COMPARISON OF INTRASPECIFIC COMPETITION BETWEEN ERUPTIVE AND LATENT AUCHENORRHYCHA (HOMOPTERA) SPECIES ON RICE: *SOGATELLA FURCIFERA* (DELPHACIDAE) VERSUS *RECILIA DORSALIS* (DELTOCEPHALIDAE) *

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Abstract A comparison of the effects of intraspecific competition between the white-backed planthopper (WBPH) *Sogatella furcifera* (Horvath) and the zigzag leafhopper (ZLH) *Recilia dorsalis* (Motschulsky), as representatives of eruptive and latent Auchenorrhycha (Homoptera) species on rice, was carried out in the laboratory. Crowding during the nymphal stage extended the duration of development of WBPH but not of ZLH. The nymphal survival rate of WBPH, sex ratio, preoviposition period and fecundity of both species were however not affected. The brachypterous percentage of WBPH and nymphal survival of ZLH were significantly reduced under high nymphal density. Crowding during the adult stage reduced fecundity and longevity significantly of both species. Fecundity and longevity were further reduced when combined with high densities during the nymphal stage. Age-specific life table analysis showed that the integrated effect of crowding on ZLH is stronger than on WBPH. The mechanism of eruptive and latent species' response to crowding during nymph and adult stages is not clearly expressed as a significant difference in fecundity. It is better described as the variation in the intrinsic rate of increase (r_m). Therefore the construction of an age-specific life table is helpful, and perhaps necessary, to understand these effects. The results showed that the main ecological characteristics of ZLH, as a latent species were its longer immature period, lower total fecundity and decreased and retailed rate of oviposition, hence the lower r_m, as compared with WBPH.

Key words age-specific life table, eruptive species, fitness, intraspecific competition, latent species, *Sogatella furcifera*, *Recilia dorsalis*

1 INTRODUCTION

The main Auchenorrhycha (Homoptera) species on rice are the brown planthopper *Nilaparvata lugens* (Stål), the white-backed planthopper (WBPH) *Sogatella furcifera* (Horvath), the small brown planthopper *Laodelphax striatellus* (Delphacidae), the green leafhoppers *Nephotettix* spp. (Cicadelidae) and the zigzag leafhopper (ZLH) *Recilia dorsalis* Motschulsky (Deltocephalidae). These plant- and leafhoppers are major destructive pests of rice in eastern and southeastern Asian countries. In China, more than half of the total amount of insecticides sprayed on paddy is intended to control these pests (Zhu 1996a). However the status of these species is not uniform, and is influenced by different temporal and spatial factors. Since the introduction of hybrid rice breeding and extension in 1970s, WBPH has been an eruptive species. Outbreaks of ZLH are only observed occasionally connected with rice virus diseases and are

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therefore categorized as a latent pest.

In south-eastern China, e.g. Zhejiang Province, WBPH immigrates every year from southern rice growing regions (Vietnam and South China) carried by the southwest-northeast monsoon, and builds up its damaging population with two wing-forms (brachypterous and macropterous) during July on the first season cropping rice and during September on the second season cropping rice. In contrast, ZLH is an endemic species with only one wing-form adult and its highest population density usually occurs during June and August.

There are many published data of density-related effects on the fitness components and population dynamics of planthoppers (Denno *et al*. 1994). On the contrary, very little research has been conducted on ZLH, as it is considered as a minor insect pest of rice. In addition, its low population size makes ecological studies with the usual methods difficult (Price 1990). Only basic data of ZLH are available on preliminary ecology in Japan (Matsumoto 1988) and population dynamics in southeastern and western China (Hu and Nie 1989, Zhu 1996b) and in the Philippines (Cook and Perfect 1989).

The females of an eruptive insect species probably do not compete for oviposition sites because of their relative undiscriminating site choice, whereas females of a latent species possibly do, and if the sites are rare, competition will be important even at low densities (Price 1990). Fitness components (survival, duration of development, longevity, and fecundity) of planthoppers are intraspecific density-dependent (Denno *et al*. 1994) with density being the prominent factor for production of migrants (Denno 1993).

