Rice Water Weevil (Coleoptera: Curculionidae) Population Dynamics in Louisiana[1]

Hanwu Shang,[2] Michael J. Stout,[3] Zhitao Zhang[4] and Jiaan Cheng[5]

Department of Entomology, Louisiana Agricultural Experiment Station, Louisiana State University Agricultural Center, Baton Rouge, LA 70803 USA

J. Entomol. Sci. 39(4): 623-642 (October 2004)

Abstract The rice water weevil, *Lissorhoptrus oryzophilus* Kuschel, has long been an important pest of rice in the U.S. and has recently emerged as a pest of rice in Asia. A systematic study of the life history and population dynamics of this insect was conducted during the 2002 growing season at the Louisiana State University Rice Research Station, Crowley, Acadia Parish, LA, an area where it is a particularly severe pest. By monitoring weevil populations using collections from overwintering sites, from plots of rice planted throughout the growing season, and from light traps, and by dissecting collected weevils to assess the conditions of their fat bodies, flight muscles and ovaries, we concluded that a portion of the weevil population in Louisiana is univoltine, another portion is bivoltine, and another portion may pass through multiple generations if young rice is continually available. However, only one generation of weevils developed in a single rice field. Adult weevils invaded rice fields in apparently large numbers prior to flooding. Weevils possessing both well-developed ovaries and well-developed flight muscles were found in both light traps and rice plots, suggesting that adults were capable of seeking new habitats by flying if rice plants were not suitable for oviposition. Weevils were able to complete a generation on ratoon-crop rice. The emergence of overwintered weevils started in late March, with peak emergence occurring during April and May. Return to overwintering sites began in early June and continued until October. Weevils appeared to move among overwintering habitats. A comparison of weevil population dynamics in rice plots planted on different dates supported the use of early planting as a management strategy.

Key Words *Lissorhoptrus oryzophilus, Oryza sativa,* population dynamics, ovarian development, flight muscles, fat bodies

The rice water weevil, *Lissorhoptrus oryzophilis* Kuschel (Coleoptera: Curculionidae), is the most widely distributed and destructive insect pest of rice, *Oryza sativa* L., in the U.S. (Bowling 1980, Way 1990). The insect is native to the eastern U.S. and was introduced into rice-producing areas of California in the late 1950's (Lance and Grigarick 1959). Populations in rice in the southeastern U.S. reproduce sexually, but the population found in California is parthenogenetic (Lange and Grigarick 1959). *L. oryzophilus* attained greater global significance after a parthenogenetic population invaded Japan In 1976 (Iwata 1976), then spread to North and South Korea (Goh and Choi 1993) and China in subsequent decades (Shang et al. 1998). Estimates of yield losses caused by this insect differ from region to region (Way 1990). In Louisiana,

[1]Received 20 October 2003; accepted for publication 18 January 2004.

[2]Zhejiang University, Hangzhou 310029, China. Current address: Plant Quarantine Station, Zhejiang Department of Agriculture, Hangzhou 310020, China.

[3]Address inquiries (email: mstout@agctr.lsu.edu).

[4]Rice Research Station, Louisiana State University Agricultural Center, P.O. Box 1429, Crowley, LA 70527.

[5]Zhejiang University, Hangzhou 310029, China.

where this insect is a particularly severe pest, yield losses typically exceed 10% (Smith 1983) and can approach 70% or more (Anonymous 1994).

Aspects of the life history of *L. oryzophilus* have been described by several authors, with the most recent detailed account given by Muda et al. (1981). Adult weevils fly to overwintering sites in summer (Smith 1983) where they presumably enter a true diapause (Knabke 1973, Nilakhe 1977). Overwintering habitats are various, including Spanish moss, leaf litter, bunch grasses, grass clumps and plant debris in and around rice fields or uncultivated areas (Webb 1914, Isely and Schwardt 1934, Grigarick and Beards 1965, Gifford and Trahan 1967). The indirect flight muscles of adults are greatly reduced during the winter. Muscle regeneration occurs in spring shortly before the adults leave overwintering sites (Muda et al. 1981, Haizlip and Tugwell 1983, Morgan et al. 1984). The emergence period in Louisiana was observed by Webb (1914) to fall between 25 March and 26 June; whereas, in Arkansas emergence was reported in late April (Isely and Schwardt 1934). Flight activity of the weevil is influenced by air temperature (Gifford and Trahan 1966). According to Isely and Schwardt (1934) and Muda et al. (1981), the seasonal history of the rice water weevil in a rice field begins after flooding. Few eggs are deposited in fields prior to flooding (Webb 1914). Adults are thought to invade fields in large numbers within a week of flooding, but their numbers soon decline (Isely and Schwardt 1934, Sooksai 1976, Muda et al. 1981). Isely and Schwardt (1934) indicated that the decline may be due to mortality or to migration to other fields with younger rice, but they believed the latter to be most important. Muda et al. (1981) reported that indirect flight muscles degenerate once the adult females establish themselves in a flooded rice field and oviposition begins. Approximately 4 to 5 wks are required for development from egg to adult (Smith 1983). Newly-eclosed weevils can be found in rice fields 5 to 6 wks after flooding (Isely and Schwardt 1934).

The importance of *L. oryzophilus* in areas where it is established and the continuing spread of this insect to major rice-producing regions necessitate a full understanding of its life history and population dynamics. Moreover, *L. oryzophilus* biology may differ sufficiently among rice-producing regions that methods for management used in one region may not be applicable in another, and an understanding of regional differences in the biology of this insect is needed to predict the behavior of this insect in areas threatened by weevil invasion. For these reasons, a systematic study of the life history and population dynamics of this insect was conducted during the 2002 growing season in Louisiana.

Materials and Methods

Major events in the seasonal history of *L. oryzophilus* were observed by monitoring weevil populations using collections from overwintering sites, from plots of rice planted throughout the growing season, and from light traps. Weevils were dissected to assess the conditions of fat bodies, flight muscles and ovaries. Use of these methods yielded information on the initiation of seasonal activity, number of generations, timing of peak abundance, return to overwintering sites, and other aspects of the life history of this pest needed to formulate effective management and containment programs.

Observations were made during the 2002 growing season at the Louisiana State University Agricultural Center Rice Research Station, near Crowley, Acadia Parish, LA. The soil at this site is a silt loam (fine, montmorillonitic, thermic Typic Albaqualf). The rice variety "Cocodrie" was used for all observations. Weevil populations were monitored in small plots that bordered larger experiments not described here. Plots were cultivated following standard agronomic practices for Southwest Louisiana, except that no insecticides or fungicides were applied to plots (except in the ratoon rice field as described below).

First-crop rice, early- and mid-season observations. Population densities of *L. oryzophilus* eggs, immature stages, and adults were systematically surveyed in plots of rice planted on three dates. Plots in each field were 6.1 m in length by 7 rows with rice plants spaced 18 cm apart. The first set of plots (field 1) was drill-seeded on 24 April, the second set (field 2) on 3 May, and the third set (field 3) on 28 May. Plots were irrigated as necessary until permanent flood was established on 16 May, 31 May and 18 June for fields 1, 2, and 3, respectively. Rice plants possessed 3 to 4 fully-expanded leaves when permanent flood was applied. Fields remained flooded until they were drained for harvest.

Sampling for all life stages of weevils was conducted from three plots in field 1 and from four plots in fields 2 and 3. Feeding scars were monitored every 3 to 5 days from emergence of rice until all of the plants in plots showed feeding scars. Adult densities were estimated at intervals of 3 to 4 days after planting early in the season, then at weekly intervals through harvest. Densities of eggs in plots were estimated from 5 to 10 plants from each plot. Plants for egg counts were taken on the same dates as adults were sampled. Densities of immature weevils (larvae and pupae) were determined by taking root/soil core samples weekly beginning 2 wks after flood or earlier. On each sampling date, 5 core samples were collected from each plot.

