularly vulnerable to injury by rice water weevil feeding, then protection of that stage should provide greater yield benefits than protection of a more tolerant stage. Protection of a less tolerant stage should result in a shallower (less negative) relationship between number of larvae and yield loss and/or a smaller yield loss at the mean value of the covariate than protection of a more tolerant stage.

The regression models describing yield losses from plots receiving a single application of carbofuran at different phases of rice growth ('early', 'mid', and 'late' treatments) were similar. Neither the slopes of these models nor the estimated yield losses at the mean of the covariate differed significantly among these treatments, although yield losses from plots of the 'early' treatment tended to be greater than yield losses from the other two treatments. Rice plants protected at an early phase of tillering but not at later phases of tillering did not exhibit lower yield losses than plots infested early but protected later. Thus, the results did not conform to the pattern predicted if rice plants are particularly sensitive to weevil injury early in the tillering period. Ostensibly, then, these models do not support the hypothesis that young rice plants are more susceptible to yield loss than older plants. Rather, they provide limited evidence for slightly increased susceptibility of rice plants later in the tillering phase.

On the other hand, the model describing yield losses from 'early + mid' treatment plots does provide some evidence for increased tolerance of rice in later phases of tillering. In these plots, which were protected from weevil feeding at the 'early' and 'mid' phases but infested during the 'late' phase of tillering, no significant relationship between larval numbers and yield loss was found; moreover, yields from plots of this treatment did not differ from yields of 'total exclusion' plots, which were protected at the 'early', 'mid', and 'late' phases of tillering. This suggests that feeding by weevil larvae on rice roots is not injurious if delayed until the latter stages of tillering, i.e. that rice plants during the latter phases of tillering are tolerant of weevil feeding.

This apparent conflict is partially resolved by an analysis of temporal patterns of infestation in plots of the different treatments. 'Early' applications of carbofuran were made within 5 to 9 days of flooding (table 1) and hence eliminated predominately small larvae. 'Early' plots were then re-

Table 3. Parameters of the regression models used to describe the relationships between adjusted total number of *Lissorhoptrus oryzophilus* larvae and standardized yield losses for five insecticide treatments.

Treatment	Y-intercept (S.E.)	Slope (S.E.)[1]	LS MEAN (S.E.)[2]
No exclusion	−9.9 (6.8)	−0.71 (0.13) b	−27.4 (4.5) c
Early	−15.0 (6.0)	−0.38 (0.19) ab	−24.4 (4.0)bc
Mid	−11.8 (4.9)	−0.26 (0.24) ab	−18.1 (5.0) b
Late	−6.3 (6.5)	−0.48 (0.16) b	−18.1 (4.2) b
Early + mid	−2.8 (4.8)	0.10 (0.24) a	−0.3 (5.7) a

[1] % yield loss per weevil; means separated using the ESTIMATE statement in PROC MIXED.

[2] The LSMEAN column shows adjusted % yield losses at the mean of the covariate (24.8 total weevils per plot over three core sampling dates). Means were separated using an LSD test.

Models were developed using pooled data from four experiments conducted in 1999 and 2000.

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infested, and over 90% of the total number of immature weevils found in these plots over the course of three sampling dates were found on 'mid' and ''late' core sampling dates, when larvae were, on average, larger. In contrast, 'mid'- and 'late'- treated plots were infested early, and applications of carbofuran made to these plots at the 'mid' or 'late' time points eliminated a mixture of small, medium, and large larvae. A higher proportion of the total number of immature weevils found in 'mid'- and 'late'- plots were small larvae found at the 'early' core sampling. The weights of *L. oryzophilus* larvae increase 9- to 10-fold with each instar, and relative feeding rates of third- and fourth-instar larvae are estimated to be 10 to 1000 times greater than relative feeding rates of first- and second-instar larvae (Wu & Wilson, 1997). Thus, the 'mid' and 'late' applications of carbofuran had a greater impact on yields (fig. 1) probably because they eliminated a greater number of large, damaging larvae than did 'early' applications. The fact that 'early' applications of carbofuran impacted yield to nearly the same degree as 'mid' or 'late' applications despite eliminating primarily small larvae is probably an indication of the high sensitivity of rice plants early in the tillering stage. If larvae at the 'early' phase of tillering had been, on average, as large as larvae at the 'mid' and 'late' phases of tillering, the yield benefits associated with 'early' application of carbofuran would undoubtedly have been greater.

Thus, the patterns of yield loss observed are best explained by hypothesizing that both the age of the plant infested and the size of the larvae infesting the plant are important determinants of yield loss in the rice–rice water weevil system. As is the case in many plant–insect systems, older (larger) *L. oryzophilus* larvae appear to be more injurious than smaller larvae (Wu & Wilson, 1997). Rice plants at the later stages of tillering appear to be capable of tolerating some feeding by weevil larvae, and young plants are probably more susceptible to yield losses from weevil feeding. However, young plants are rarely, if ever, exposed to large larvae because larval infestation does not commence until fields are flooded. The dual importance of pest size and plant age has also been recognized for root-feeding pests of corn (Culy, 2001).

Clearly, management practices for *L. oryzophilus* should focus not only on reducing densities of large, damaging larvae on tillering rice, but also on delaying infestation as long as is feasible. These goals can, of course, be achieved using insecticides, but they can also be achieved by the cultural practice of delaying flooding. In southwest Louisiana, growers flood many fields before rice has begun to tiller. This cultural practice, although it suppresses the germination of important weed pests, results in the infestation of rice roots when they are young and vulnerable to injury. Delaying the application of permanent flood until rice is older may therefore be an effective contributing strategy for management of the rice water weevil because it reduces the numbers of larvae infesting rice during the vulnerable tillering phase. The introduction of herbicide-resistant rice, anticipated within a few years, should reduce the need for early flooding of rice fields and make the use of delayed flooding a feasible strategy for rice water weevil management.

Acknowledgements

The authors gratefully acknowledge the technical assistance of Blake Henry and Li Zou and the advice of Dr D. Blouin on statistical analyses. The manuscript was improved by comments from Drs Frank Guillot and Linda Hooper. Research was supported by the Louisiana Rice Research Board and grants from the USDA Pest Management Alternatives Program (97-34365-5030) and the USDA-NRICGP (Biologically-Based Pest Management Program, 00-35316-9251). Approved for publication by the director of the Louisiana Agricultural Experiment Station, manuscript no. 01-17-0340.

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(Accepted 26 November 2001)
CAB *International*, 2002

https://doi.org/10.1079/BER2001147 Published online by Cambridge University Press