The effects of intraspecific crowding on the fitness components and population parameters of the white-backed planthopper *Sogatella furcifera* and the zigzag leafhopper *Recilia dorsalis* are described in this paper to elucidate the intrinsic causes of the eruptive or latent status of a species.

2 MATERIALS AND METHODS

2.1 Insects

Late instar nymphs of *Recilia dorsalis* and *Sogatella furcifera*, collected from paddies in Zhejiang University Experimental Farm in mid August 1994, were maintained in glass tubes (1.8 cm in diameter and 18 cm high) on rice seedlings of 20 – 40 days after sowing (variety: Guangluai 4, *indica*) at 25 – 26℃ and at a 14:10 hour day-night rhythm. (Our earlier experiments had showed that this instrument is good for planthoppers and leafhoppers and their egg parisitoids (Zhu *et al*. 1991, 1993, 1994b). In a recent experiment by this instrument, mean lifespan fecundity of *S. furcifera* was observed as 704, the highest one in the literature.) The emerged adults were paired and maintained in the same conditions as the nymphs. The rice seedlings were renewed every 2 days and the seedlings, embedded with insect eggs, were maintained in the insectary at an average temperature of 28℃ and in a natural light regime. The newly hatched first-instar nymphs (less than 8 hours old) were used in the experiment. Experimental insects were maintained as described above unless stated otherwise.

2.2 Intraspecific competition during nymphal stage

Four nymphal stage density categories were established, i.e. 1, 2, 4, and 8 (or 7) per plant- or leafhoppers per glass tube (seedling), each having 16 to 62 replicates. The wingform, sex, survival and duration of development to adults were recorded when the insects emerged.

2.3 Intraspecific competition during adult stage

Adult females that emerged on the same day from identical nymphal densities were aspirated into new tubes. The females were kept single (S), irrespective of nymphal density (1S, 2S, 4S, 8S) or at the same density as during the nymphal period (2M, 4M, 8M). In each tube one male was added. The seedlings which had been used for food and as oviposition sites for the adults were maintained in an incubator at 15 or 25℃ to regulate the rate of egg development so that they could be dissected at a convenient time.

Age-specific life tables of each treatment were established following the methodology of Andrewarth and Birch (1954) with mean egg development periods of 7 and 9 days for WBPH and ZLH respectively, derived from statistical values of observations of a control group (7.18 ± 0.05 (n = 126) and 9.20 ± 0.04(n = 161) days for WBPH and ZLH respectively (n = no. of observations)). The nymph development periods and survival rates obtained from intraspecific competition treatments were used for life table analysis. Based upon the genetics of these insects and our observations, a sex ratio of 0.5 (female/(female + male)) was used for all treatments. Population parameters (the net reproductive rate $R_0 = \sum l_x m_x$, the mean duration of the generation $T = \sum l_x m_x x / \sum l_x m_x$, the intrinsic rate of increase $r_m = lnR_0/T$, the finite increase rate $\lambda = \exp(r_m)$, the population doubling time p.d.t. $= ln(R_0)/2$, where l_x, m_x are age-specific survival and reproductive rate at age x (days) respectively) were calculated for each treatment using these age-specific life tables.

2.4 Statistical methods

Mean values of different treatments were analysed for significance using Student's t-test or analysis of variance (ANOVA). Differences between treatment means were tested for significance using Duncan's multiple range test (LSD) at $P = 0.05$ or 0.01 if the treatment was significant by ANOVA.