Ratoon rice field, late-season observations. A survey of weevil populations was conducted in second (ratoon)-crop rice following the observation, on 2 August, of a number of gravid females in the ratoon field. The survey was conducted in plots of rice bordering another experiment designed to investigate the relationship between planting date and rice yield. Plots in this field measured 4.9 m in length and 1.4 m in width. The ratoon-crop field was water-seeded on 24 April and flooded on 10 May. The first crop in this field was harvested on 15 August. Additional nitrogen was applied to the field and the field was re-flooded immediately after harvest. The ratoon crop was harvested on 31 October. Karate® (0.03 kg ha^{-1}, lambda-cyhalothrin, Syngenta Crop Protection, Greensboro, NC) was sprayed to control an infestation of rice stink bug, *Oebalus pugnax* (F.), on 2 August and 17 September. Five core samples were taken weekly from 27 August until harvest from 8 plots. Egg samples were taken only twice from the ratoon field because rice plants in this field were too large and tough to accurately determine egg densities. At least 15 adults were collected weekly for determination of sex ratio and reproductive status of weevils.

Sampling methods. Feeding of adult weevils in fields was monitored by noting the proportion of leaves on plants with feeding scars. Densities of adult rice water weevils in flooded fields were estimated with the aid of a sampling device consisting of a 30-mesh metal kitchen strainer, 20 cm in diam, to which was attached a 50 × 30 cm rectangular section of 20-mesh wire screening. Adults were sampled by striking plants over the sampling device and counting the number of adults falling into the strainer portion of the device. One sample consisted of weevils collected from an entire 6.1 m row of rice plants. This method is similar to that used in Asia to estimate densities of the brown planthopper (Dyck et al. 1979). Adult weevils also were captured in two CDC Miniature light traps (BioQuip products, Gardena, CA), one with a UV light source (4 watt) and one with an incandescent light source. Light traps were positioned on levees near experimental plots. Each trap was programmed to switch on at 1730 and off at 0530 the next morning. Light traps were connected to collection bottle rotators (BioQuip products, Gardena, CA) with 8 plastic collecting jars programmed to rotate every 24 h, when lights switched on. Sampling was terminated on 21 August after light traps were destroyed by a hurricane.

Densities of adults from an overwintering site were estimated following the methods of Gifford and Trahan (1969a). Samples were taken near the boundary of a pasture and a wooded area on the grounds of the LSU Rice Research Station. This area is a known overwintering site for weevils (M.J.S., unpubl. data). Samples were taken 3 to 4 times a month from August 2001 until December 2002. Typically, two samples were taken from leaf litter in the wooded area and two samples were taken from pasture grasses within 3 m of the wooded area; however, between 23 April and 23 September 2002, four samples were taken exclusively from pasture grasses. A metal square measuring 50 cm^2 was used to define an area of grass or leaf litter, and a shovel was used to collect grass or litter and approximately 1 cm of soil into a plastic bag. The contents of plastic bags were emptied into garbage cans and covered with trash-can lids with a single hole drilled into the center of the lid. Garbage cans were then filled to the level of the lid with warm water, causing adults to surface through the hole in the lid (Gifford and Trahan 1969a). Adults were counted over a 4-h period and dissected or sexed.

Densities of weevil eggs were estimated following the methods of Gifford and Trahan (1969b). Individual plants were pulled from rice fields, labeled, washed free of soil, trimmed of excess root and leaf material, and placed in 95% alcohol. After plants were bleached, eggs were counted by carefully dissecting the leaf sheaths of plants under a dissecting scope (10× to 25× magnification). Egg densities are expressed as number of eggs per plant.

Densities of immature stages of the rice water weevil were estimated by counting the number of larvae and pupae contained in a root-soil core sample. The cylindrical core sampler used had a diameter of 9.2 cm and a depth of 7.6 cm. Soil, larvae, and debris in core samples were washed from roots into a 40-mesh screen sieve bucket that retained the larvae. When the bucket was submerged in salt water, the larvae and pupae floated to the surface and were counted.

Reproductive and flight status of weevils. Adults collected from light traps, overwintering sites, and rice fields were dissected to monitor the development status of flight muscles, fat bodies and ovaries. Adult weevils collected from rice fields, light traps, and overwintering sites were dissected immediately under a dissecting microscope at 25× to 45× magnification or stored frozen at −18°C for later dissection. The weevils were held and fixed with a pair of surgical forceps while another pair of forceps was used to remove the elytra and thoracic tergum for assessment of flight muscles (Haizlip and Tugwell 1983). Sternite VII of the abdomen was then gently pulled away from the abdomen to expose ovaries and gut. Ovaries were examined, and their condition and number of eggs recorded. Only mature eggs were counted. Fat bodies were categorized as poorly developed (few fat bodies), partially developed (scattered particle and droplet fat bodies) and well-developed (full, white or yellowish, spongy, hypertrophic, fat bodies) (Zhai et al. 1999b). Flight muscles were categorized as degenerate (very weak or no visible flight muscles), partially developed (less compact and fragile bundles, narrow flight muscles), and fully developed (firm, compact and strong flight muscles) (Zhai et al. 1999a). Ovaries were classified according to the following scale: 0, no oocytes; I, previtellogenic; II, gravid (vitellogenic to chorionated oocytes); III, ovipositing (chorionated eggs stored in the egg calyxes); IV, late ovipositing; V, empty ovarioles (enlarged egg calyxes and with corpus luteum at base of oviducts) (Zhai et al. 1999a).

Typically, 30 individuals were collected and dissected on each sampling date, but sometimes, depending on availability, more or fewer weevils were dissected. Weevils were sexed following the methods of Everett and Newsom (1964).

Results

Early- and mid-season rice. Feeding scars were found on plants prior to flooding. Rice planted later in the season sustained more feeding damage at comparable time points than plants in fields planted earlier in the season. For example, only 5.5% of rice in plots planted on 24 April (field 1) showed feeding scars on the day of flooding, whereas 100% of the plants in fields planted on 28 May (field 3) showed feeding scars on the day of flooding.

Densities of rice water weevil adults, eggs and immatures in fields 1, 2, and 3 are shown in Figure 1. Adults were found on most sampling dates, from the day of flooding until harvest. Maximal densities of adults were found sooner after flooding in plots planted late in the season than in plots planted earlier in the season. There were two distinct peaks of adult densities in field 1, the first occurring 12 to 19 d after flooding and the second 41 to 47 d after flooding. In field 2, there were also two periods of high adult densities, the first 4 to 11 d after flooding, the second 33 to 46 d after flooding. In field 3, peaks of adult densities were less distinct than in the first two fields. The highest density of adults was observed on the day of flooding (1 h after flooding). Weevil densities in this field exceeded 8 adults per row for 42 d after flooding, with peaks of adults at 14 d and 28 d after flooding.

There were distinct peaks of eggs in the two fields planted on 24 April and 3 May, but no apparent peak in the late-planted field of 28 May (Fig. 2). In field 1, eggs were first found 4 d after flooding. Egg density increased gradually to a maximum of 14.5 eggs per plant 19 d after flooding and decreased thereafter until no eggs were found 29 d after flooding. In field 2, high numbers of eggs were found 4 d after flooding, and densities peaked 11 d after flooding. Egg densities decreased thereafter, and no eggs were found 32 d after flooding. In field 3, a few eggs were found before flooding, and low densities of eggs were found throughout the surveillance period.

There was generally only a single major, distinct peak of immature densities in plots (Fig. 1). In field 1, maximum densities of immature weevils were found 38 d after flooding, and densities were above 20 per core from 27 to 49 d after flooding. In field 2 larval densities were highest 18 d after flooding and declined thereafter, although densities remained above 20 immatures per core until 54 d after flooding. In the third field, highest densities were reached 28 d after flooding then decreased gradually.

Over half the weevils collected immediately after flooding in field 1 had mature eggs in their ovaries, with an average of 3.8 eggs found per female (Table 1). The percentage of gravid females in this field remained above 65% over the next 4 wks. More than a third of the weevils collected during this period also had well-developed flight muscles, but the fat bodies on these weevils were poorly-developed. Females with undeveloped ovaries and well-developed fat bodies began to appear in high frequencies 5 wks after flooding, and weevils with undeveloped ovaries represented over half the weevils collected in the 6th wk after flooding. Most of the weevils collected later in the season in this field had poorly developed ovaries and well-developed flight muscles and fat bodies. Sex ratios were biased toward females, particularly for weevils collected 4 or more weeks after flooding, (Table 1).

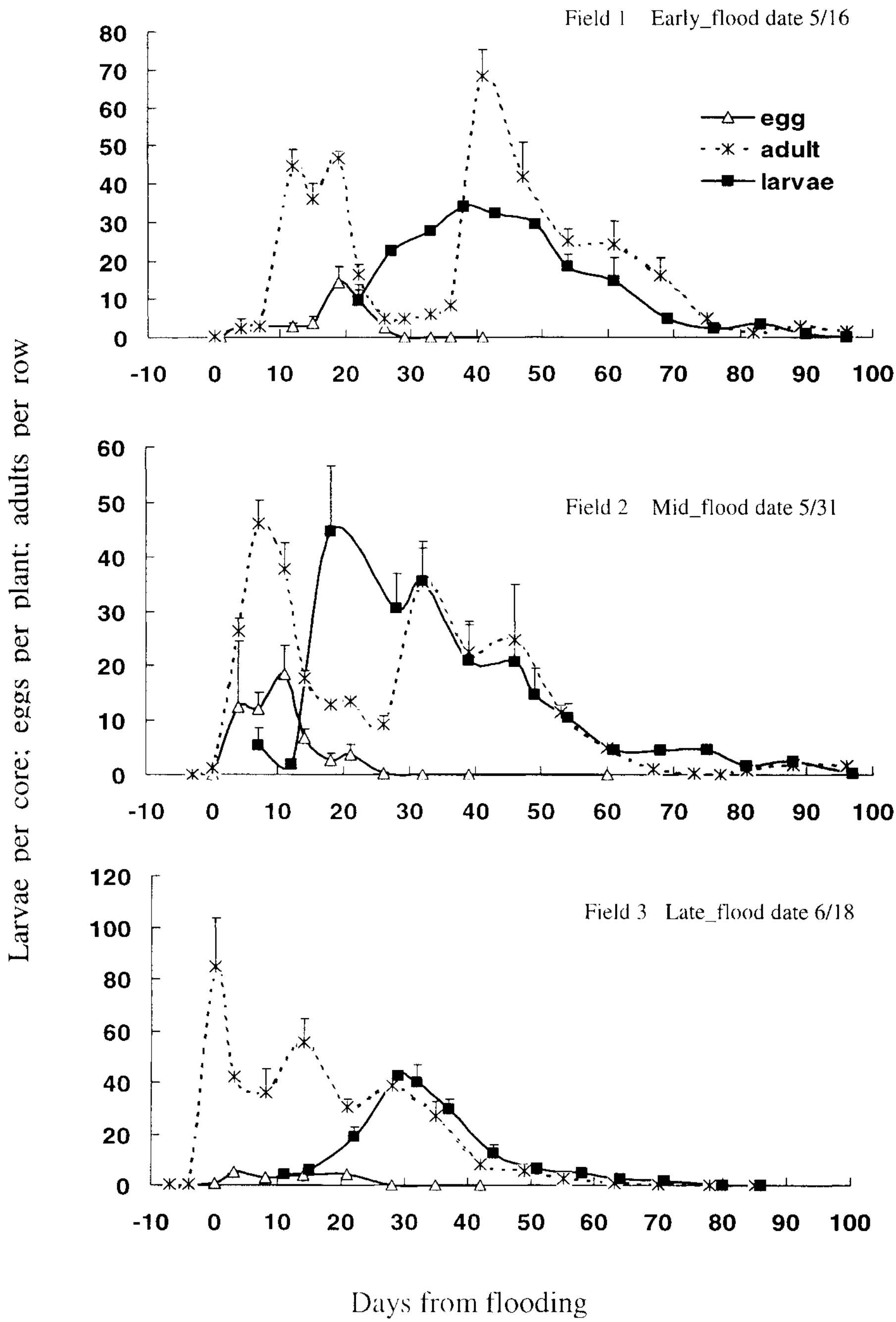

Fig. 1. Mean densities (+SE) of rice water weevil eggs (eggs plant^{-1}), adults (adults row^{-1}), and immatures (larvae and pupae core^{-1}) over time in fields 1, 2, and 3, Rice Research Station, Crowley, LA, 2002.

Table 1. Development of ovaries, flight muscles, and fat bodies in rice water weevils collected from rice plots, Rice Research Station, Crowley, LA, 2002*

Crop type	No. of field	Sampling dates	Days after flood	No. dissected	Sex ratio F:M	Ovarian development %**						Matured eggs†	Flight muscles development %‡			Fat body development %‡		
						0	I	II	III	IV	V		0	I	II	0	I	II
First crop	Field 1	5/17-23	1-7	56	1.95	10.8	13.5	5.4	64.9	2.7	2.7	3.8 ± 0.6	60.7	5.3	33.9	89.3	10.7	0.0
		5/24-30	8-14	53	1.65	0.0	6.1	3.1	78.8	9.1	3.0	8.0 ± 0.9	52.8	3.8	43.4	75.5	24.6	0.0
		5/31-6/6	15-21	66	2.88	0.0	4.1	4.1	65.3	18.4	8.1	6.8 ± 0.8	47.0	18.2	34.9	72.7	28.8	0.0
		6/07-13	22-28	68	0.79	6.7	0.0	0.0	80.0	6.7	6.7	6.1 ± 0.9	44.5	7.5	48.0	60.3	39.7	0.0
		6/14-20	29-35	52	1.60	12.5	0.0	0.0	37.5	25.0	25.0	2.8 ± 0.6	76.0	12.9	11.2	72.3	16.5	11.2
		6/21-27	36-42	68	1.62	57.2	2.4	0.0	11.9	9.5	19.0	1.2 ± 0.5	75.0	8.8	16.2	44.2	5.9	50.0
		6/28-7/4	43-49	40	4.71	78.8	6.1	0.0	15.2	0.0	0.0	1.1 ± 0.5	67.5	2.5	30.0	7.5	10.0	82.5
		7/05-11	50-56	48	3.00	80.0	0.0	0.0	10.0	10.0	0.0	0.5 ± 0.3	56.3	12.5	31.2	21.9	28.1	50.0
		7/12-18	57-63	32	7.00	75.0	14.3	0.0	3.6	0.0	7.1	0.2 ± 0.2	46.9	3.1	50.0	12.5	12.5	75.0
		7/19-25	64-70	32	2.20	100.0	0.0	0.0	0.0	0.0	0.0	0.0	56.3	3.1	40.6	6.3	15.6	78.1
		7/26-8/1	71-77	8	8.00	87.5	0.0	0.0	12.5	0.0	0.0	0.8 ± 0.6	94.4	5.6	0.0	5.6	27.8	66.7
		8/2-8/8	78-84	5	–	100.0	0.0	0.0	0.0	0.0	0.0	0.0 ± 0.0	80.0	0.0	20.0	0.0	40.0	60.0
		8/9-15	85-91	11	4.50	44.4	0.0	0.0	22.2	11.1	22.2	0.8 ± 0.5	54.5	0.0	45.5	0.0	63.6	36.4
		8/16-22	92-98	5	–	60.0	0.0	0.0	40.0	0.0	0.0	2.2 ± 1.4	80.0	0.0	20.0	20.0	40.0	40.0

Table 1. Continued.