3 RESULTS

3.1 Intraspecific competition during the nymphal stage

No significant ($P > 0.05$) difference was observed for the different nymphal densities in the duration of nymphal development (Table 1) of ZLH, in survival of the WBPH nymphs (Table 2), in fecundity of females of both species kept as single (Table 4) and in sex ratio of the emerged adults (Table 2). The mean fecundity of adult ZLH decreased however with increasing nymphal density (Table 4). The survival of ZLH nymph in the treatment with density 8 was significantly lower ($P < 0.05$) than in the densities 1, 2 and 4 (Table 2). When subjected to a high density, WBPH extended significantly ($P < 0.05$) its duration of nymphal development (Table 1). The male hoppers of both species developed faster than female cospecific ones in all density treatments, although differences were only significant for one treatment in WBPH and two treatments in ZLH. The grand averages for the five density treatments were likewise significantly as well (Table 1, $P < 0.05$).

Table 1 Duration of development (days, mean ± S.E.(number of observations)) in different nymphal densities of the white-backed planthopper *Sogatella furcifera* (WBPH) and the zigzag leafhopper *Recilia dorsalis* (ZLH)[a].

Density (No./tube)	WBPH		ZLH	
	Female	Male	Female	Male
1	12.63 ± 0.179(24)b	12.19 ± 0.245(16)b	14.95 ± 0.195(24)a	13.67 ± 0.232(21)a[1)]
2	12.53 ± 0.316(28)b	12.07 ± 0.299(28)b	14.63 ± 0.298(22)a	14.28 ± 0.239(22)a
4	13.75 ± 0.250(20)a	13.35 ± 0.242(28)a	14.65 ± 0.256(31)a	14.06 ± 0.211(34)a
8	13.41 ± 0.176(62)a	12.31 ± 0.205(58)b[1)]	14.91 ± 0.227(36)a	13.82 ± 0.234(45)a[2)]
Mean	13.14 ± 0.120(134)	12.47 ± 0.133(130)[2)]	14.79 ± 0.123(113)	13.97 ± 0.119(132)[3)]

[a] The means in same column followed by same letter are not significantly different ($P < 0.05$, Duncan's multiple range test); 1) Significant effect of sex in the density treatments ($P < 0.05$, t-test). Significant effect of sex (grand mean for four density treatments, 2) $P = 0.0011$, $t = 3.7569$, $df = 259$, in WBPH; 3) $P = 1.1E\text{-}06$, $t = 4.8431$, $df = 240$, in ZLH, t-test).

Table 2 Effects of intraspecific crowding during nymph stage of *Sogatella furcifera* (WBPH) and *Recilia dorsalis* (ZLH) on survival and sex ratio[a].

Density (No./tube)	WBPH	ZLH
	Survival(%, mean ± S.E.)	
1	86.45 ± 2.92(11,16,21)a	96.49 ± 3.51(9,19,15)a
2	82.78 ± 4.34(24,20,24)a	95.84 ± 2.41(10,24,24)a
4	83.06 ± 1.94(20,20,24)a	85.09 ± 7.64(25,27,27)a
8	86.12 ± 0.69(48,48,55)a	65.25 ± 2.16(21,29,40,56)b
	Sex ratio(female/(female + male))	
1	0.5782 ± 0.0808(10,14,17)a	0.5051 ± 0.0481(9,17,15)a
2	0.4981 ± 0.0305(18,18,20)a	0.3437 ± 0.0236(10,21,20)a
4	0.4216 ± 0.0427(17,17,16)a	0.4869 ± 0.0204(21,24,19)a
8	0.5290 ± 0.0091(41,32,46)a	0.4058 ± 0.0478(11,15,27,32)a

[a] Numbers in parentheses are the numbers of individuals observed in each group. The means in same column under same parameter followed by same letter are not significantly different ($P < 0.05$, Duncan's multiple range test).

The percentage of brachypterous female WBPH of the total of emerged adults was 8.33 ± 4.81(24), 17.44 ± 8.74(28), 0 (21) and 0 (63) for densities of 1, 2, 4 and 8 nymphs per tiller (tube) respectively (three groups for each density, the number in brackets is the total number of samples in corresponding density). The proportion decreased as the density increased. No brachypterous males were found in any of the treatment.

3.2 Intraspecific competition during the adult stage

Even though the development periods of WBPH were extended by nymph crowding (Table 1), there were no significant differences in the preoviposition periods in the five densities during adulthood of both species (Table 3). The longevity of WBPH female adults kept at one per tiller

(1S, 2S, 4S and 8S) was independent from different crowding levels during the nymphal stage. High ZLH nymph densities reduced the adult longevity significantly ($P < 0.05$) even when kept single (Table 3).

The survival and fecundity of both species under adult crowding were reduced significantly ($P < 0.05$) except for females maintained at a density of 2 per tiller (tube) versus single (2M/2S) (Tables 3 and 4). The probabilities of difference (Table 5) showed clear increase in differences of survival and fecundity within pairs of increasing density (2M/2S, 4M/4S, 8M/8S).

The data in Table 5 clearly indicate higher reductions of fecundity and longevity of WBPH in same density treatment pairs as compared with those of ZLH.

Table 3 Preoviposition period and female longevity (days) under adult crowding of *Sogatella furcifera* (WBPH) and *Recilia dorsalis* (ZLH)[a].

Density (No./tube)	Preoviposition		Longevity	
	WBPH	ZLH	WBPH	ZLH
1S	3.90 ± 0.34(20)b	4.77 ± 0.57(17)a	18.60 ± 1.11(20)b	33.59 ± 4.07(17)a
2S	5.80 ± 0.80(10)a	4.78 ± 0.52(9)a	24.40 ± 2.53(10)a	23.89 ± 2.73(9)ab
4S	4.50 ± 0.50(8)ab	6.69 ± 1.46(13)a	19.50 ± 2.06(8)ab	23.40 ± 3.10(15)b
8S	4.80 ± 0.50(20)ab	6.87 ± 1.78(13)a	22.80 ± 1.85(20)a	21.00 ± 1.90(20)bc
2M	4.14 ± 0.86(14ab	4.64 ± 0.75(22)a	10.14 ± 2.04(14)c	25.55 ± 3.87(22)ab
4M	4.50 ± 1.50(16)ab	4.00 ± 0.58(14)a	13.50 ± 1.53(16)c	15.71 ± 2.40(14)c
8(7)M	4.20 ± 0.80(40)ab	3.67 ± 1.33(21)a	13.05 ± 1.40(40)c	14.62 ± 2.16(21)c
Mean	4.54 ± 0.24(128)	5.44 ± 0.50(118)	16.47 ± 1.38(128)	22.42 ± 1.28(118)

[a] mean ± S.E. (number of observations, * denotes the number of observations of groups). S-Single insect per tiller during adult stage, M-Multiple insects (number as those during nymphal stage) put together in one tube during adult stage. The means in one column followed by same letter are not significantly different ($P < 0.05$, Duncan's multiple range test).

Table 4 Fecundity (No. of eggs /female) under nymph and/or adult crowding treatments of *Sogatella furcifera* (WBPH) and *Recilia dorsalis* (ZLH)[a].

Density (No./tiller)	WBPH	ZLH
1S	447.25 ± 43.63(20)a	131.00 ± 18.68(17)a
2S	569.90 ± 89.13(10)a	122.67 ± 17.58(9)a
4S	434.13 ± 49.54(8)a	106.92 ± 16.60(13)a
8S	480.15 ± 47.57(20)a	88.73 ± 10.30(15)a
2M	199.64 ± 50.14(14)b	107.82 ± 7.59(14)a
4M	146.25 ± 14.02(16)b	45.56 ± 1.52(14)b
8(7)M	117.75 ± 4.93(40)b	28.05 ± 0.94(21)c
Mean	305.19 ± 14.79(120)	84.71 ± 4.08(116)

[a] (Mean ± S.E. (number of observations)). The means in one column followed by the same letter are not significantly different ($P < 0.05$, Duncan's multiple range test).

Table 5 Statistical differences' level (*P* value, *t*-test assuming unequal variance) and reduction percentage in fecundity, longevity between crowded adults and single adults of *Sogatella furcifera* (WBPH) and *Recilia dorsalis* (ZLH).