Crop type	No. of field	Sampling date	Days after flood	No. dissected	Sex ratio F:M	Ovarian development %**						Matured eggs†	Flight muscles development %‡			Fat body development %‡		
						0	I	II	III	IV	V		0	I	II	0	I	II
First crop	Field 2	5/31	0	17	3.25	15.4	30.8	15.4	7.7	0.0	30.8	0.3 ± 0.2	17.6	5.9	76.5	11.8	82.4	5.9
		6/1-7	1-7	31	0.94	26.7	6.7	6.7	46.7	13.3	0.0	4.1 ± 1.2	35.5	0.0	64.5	51.6	32.3	16.1
		6/8-14	8-14	74	1.55	4.5	31.1	2.2	53.3	8.9	0.0	3.4 ± 0.7	28.4	9.5	62.2	40.6	55.4	4.1
		6/15-21	15-21	53	2.31	8.1	16.2	5.4	43.2	21.6	5.4	2.9 ± 0.7	49.1	21.8	29.1	60.0	32.0	8.0
		6/29-7/5	29-35	31	2.10	14.3	14.3	4.8	42.9	14.3	9.5	2.4 ± 0.6	61.3	0.0	38.7	51.6	35.5	12.9
		7/6-12	36-42	53	1.94	68.8	0.0	0.0	12.5	0.0	18.8	0.3 ± 0.2	66.7	0.0	33.3	46.4	10.7	42.9
		7/13-19	43-49	30	14.00	82.1	0.0	0.0	17.9	0.0	0.0	1.0 ± 0.5	63.3	0.0	36.7	13.3	23.3	63.3
		7/20-26	50-56	33	1.54	60.0	0.0	0.0	20.0	20.0	0.0	1.4 ± 0.5	24.2	6.1	69.7	12.1	51.5	36.4
		7/27-8/2	57-63	31	2.88	91.3	4.3	0.0	4.3	0.0	0.0	0.1 ± 0.1	67.7	3.2	29.0	0.0	19.4	80.6
		8/3-9	64-70	10	9.00	100.0	0.0	0.0	0.0	0.0	0.0	0.0	80.0	0.0	20.0	0.0	30.0	70.0
		8/10-16	71-77	1	–	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	100.0
		8/17-23	78-84	3	–	66.7	0.0	0.0	0.0	0.0	33.3	0.0	100.0	0.0	0.0	33.3	0.0	66.7
		8/24-30	85-91	5	–	80.0	20.0	0.0	0.0	0.0	0.0	0.0	80.0	0.0	20.0	20.0	20.0	60.0
		8/31-9/6	92-98	5	4.00	100.0	0.0	0.0	0.0	0.0	0.0	0.0	60.0	0.0	40.0	0.0	0.0	100.0

Table 1 Continued.

Crop type	No. of field	Sampling date	Days after flood	No. dissected	Sex ratio F:M	Ovarian development %**						Matured eggs†	Flight muscles development %‡			Fat body development %‡		
						0	I	II	III	IV	V		0	I	II	0	I	II
	Field 3	6/14	-4	16	0.78	28.6	28.6	0.0	42.9	0.0	0.0	3.6 ± 1.1	6.3	6.3	87.5	25.0	43.8	31.3
		6/19-26	1-7	33	1.20	27.8	16.7	5.6	44.4	5.6	0.0	3.6 ± 0.9	57.7	3.8	38.5	73.1	23.1	3.8
		6/27-7/13	8-14	60	1.61	0.0	10.8	5.4	54.1	21.6	8.1	4.2 ± 0.9	65.0	8.3	26.7	63.3	31.6	5.0
		7/4-10	15-21	58	2.22	2.5	7.5	5.0	55.0	22.5	7.5	3.6 ± 0.5	51.2	5.2	43.7	70.6	20.8	8.6
		7/11-16	22-28	30	2.75	13.6	22.7	0.0	31.8	22.7	9.1	2.5 ± 0.6	43.3	3.3	53.3	46.7	26.7	26.7
		7/17-23	29-35	30	1.50	22.2	0.0	0.0	50.0	16.7	11.1	3.2 ± 0.8	50.0	3.3	46.7	30.0	33.3	36.7
		7/24-30	36-42	24	3.80	57.9	0.0	0.0	26.3	5.3	10.5	1.0 ± 0/4	45.8	0.0	54.2	12.5	25.0	62.5
		7/31-6	43-49	19	2.17	92.3	0.0	0.0	0.0	0.0	7.7	0.0	94.7	0.0	5.3	0.0	36.8	63.2
		8/7-13	50-56	11	4.50	88.9	0.0	0.0	0.0	0.0	11.1	0.0	54.5	0.0	45.5	18.2	18.2	63.6
		8/14-20	57-63	8	-	100	0.0	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	100
		9.10-16	85-91	1	-	100	0.0	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	100
Second crop (Ratoon Rice)	Field 4	8/16-22	1-7	20	19.00	10.5	5.3	0.0	63.2	15.8	5.3	3.9 ± 0.5	75.0	10.0	15.0	40.0	45.0	15.0
		8/23-29	8-14	41	9.25	0.0	0.0	0.0	89.2	2.7	8.1	7.8 ± 0.9	90.2	0.0	9.8	36.6	58.5	4.9
		8/30-9/5	15-21	26	12.00	0.0	0.0	0.0	95.7	0.0	4.3	7.5 ± 0.7	92.3	3.8	3.8	57.7	42.3	0.0
		9/6-13	22-28	21	6.00	0.0	0.0	0.0	72.2	16.7	11.1	3.8 ± 0.7	100.0	0.0	0.0	76.2	23.8	0.0
		9/14-20	29-35	1	-	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	100.0
		9/21-27	36-42	20	-	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	100.0
		10/5-11	50-56	18	-	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	100.0
		10/12-18	57-63	13	-	92.3	0.0	0.0	0.0	0.0	7.7	0.0	100.0	0.0	0.0	0.0	0.0	100.0
		10/19-25	64-70	41	-	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	100.0

* Fields 1, 2, and 3 were drill-seeded on 24 April, 3 May, and 28 May and flooded on 16 May, 31 May, and 18 June. The second crop plots were water-seeded on 24 April, flooded 10 May, and harvested 15 August (first crop), then re-flooded on 15 August.

** Developmental stages of ovaries: 0, no oocyte; I previtellogenic; II gravid (vitellogenic to chorionated oocyte); III ovipositing (a number of chorionated eggs are stored in the egg calyxes); IV late ovipositing; V empty ovarioles.

† Means ± SE.

‡ Developmental stages of flight muscles and fat bodies: 0 poorly developed or degenerated; I partially developed; II well developed.

§ Ratoon rice field sprayed with Karate on 2 August and 17 September.

Similar patterns of ovarian, fat body, and flight muscle development were observed in fields 2 and 3 (Table 1). The ovaries of many of the weevils collected in these fields within a few days of flooding were categorized as stage III, IV, or V, and their flight muscles were generally well-developed. Most of the weevils collected during the first 3 wks after flooding had well-developed ovaries and poorly-developed fat bodies, and the flight muscles of a significant proportion were well-developed. Weevils with undeveloped ovaries and well-developed fat bodies began to increase after 4 wks, and, as in field 1, weevils with undeveloped ovaries and well-developed flight muscles and fat bodies represented a majority of collected weevils later in the season. Sex ratios were biased toward females, particularly later in the season.

Ratoon rice. Weevils of all life stages were found associated with second crop rice. An average of 3.7 eggs per plant was found on 23 August, 8 d after harvesting of the first crop. Feeding scars and adults were found easily. The occurrence of larvae and pupae in ratoon rice is shown in Figure 2. The initial sampling date was 12 d after re-flooding. Density of immatures was 2.2 ± 0.4 small larvae per core on this first sampling date. Larval densities reached a maximum 27 d after re-flooding. Pupae were first found 34 d after flooding, and pupal densities were highest 40 d after harvesting. The density of immatures decreased sharply 56 d after flooding, but immatures were still present until harvesting of the second crop. Adult densities were not estimated until 40 d after flooding. Adult densities were 2.4 to 6.8 per row from 40 d after re-flooding until harvest; the highest density was found 1 wk before harvest. Similar densities of adults were found at this time in commercial second-crop rice fields (H.W.S. unpubl. data).

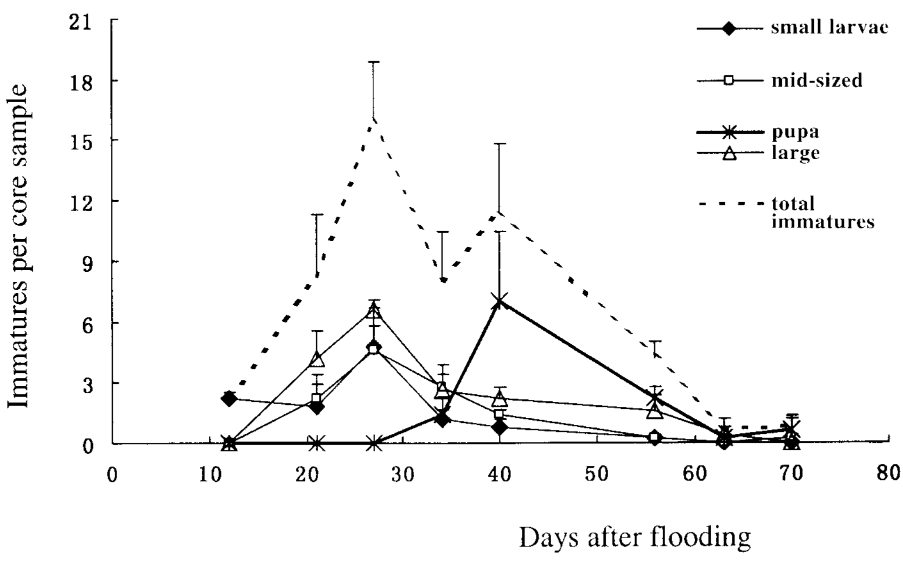

Fig. 2. Densities of larvae and pupae (larvae or pupae core^{-1} +S.E.) over time in a ratoon rice field, Rice Research Station, Crowley, LA, 2002. The first crop was harvested on 15 August; the field was re-flooded on 15 August and the ratoon crop was harvested on 31 October.