	Fecundity				Longevity			
	WBPH		ZLH		WBPH		ZLH	
	Reduction perentage	*P*	Reduction perentage	*P*	Reduction perentage	*P*	Reduction perentage	*P*
2M vs 2S	64.97	0.0013	12.11	0.2273	58.44	0.0032	-6.95	0.3644
4M vs 4S	66.31	0.0026	57.39	0.0016	30.77	0.0169	33.49	0.0303
8(7)M vs 8S	76.25	1.56E-07	68.39	2.0E-05	42.76	7.2E-05	37.52	0.0150

3.3 Integrated effects

Table 6 shows the integrated effects of the population parameters of nymph and adult crowding. For both species, as nymph density increased, the net replacement rate (R_0) decreased, and the mean duration of the generation (T) increased. This resulted in a lower intrinsic rate of increase (r_m) and the periodical increase rate (λ), and the population doubling times (p.d.t.) of both species were extended.

Table 6 Population growth parameters of *Sogatella furcifera* (WBPH) and *Recilia dorsalis* (ZLH) for the different combinations of density treatment in nymphal and adult stages.

	R_0 (FF[a]/Generation)		T(days)		r_m (FF/F[b]/day)		λ (No.times/day)		p.d.t.(days)	
	WBPH	ZLH	WBPH	ZLH	WBPH	ZLH	WBPH	ZLH	WBPH	ZLH
1S	190.22	63.11	33.20	43.41	0.1581	0.0955	1.1713	1.1002	4.38	7.26
2S	234.42	58.78	36.41	38.45	0.1499	0.1060	1.1617	1.1118	4.63	6.54
4S	174.91	45.49	33.30	42.18	0.1551	0.0905	1.1677	1.0947	4.47	7.66
8S	201.78	31.69	35.68	39.60	0.1488	0.0873	1.1604	1.0912	4.66	7.94
2M	66.59	53.55	33.13	43.72	0.1268	0.0911	1.1351	1.0953	5.47	7.61
4M	58.64	18.19	33.70	37.81	0.1208	0.0767	1.1284	1.0798	5.74	9.03
8M	54.51	9.61	36.45	37.82	0.1097	0.0598	1.1160	1.0617	6.32	11.59

[a] FF-Females; [b] F-female.

For the same nymphal density, the proportion of r_m of crowded adults versus single adult was calculated. Low and intermediate adult density showed a higher reduction degree for WBPH than for ZLH, while at higher density, ZLH suffered more than WBPH (r_m proportion 0.69 versus 0.74, Fig. 1a). A comparison of crowding and single treatment during the entire lifespan, showed a more abrupt r_m reduction for ZLH than for WBPH (Fig. 1b). The density treatment range influences the density-dependent r_m of both species.

The logarithmic regression analysis of the two variables, proportion of r_m and nymph densities (Fig. 2) showed a lower regression coefficient for ZLH (b = −0.1378) than for WBPH (b = −0.1232), indicating a stronger crowding effect in the former than in the latter.

4 DISCUSSIONS

4.1 Intrinsic ecological characteristics of eruptive and latent hoppers

Although there are significant ($P < 0.05$) positive correlations between longevity and fecundity in both WBPH and ZLH (Fig. 3), which show that a compensatory effect exists, ZLH extends its longevity to maximize fecundity. On the other hand, WBPH has a higher fecundity but lives for a shorter time than ZLH, also WBPH develops faster. To compare reproduction dynamics in the same scale, the two equations in Fig. 3. were transformed as follows:

$$\text{WBPH}: y = 894.72x';$$
$$\text{ZLH}: y = 267.92x',$$

x' means proportional longevities to maximum ones (40 and 70 days for WBPH and ZLH respectively), while y means the fecundity. The higher slope for WBPH indicates that WBPH not only lays more eggs but also quicker, which is one of the most important characteristics causing population outbreak. The higher intrinsic rate of increase (r_m) of WBPH characterizes WBPH as an eruptive species compared with ZLH.

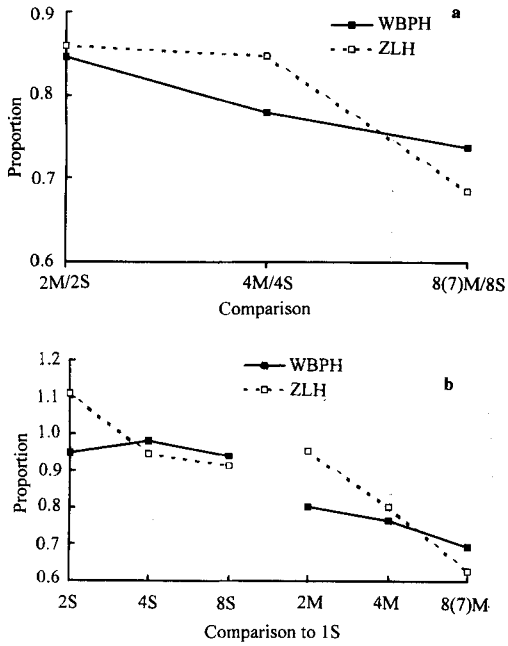

Fig.1. Proportions of intrinsic rate of increase (r_m) of white-backed planthopper *Sogatella furcifera* (WBPH) and zigzag leafhopper *Recilia dorsalis* (ZLH) compared under crowding conditions during adult stage and kept single (a); and such proportions of both under single and crowding during adult stage compared with females kept single throughout nymphal and adult stage (b).

Average clutch size is considered one of the main differences in eruptive and latent species in forestry insects (Price 1990). ZLH with a mean clutch size of 1.4 (Zhu *et al*. unpublished data) is considered a typical latent species whereas WBPH with a mean clutch size of 6.9 (even though the clutch size is affected by female density, age, host plant quality, temperature as so on (Zhu *et al*. 1994a, b)) is a typical eruptive species. As a consequence, WBPH's offspring will have to compete for nutrition in the field which results in lower fitness. The experiments subjected ZLH to higher densities than those occurring in nature which might affect their fitness.

4.2 Different responses of eruptive and latent species to intraspecific competition

Extension of nymph development period of planthoppers at high density has been observed often (Denno *et al*. 1994). Fecundity reduction at high female density was also observed in *Nilaparvata lugens* (Stål) (Heong 1988) and *Prokelisia marginata* (Denno and McCloud 1985). Such effects on leafhoppers are relative fewer. The data presented in this paper show that threshold nymphal density of WBPH for significantly reducing nymphal survival is higher