Dissection results showed that the majority of the adults collected from ratoon rice in the first 4 wks after re-flooding were gravid (ovaries in stages III and IV), with an average of 3.8 to 7.8 mature eggs per female (Table 1). Most of the weevils collected during this time period also had undeveloped flight muscles and poorly-developed fat bodies. An application of insecticides was made to this field on 17 September to manage an infestation of rice stink bugs. Adults collected after this application of insecticide had undeveloped ovaries and well-developed flight muscles and fat bodies. Few males were found in the second-crop rice, with sex ratios ranging between 6:1 and 9:1 (female:male).

Overwintering sites. Rice water weevil adults were found in overwintering habitats throughout the year (Fig. 3). Densities of weevils in both leaf litter and prairie samples fluctuated considerably over time. A transient increase in weevil densities in prairie samples was observed in mid-April and early May, just as weevil flights were being detected in light traps near experimental plots. A marked increase in weevil densities in prairie samples was observed beginning in late June. Weevil densities in this habitat remained high during the summer (leaf litter samples were not taken during this time), but declined in September. Densities of adults during fall and winter (October to January) were higher in leaf litter samples than in prairie samples (Fig. 3).

The sex ratio of weevils in overwintering sites varied throughout the season, with the average ratio biased towards females (1.55 ± 0.25:1, range 0.4 to 6.0) (Table 2). Dissections of over 1,000 weevils from overwintering sites revealed that the ovaries

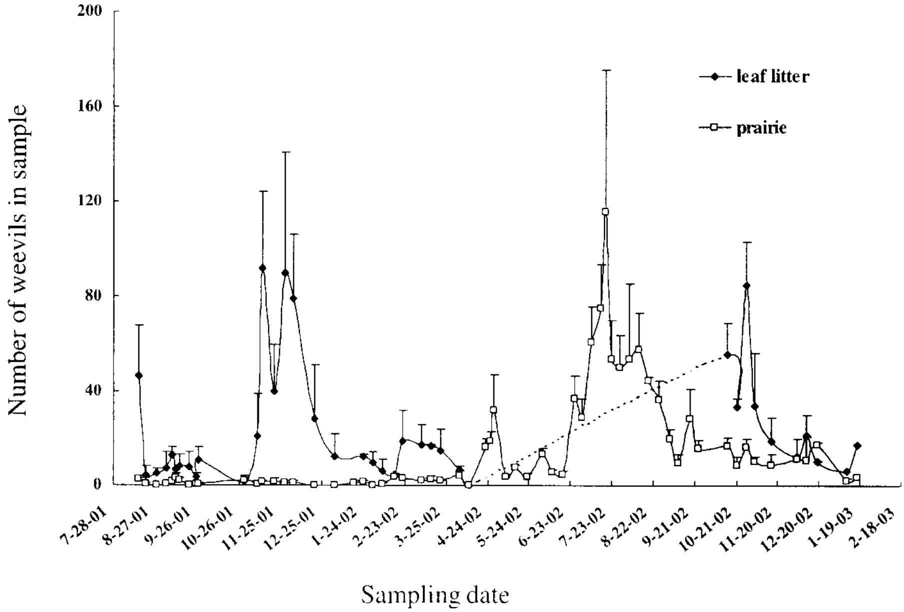

Fig. 3. Occurrence of rice water weevil adults at an overwintering site (no. of weevil adults +S.E.). Samples were taken from leaf litter in a wooded area or grasses in a nearby pasture, Rice Research Station, Crowley, LA, August, 2001 to December, 2002.

of weevils were undeveloped in summer and winter with the exception of a single gravid weevil found on 8 July. Ovaries of weevils collected in April and May were partially developed. The fat bodies of most weevils collected in April and May were degenerate, with none of the fat bodies categorized "well developed." The proportion of well-developed fat bodies increased in June, and almost all weevils had well-developed fat bodies from 5 July to December. A high proportion (75% or more) of weevils in spring had developing or well-developed flight muscles. This proportion decreased to 50 to 60% in mid-June and decreased gradually thereafter, such that most weevils had degenerated flight muscles after August. A small proportion of the weevils collected in late September to mid-October had well-developed flight muscles (Table 2).

Light trap catches. Two light traps were set up near experimental plots in early spring, before planting. There were two major periods of weevil flight activities, one in spring and the second in early summer (Fig. 4). The initial catch of weevils in the UV trap was made on 2 April. The highest catch of weevils in the spring flight period occurred on 24 April. The initial catch from the incandescent trap was on 14 April, with the highest catch on 25 April. The period of flight activity in summer lasted about 2.5 months beginning on 6 June and peaking on 25 June. Numbers of weevils captured in light traps were higher during the summer flight period than during the spring flight period. Light traps were destroyed on 21 August by a hurricane. Dissection of weevils collected from both incandescent and UV light traps showed that virtually all weevils had well-developed flight muscles. Fat bodies of most weevils caught in April and May were poorly developed, but the proportion of weevils with well-developed fat bodies increased to 20% in July and August. Unexpectedly, a proportion of weevils caught in both types of traps from May to August had well-developed ovaries (Table 3).

Discussion

The rice water weevil, *L. oryzophilus,* has long been an important pest of rice in the U.S. and has recently emerged as a major pest of rice in Asia (Heinrichs and Quisenberry 1999). For example, *L. oryzophilus* is now an important quarantine pest in China, and a nation-wide eradication program has been implemented since its invasion in 1988 (Shang and Zhai 1997). Effective management programs for this pest are needed to control it where it is established and to prevent or retard its spread to new areas. Development of such strategies depends on a better understanding of the population dynamics and biology of this pest in different areas. The research reported here was conducted to characterize the life history and population dynamics of this insect in an area where it is a particularly severe pest.

Adult weevils overwinter in a state of reproductive diapause (Knabke 1973, Nilakhe 1977). Weevils collected from overwintering habitats in winter possessed atrophied ovaries and well-developed fat bodies. Overwintering weevils appeared, however, to be very active. Considerable temporal fluctuations in weevil densities were observed in both the wooded habitat (leaf litter samples) and the prairie habitat. These temporal and spatial fluctuations in densities of overwintering weevils suggest that weevils move among overwintering habitats during the course of a year (Gifford and Trahan 1967).

Emergence of adults from overwintering sites and flight to rice fields in spring is a protracted process partially controlled by temperature (Muda et al. 1981, Morgan et al. 1984, Matsui 1985). In our study, weevils were initially caught by light traps near

Table 2. Ovary, flight muscle, and fat body development of rice water weevil in overwintering quarters, Crowley, April-December 2002

Sample date	No. dissected	Sex ratio F:M	Ovarian development %						Matured eggs†	Flight muscles development %			Fat body development %		
			0	I	II	III	IV	V		0	I	II	0	I	II
April	200	0.94	87.1	12.9	0.0	0.0	0.0	0.0	0.0	8.2	22.6	69.2	54.4	45.6	0.0
May	29	4.80	91.7	8.3	0.0	0.0	0.0	0.0	0.0	10.3	13.8	75.9	76.7	23.3	0.0
June	96	2.34	91.7	8.3	0.0	0.0	0.0	0.0	0.0	47.4	5.2	47.4	40.2	16.5	43.3
July	133	0.99	95.5	1.5	0.0	1.5	0.0	1.5	0.05 ± 0.05	80.1	2.2	17.6	0.8	2.3	97.0
August	144	1.00	98.6	1.4	0.0	0.0	0.0	0.0	0.0	98.3	0.0	1.7	0.0	0.8	99.2
Sept.	224	1.04	100.0	0.0	0.0	0.0	0.0	0.0	0.0	94.2	5.4	0.4	0.0	0.0	100.0
Oct.	493	1.77	100.0	0.0	0.0	0.0	0.0	0.0	0.0	97.9	0.3	1.8	0.0	0.0	100.0
Nov.	141	1.10	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	100.0
Dec.	145	1.50	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	100.0

* Developmental stages of ovaries: 0, no oocyte; 1 previtellogenic; II gravid (vitellogenic to chorionated cycle); III ovipositing (a number of chorionated eggs are stored in the egg calyxes); IV late ovipositing; V empty ovarioles.