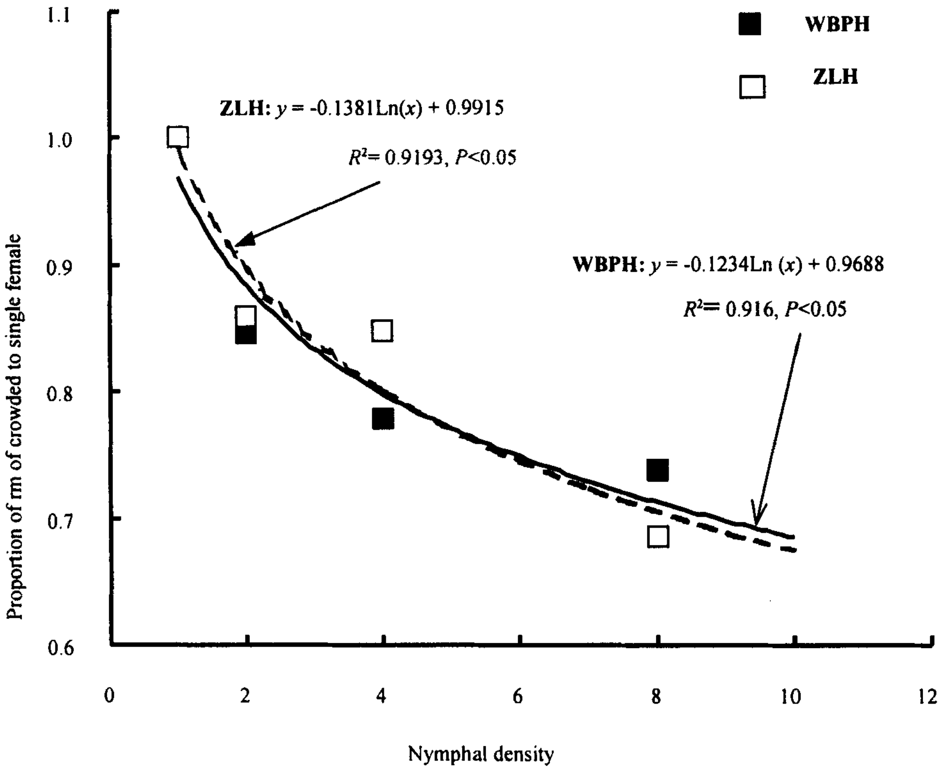

Fig.2 The relationship between relative r_m of the white-backed planthopper *Sogatella furcifera* (WBPH) and the zigzag leafhopper *Recilia dorsalis* (ZLH) of crowded to single female during adult stage and nymphal density.

than that of ZLH. Furthermore, the longevity of singly reared adult ZLH which experienced crowding during nymphal stage was significantly shorter than which did not experienced crowding, while that of WBPH had not such phenomena. This implies that ZLH has a lower ability to recover its sufferance than WBPH. The higher reduction range of WBPH fecundity in pairs of crowding and non-crowding during adult stage than ZLH might be only one of the fitness components had been influenced. It should be more clear if it is considered in a more comprehensive approach.

In addition, crowding induces a higher proportion of macropterous females of WBPH, that will emigrate (Zhu *et al*. 1994c) and build new population elsewhere, therefore the population density of WBPH in the following generation in the original habitat will be regulated (Denno *et al*. 1994). ZLH however has not evolved such heritable trait. It is wing mono-morph.

Therefore the change in fitness components of the two species of hoppers on rice, WBPH and ZLH, gives an order of susceptibility to density (ZLH > WBPH) parallel to salt marsh planthoppers (*Prokelisia marginata* > *P. dolus*) (Denno and Roderick 1992).

Taking account of methodology of the analysis, we think that the response of eruptive and latent species to crowding during nymph and adult stage cannot always be expressed as a signifi-