** Developmental stages of flight muscles and fat bodies: 0 poorly developed or degenerated; I partially developed; II well developed.

† Means ± SE.

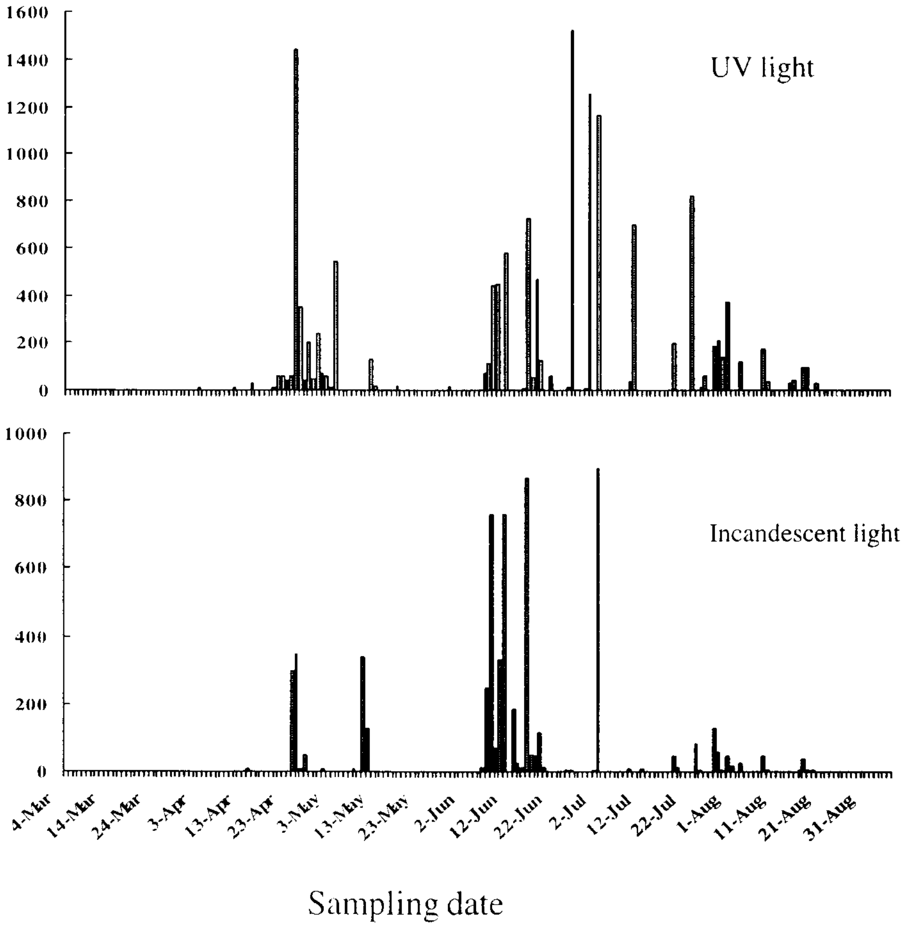

Fig. 4. Number of rice water weevils captured in light traps with a UV light source (4 March to 21 August) or an incandescent light source (4 April to 15 October), Rice Research Station, Crowley, LA, 2002. Bars from April to May represent 10× the actual numbers of weevils caught.

experimental plots on 2 April. Appearance of weevils in light traps in April was preceded slightly by a decrease in densities of overwintering adults in leaf litter samples and an increase in densities of overwintering adults in prairie samples. This pattern undoubtedly reflects movement of weevils to grasses for feeding in preparation for spring flight. It was impossible to determine with confidence when emergence from overwintering ended. Data from light traps suggest a cessation of flight activity in mid-May. However, overwintered weevils, distinguished by the presence of poorly developed fat bodies, atrophied ovaries, and worn scales, were found in overwintering habitats until 26 June, suggesting that some weevils may have emerged from overwintering later than mid-May, if at all (Nilakhe 1977). These observations are consistent with Webb (1914), who concluded that emergence in Louisiana occurred

Table 3. Ovary, flight muscle, and fat body development of rice water weevils caught from light traps, Crowley, April-August 2002

Light traps	Sample date	No. dissected	Sex ratio F:M	Ovarian development %						Matured eggs†	Flight muscles development %			Fat body development %		
				0	I	II	III	IV	V		0	I	II	0	I	II
Incandescent trap	April	44	2.14	46.7	53.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	64.6	35.4	0.0
	May	60	4.45	47.5	40.0	5.0	7.5	0.0	0.0	0.7 ± 0.4	0.0	2.0	98.0	72.0	28.0	0.0
	June	85	1.24	29.8	34.0	0.0	29.8	4.3	2.1	1.4 ± 0.4	0.0	0.0	100.0	21.4	58.3	20.2
	July	85	1.63	17.3	50.0	0.0	9.6	5.8	17.3	0.6 ± 0.2	0.0	0.0	100.0	15.5	61.9	22.6
	August	56	5.22	19.4	11.1	0.0	33.3	5.6	30.6	2.1 ± 0.4	0.0	2.2	97.8	24.4	57.8	17.8
UV trap	June	115	1.80	28.4	39.2	2.7	24.3	2.7	2.7	0.9 ± 0.2	0.0	0.0	100.0	32.2	53.9	13.9
	July	96	3.00	20.8	16.7	1.4	33.3	9.7	18.1	1.7 ± 0.3	0.0	0.0	100.0	20.6	58.8	20.6
	August	90	5.92	53.3	26.7	0.0	20.0	0.0	0.0	2.8 ± 0.4	0.0	1.1	98.9	14.4	62.2	23.3

* Developmental stages of ovaries: 0, no oocyte; I previtellogenic; II gravid (vitellogenic to chorionated oocyte); III ovipositing (a number of chorionated eggs are stored in the egg calyxes); IV late ovipositing; V empty ovarioles.

** Developmental stages of flight muscles and fat bodies: 0 poorly developed or degenerated; I partially developed; II well developed.

† Means ± SE.

between 25 March and 26 June. Emergence in Arkansas appears to occur slightly later than in Louisiana (Muda et al. 1981).

Contrary to published observations (Isely and Schwardt 1934, Muda et al. 1981), adult weevils invaded experimental plots in apparently large numbers prior to flooding. Presence of weevils in unflooded fields was indicated by the presence of feeding scars on plants and by direct observations of weevils taking refuge in crevices in soil or feeding on seedlings (H.S and M.J.S, unpubl. observations). The prevalence of feeding scars in field 3 before flooding indicates that pre-flood populations of adult weevils were higher in these late-planted plots than in plots planted in March and April.

Patterns of adult, egg, and immature densities in fields 1 and 2 strongly suggest that only a single generation of weevils developed in these fields during the growing season. Initial peaks of adults in fields 1 and 2 were followed by a decline in adult densities within 2 wks and a second peak of adult densities approximately 4 wks later. The second peak of adults in these fields consisted primarily of newly-eclosed adults based on the timing of their appearance, their outward appearance (soft elytra and absence of worn scales), and on the condition of their ovaries (undeveloped) and fat bodies (well-developed). However, only single peaks of eggs and immatures were found in fields, and densities of these life stages did not increase following the appearance of newly-eclosed adults in fields. Thus, it appears that newly-eclosed adults only rarely lay eggs in fields in which they developed. Muda et al. (1981) also found that few, if any, first-generation weevils produced eggs in the plots of rice in which they developed in Arkansas.

A decline in densities of adult weevils in rice fields within a few weeks of flooding has been noted by previous authors (Isely and Schwardt 1934, Muda et al. 1981, Haizlip and Tugwell 1983). This decline has been attributed to mortality of weevils or to movement of weevils to other fields or habitats (Isely and Schwardt 1934). Mass mortality of weevils does not seem likely, given that these weevils are very long-lived when maintained in the laboratory (Nilakhe 1977, H.S. and M.J.S., unpubl. obs.). Moreover, disappearance of weevils from fields 1 and 2 in early to mid-June in the current study coincided with an increase in numbers of weevils caught in light traps and found in other fields (e.g., field 3), a fact consistent with movement of weevils to other fields. Interestingly, many weevils caught in light traps or collected from fields in May and June (and throughout the season, for that matter) possessed both well-developed ovaries and well-developed flight muscles. The strong reciprocal relationship between development of flight muscles and ovaries found in Arkansas and Asia (Muda 1981, Matsui et al. 1983, Zhai et al, 1999b) was not as evident in the weevils collected in this study. Thus, some gravid weevils in rice fields in this study were apparently capable of seeking new habitats by flying if hosts were not suitable for oviposition. This agrees with Rolston and Rouse's (1964) observation that the adult rice water weevil appeared to move among fields, congregating on rice in the most attractive stage of development.

An influx of adult weevils into overwintering sites (prairie samples) was observed beginning in early June, with large numbers found beginning in late June. These weevils possessed undeveloped ovaries and generally well-developed fat bodies, and the timing of their appearance in overwintering sites corresponded to a period of elevated flight activity near rice fields that was reflected in light trap catches. Thus, these weevils were probably recently emerged, first-generation weevils returning to overwintering sites. This return to overwintering sites was earlier than that found in Arkansas (Muda et al. 1981, Morgan et al. 1984). Arrival of these newly-emerged weevils to overwintering sites began at a time when overwintering weevils from the previous winter were still present in overwintering habitats.

Population dynamics of weevils in field 3, which was planted (28 May) and flooded (18 June) much later than is typical for the region, differed somewhat from population dynamics of weevils in fields 1 and 2. This field was heavily infested by adults before flooding, a fact reflected in the high densities of weevils found immediately after flooding. Most of these adult weevils departed quickly; in fact, numerous weevils were observed leaving this field and moving to levees on the day of flooding (H.S., pers. obs.). The ultimate destination of these emigrants is unknown, but movement to overwintering sites is likely. Adult densities were about half as high at the next sampling date. Dissections of females collected on the first few sampling dates revealed a mixture of weevils with well-developed and undeveloped ovaries. The weevils with well-developed ovaries were probably remnants of the overwintering generation, as adults of this species are known to be long-lived and to oviposit over a long period of time (Grigarick 1984). The weevils with undeveloped ovaries were probably first generation weevils, newly emerged from other rice fields. The percentage of weevils with undeveloped ovaries declined over the next few weeks, suggesting ovarian development in these first-generation weevils. The immature weevils produced in field 3 were likely the offspring of weevils from both the overwintering generation and the newly-emerged first generation.

The activities of weevils in second-crop (ratoon) rice had been noted (Isely and Schwardt 1934, Way and Wallace 1993), but not extensively documented previously. Adults were found in this field until harvesting of the second crop (31 October). Most of these adults were probably first generation weevils. As noted above, however, adults of this species are long-lived, in some cases living 4 months or more beyond emergence from overwintering, and thus it is possible that some of the adults found in ratoon-crop rice were members of the overwintering generation. It is also possible that some of the adult weevils found in ratoon rice were second-generation weevils, newly emerged from late-planted first-crop rice fields, because sufficient time had passed for development of a second generation. Densities of immatures in ratoon rice were substantial, at times exceeding 10 larvae per core sample. Moreover, the appearance in late September of newly-eclosed weevils in this field indicates that immature weevils were able to complete their development on ratoon-crop rice.

Previous estimates of the number of generations of rice water weevils occurring during a growing season in Louisiana have varied from one and a partial second (Webb 1914) to two and a partial third (Gifford and Trahan 1966, Gifford et al. 1973). Everett (1966) estimated that as many as four generations could develop in Louisiana rice, but this estimate was based only on the length of the weevil life cycle. Data obtained in this study indicate that a portion of the weevil population in Louisiana is univoltine. This is suggested by the development of only one generation of weevils in a single rice field and by the influx of weevils into overwintering sites as early as June. Additional data from field 3 and data from the ratoon rice field indicate that another portion of the weevil population in Louisiana is bivoltine. The existence of a third generation cannot be completely discounted by the data in this study. However, the existence of multiple generations in Louisiana probably depends on the continuing presence of young rice, for which ovipositing weevils show a preference (Isely and Schwardt 1934, Bang and Tugwell 1976). The seasonal history of weevils in Louisiana resembles the seasonal history of weevils in Southeast China, where most first-generation adults emigrate from rice fields to overwintering sites, and only a small proportion of weevils pass through a second generation (Zhai et al. 1997). Muda et al.

(1981) reported the occurrence of only one complete generation and a partial second generation in Arkansas. Parthenogenetic populations in California and Asia are thought to pass through 1 to 3 generations per year, depending on location (Grigarick 1993).

Early planting has been suggested as a cultural strategy for management of the rice water weevil in Louisiana (Isely and Schwardt 1934, Thompson et al. 1994). Although none of the rice in this study can be considered early-planted (recommended planting dates for rice in southwest Louisiana are from mid-March through 30 April), a comparison of weevil population dynamics in the plots planted on 24 April (field 1) with plots planted in May lends support to the use of early planting as a management strategy. Maximum densities of larvae were lower in field 1 than in fields 2 and 3. Perhaps more importantly, the timings of peak infestations of adults, eggs, and larvae were delayed in field 1 relative to fields 2 and 3. Thus, early planting may affect both the timing and severity of weevil infestations. Delays in infestation may be important (regardless of severity of infestation) because they may allow rice plants to develop for a longer period of time in the absence of severe infestation, and tolerance of rice to weevil feeding increases as plants age (Stout et al. 2002).

In contrast to Thompson (1970), who found an overall 1:1 sex ratio, the genders of weevils dissected in this study were biased toward females. This bias was particularly extreme in weevils collected in rice fields in August and September and for weevils collected in light traps. The bias was not as marked for weevils collected from overwintering sites. One probable explanation for the bias in sex ratios (particularly in late-season rice) is the fact that males typically have shorter life spans than females (Nilakhe 1977). The variability of sex ratios in different habitats and at different times suggests differences in behavior among the sexes. Also, the scarcity of male weevils in late-season rice and the presence of immature weevils on rice at these times suggest the possibility that a portion of female weevils are capable of reproducing parthenogenetically.

These data represent the most comprehensive study of the life history and biology of rice water weevil in Louisiana. Most aspects of the life history and population dynamics were similar to those of this pest in Arkansas and Asia, but a few differences were found. Some of these differences can be accounted for by climatic differences between regions (e.g., possible differences in the numbers of generations passed by weevils in a growing season, and variation in emergence from and return to overwintering sites). Other differences may represent real differences between regions (e.g., the lack of a strong inverse relationship between development of ovaries and flight muscles in Louisiana females, the female-biased sex ratio). However, the cultural practices used in this study do not represent the full range of cultural practices used in Louisiana, and the small size of experimental plots may have affected aspects of weevil biology. Moreover, the availability of all stages of rice throughout the growing season at the Rice Research Station is not representative of commercial rice production in Louisiana. Additional work on aspects of rice water weevil biology in rice fields, including movement between fields, habitat choice, and reproductive capacity (parthenogenetic and sexual) of adults, are needed to develop more effective management and containment strategies.

Acknowledgments

We thank R. Pousson, S. D. Linscombe, J. Musick and Q. Chu for their support and assistance with experiments. The manuscript was improved by comments from B. Castro, Q. Chu and C. Carlton. This work was supported by grants from the Louisiana Rice Research Board. This manuscript was approved for publication by the director of Louisiana Agricultural Experimental Station, manuscript number 04-26-0090.

References Cited

Anonymous. 1994. Rice pesticide usage report and integrated pest management of rice in Louisiana. Louisiana State Univ. Agric. Center. Baton Rouge, LA. 27 pp.

Bang, Y. H. and N. P. Tugwell. 1976. Adult rice water weevil feeding preferences for rice plants and leaves of different ages. Arkansas Experiment Station Report Series 231: 1-12, Univ. of Arkansas, Fayetteville.