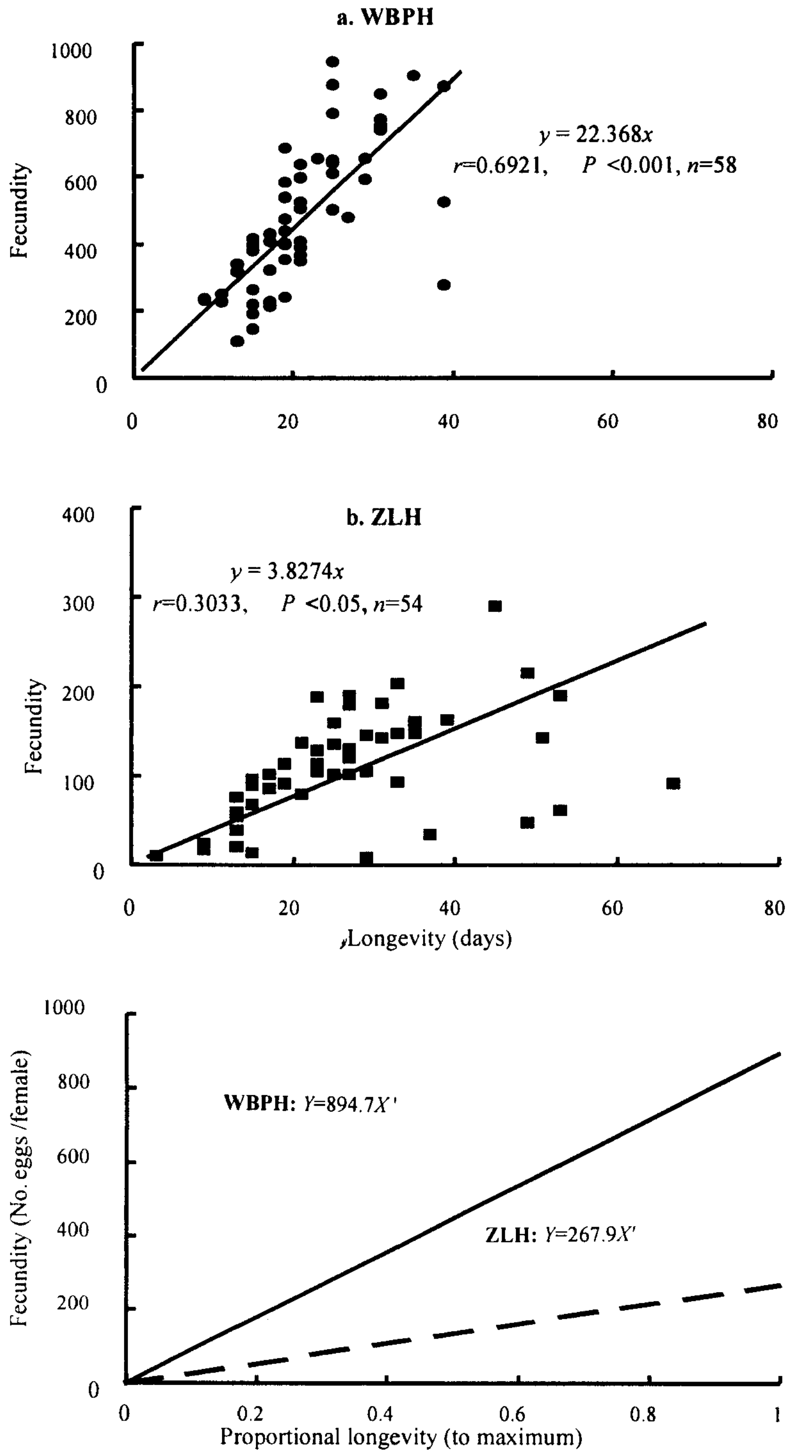

Fig.3 The regressional relationships between fecundities and longevity of the white-backed planthopper *Sogatella furcifera* (WBPH) and the zigzag leafhopper *Recilia dorsalis* (ZLH).

cant difference in fecundity and survival (longevity). In this experiment, the significant differences between fecundity and longevity of crowded adults versus single ZLH adult were less than those of WBPH, but the r_m, one of the integrated parameters of former is much lower than that of latter. So age-specific life table analysis, which integrates survival and reproduction dynamics with average fecundity and longevity and makes a more accurate assessment of the effect of crowding feasible, is helpful and perhaps necessary for understanding the different response mechanisms of eruptive and latent Auchenorrhycha species to density.

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常发性害虫白背飞虱与潜在性害虫电光叶蝉的种内竞争效应比较

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实验室研究表明若虫期拥挤显著延长了白背飞虱 *Sogatella furcifera* 的发育历期,但电光叶蝉 *Recilia dorsalis* 的历期受影响不显著;白背飞虱的若虫存活率、两种的性比、产卵前期和繁殖力不显著。若虫期高密度下的白背飞虱短翅率、电光叶蝉的若虫存活率显著降低。繁殖力和成虫寿命在成虫期也拥挤的条件下将进一步受到影响。特定年龄生命表分析表明拥挤对白背飞虱的综合影响程度比对电光叶蝉小。常发性、潜在性昆虫对若虫期、成虫期拥挤的反应并不总是如文献中所言表现为繁殖力的差异,本研究表明内禀增长力可较完整地描绘这种反应。白背飞虱作为一常发性昆虫与潜在性昆虫电光叶蝉的生态学特性的差异表现在:未成熟期短、繁殖力和产出卵速率均高,因而内禀增长力也高。

关键词 白背飞虱 电光叶蝉 种内竞争 适合度 常发性害虫 潜在性害虫