Bowling, C. C. 1980. Insect pests of the rice plant. Pp. 260-288. *In* B. S. Luh [ed.], Rice: production and utilization. AVI, Westport, CO.

Dyck, V. A., B. C. Misra, S. Alam, C. Chen, G. Y. Hsieh and R. S. Rejesus. 1979. Ecology of the brown planthopper in the tropics, Pp. 61-98. *In* IRRI (International Rice Research Institute) [ed.], Brown Planthopper: Threat to rice production in Asia. Manila, Philippines.

Everett, T. R. and L. D. Newsom. 1964. External characters for separating the sexes of the rice water weevil, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera, Curculionidae). Ann. Entomol. Soc. Amer. 57: 514-515.

Gifford, J. R., S. S. Nilakhe and G. B. Trahan. 1973. Host plant resistance to rice insects. Ann. Prog. Rept. Rice Exp. Eta., Crowley, Louisiana. 65: 131-139.

Gifford, J. R. and G. B. Trahan. 1966. Flight activity of rice water weevil and the green nice leafhopper. Ann. Prog. Rept. La. Rice Exp. Sta. Crowley, LA. 58: 161-165.

1967. Overwintering of the rice water weevil in Louisiana. J. Econ. Entomol. 60: 173-175.

1969a. Apparatus for removing overwintering adult rice water weevils from bunch grass. J. Econ. Entomol. 62: 752-754.

1969b. Staining technique for eggs of rice water weevils oviposited intracellularly in the tissue of the leaf sheaths of rice. J. Econ. Entomol. 62: 740-741.

Goh, H. G. and K. M. Choi. 1993. Forecasting methods of the rice water weevil in Korea, Pp. 133-162. *In* K. Hirai [ed.], Establishment, Spread, and Management of the Rice Water Weevil and Migratory Rice Pests in East Asia, 20-24 September 1992, Suwon, Korea. NARC, Tsukuba, Japan.

Grigarick, A. A. and G. W. Beards. 1965. Ovipositional habits of the rice water weevil in California as related to a greenhouse evaluation of seed treatments. J. Econ. Entomol. 58: 1053-1056.

Grigarick, A. A. 1993. Study of the rice water weevil, past, present, and future in the United States with emphasis on California, Pp. 12-31. *In* K. Hirai [ed.], Establishment, Spread, and Management of the Rice Water Weevil and Migratory Rice Pests in East Asia, 20-24 September 1992, Suwon, Korea. NARC, Tsukuba, Japan.

1984. General problems with rice invertebrate pests and their control in the United States. Protec. Ecol. 7: 105-114.

Haizlip, M. B. and N. P. Tugwell. 1983. Degeneration and regeneration of indirect flight muscle in the rice water weevil (Coleoptera: Curculionidae). J. Kansas Entomol. Soc. 56: 164-168.

Heinrichs, E. A. and S. S. Quisenberry. 1999. Germplasm evaluation and utilization for insect resistance in rice, Pp. 3-23. *In* S. L. Clement and S. S. Quisenberry [eds.], Global plant genetic resources for insect-resistant crops. CRC, Boca Raton, FL.

Isely, D. and H. H. Schwardt. 1934. The rice water weevil. Univ. of Arkansas College of Agric., Agricultural Experiment Station Bulletin No. 299. 43 pp.

Iwata, T. 1976. Occurrence of the American rice water weevil in Japan. Intern. Rice Research Newsl. 1(2): 17.

Knabke, J. J. 1973. Diapause in the rice water weevil, *Lissorhoptrus oryzophilus* Kuschel, (Coleoptera: Curculionidae) in California. Ph.D. dissertation, Univ. California, Davis, CA.

Lange, W. H. and A. A. Grigarick. 1959. Rice water weevil: Beetle pest in rice growing areas of southern states discovered in California. Calif. Agric, Aug. Pp. 10-11.

Matsui, M. 1985. Temperature dependence of flight muscle development and flight activity of overwintered adults of the rice water weevil adult, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae). Jpn. J. Appl. Ent. Zool. 29: 62-72.

Matsui, M., K. Ito, M. Okada and R. Kisimoto. 1983. Morphological changes in the flight muscles and the ovary of the rice water weevil adult, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae), collected at various sites during the period of migration. Jpn. J. Appl. Ent. Zool. 27(3): 183-188.

Morgan, D. R., P. H. Slaymaker, J. F. Robinson and N. P. Tugwell. 1984. Rice water weevil (Coleoptera: Curculionidae) indirect flight muscle development and spring emergence in response to temperature. Environ. Entomol. 13: 26-28.

Muda, A. R., N. P. Tugwell and M. B. Haizlip. 1981. Seasonal history and indirect flight muscle degeneration and regeneration the rice water weevil. Environ. Entomol. 10: 685-690.

Nilakhe, S. S. 1977. Reproductive status of overwintering rice water weevils. Ann. Entomol. Soc. Am. 70: 599-601.

Rolston, L. H. and P. Rouse. 1964. Some factors influencing larval infestations of the rice water weevil. J. Kansas Entomol. Soc. 37: 29-35.

Shang, H., J. Cheng, L. Lv, Y. Lin and B. Zhai. 1998. Spread and management of the rice water weevil in Zhejiang Province, Pp. 429-433. *In* J. Cheng and W. Zhou [eds.], Research on Agricultural Development Beyond the Century. Chinese National Environment Press, Beijing, China.

Shang, H. and B. Zhai. 1997. The spread of rice water weevil in southern China and the tactics of its control. Pp. 217-221. *In* X. Yang and H. Wu [eds.], Advances in entomological research. House of Chinese Forestry, Beijing. China.

Smith, C. M. 1983. The rice water weevil, *Lissorhoptrus oryzophilus* Kuschel, Pp. 3-9. *In* K. G. Singh [ed.], Exotic plant quarantine pests and procedures for introduction of plant materials. Asian (Planti), Selangor, Malaysia.

Sooksai, S. 1976. Rice water weevil (*Lissorhoptrus oryzophilus* Kuschel) feeding scars-larval density relationship. M.S. Thesis, Univ. of Arkansas, Fayetteville.

Stout, M. J., W. C. Rice. and D. R. Ring. 2002. The influence of plant age on tolerance of rice to injury by the rice water weevil *Lissorhoptrus oryzophilus* (Coleoptera: Curculionidae). Bulletin of Entomological Research. 92: 77-184.

Thompson R. G. 1970. The relationship of the development of the rice plant to the rice water weevil, *Lissorhoptrus oryzophilus,* Kuschel, and root damage. M.S. Thesis, Univ. of Arkansas, Fayetteville.

Thompson, R. A., S. S. Quisenberry, F. K. N'Guessan, A. M. Heagler and G. Giesler. 1994. Planting date as a potential cultural method for managing the rice water weevil (Coleoptera: Curculionidae) in water-seeded rice in southwest Louisiana. J Econ. Entomol. 87: 1318-1324.

Way, M. O. and R. G. Wallace. 1993. Rice water weevil integrated pest management in the United States with emphasis on the South, Pp. 58-82. *In* K. Hirai [ed.], Establishment, Spread, and Management of the Rice Water Weevil and Migratory Rice Pests in East Asia, 20-24 September 1992, Suwon, Korea. NARC, Tsukuba, Japan.

Way, M. O. 1990. Insect pest management in rice in the United States, Pp. 181-189. *In* B. T. Grayson, M. B. Green and L. G. Copping [eds.], Pest management in rice. Elsevier Science Publ Co., Inc., New York. NY.

Webb, J. L. 1914. Notes on the rice water weevil. J. Econ. Entomol. 7: 432-439.

Zhai, B., H. Shang and J. Cheng. 1999. Classifying the ovarian development of rice water weevil and its application. Chinese Journal of Rice Science. 13: 109-113.

Zhai, B., J. Cheng, E. Huang, H. Shang, X. Zheng, J. Wu and X. L. 1999. The oogenesis-flight syndrome of rice water weevil, *Lissorhoptrus oryzophilus* Kuschel. ACTA Ecologica Sinica 19: 242-249.

Zhai, B., J. Cheng, E. Huang, H. Shang, X. Zheng, J. Wu, Y. Fang, W. Xia and X. L. 1997. Population dynamics of rice water weevil in double rice cropping area of Zhejiang province, China. Scientia Agricultura Sinica. 30: 23-29.