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Impact of nitrogenous-fertilization on the population dynamics and natural control of rice leaffolders (Lep.: Pyralidae)

(*Keywords: Cnaphalocrocis medinalis, Marasmia patnalis,* natural enemies, nitrogenous fertilization, population dynamics, rice)

J. DE KRAKER*†‡, R. RABBINGE†, A. VAN HUIS‡, J. C. VAN LENTEREN‡ and K. L. HEONG§

†*Laboratory of Theoretical Production Ecology, Wageningen University, Wageningen, The Netherlands*
‡*Laboratory of Entomology, Wageningen University, Wageningen, The Netherlands*
§*International Rice Research Institute, Los Baños, Philippines*

Abstract. The effect of nitrogenous-fertilization on the population dynamics and natural control of rice leaffolders was studied in an irrigated rice area in the Philippines. Nitrogen was applied at three levels (0, 75 and 150 kg N ha^{-1}), and its impact on crop growth and yield, arthropod abundance, and rates of leaffolder parasitism and survival was assessed with weekly samples. Rice plants were taller and had a higher leaf nitrogen content with increasing levels of nitrogenous-fertilization, but grain yield was highest at the medium nitrogen level. Herbivores, predators, and parasitoids increased in abundance with nitrogenous-fertilization level. The average density of rice leaffolder larvae at the highest nitrogen level was eight times the density at zero nitrogen level, and the peak percentage injured leaves increased from 5 to 35%. The strong increase in larval density was due to the positive effect of nitrogenous-fertilization on egg recruitment and survival of medium-sized larvae. The percentage parasitism of eggs and larvae was not affected by nitrogenous-fertilization. The increase in survival of medium-sized larvae with nitrogen levels was associated with lower predator to leaffolder ratios. The strong effect of nitrogenous-fertilization in the present small-scale experiment was attributed mainly to allowing the moths an oviposition choice between plots with different application levels of nitrogen. Therefore it is hypothesized that the effect of increasing nitrogenous-fertilization level on leaffolder larval densities will be less pronounced when implemented over a large area.

1. Introduction

Since the mid-1960s rice leaffolders (*Cnaphalocrocis medinalis* (Guenee) and *Marasmia* spp., Lepidoptera: Pyralidae) have increased in abundance, and in many Asian countries they are now considered as important pests (Reissig *et al.*, 1986; Khan *et al.*, 1988; Dale, 1994). The shift from minor to major pest status has been attributed to the adoption of new rice growing practices that accompanied the introduction of high yielding varieties (Kulshreshtha *et al.*, 1970; Litsinger, 1989). These practices included increased cropping intensity, irrigation and a high input of nitrogenous fertilizers and pesticides (Loevinsohn *et al.*, 1988). In particular the effects of variety and nitrogenous-fertilizer on rice leaffolder infestation have been the topic of numerous studies. The adoption of modern varieties *per se* does not seem to be the cause of increased leaffolder abundance, because their level of resistance to rice leaffolder does not differ from that of the traditional cultivars (Heinrichs *et al.*, 1985, 1986; Khan and Joshi, 1990). A large number of field trials, however, have shown that increasing nitrogenous-fertilization usually leads to higher leaffolder injury levels (Dale, 1994). The effects of nitrogenous-fertilization on leaffolder population dynamics were not determined in these field trials, nor were the mechanisms underlying the increased injury levels identified. Laboratory experiments showed that nitrogenous-fertilization affects several bionomic characteristics of rice leaffolders (table 1). As is usual for herbivores (Mattson, 1980), nitrogen appears to be a limiting factor for growth, reproduction and survival. The reported increase in leaffolder injury with nitrogenous-fertilization level may thus have various causes, but the relative importance of these factors under field conditions is not yet known.

In insecticide-free fields with current farmer crop management practices, rice leaffolder infestations in the Philippines are generally low and natural control seems to be effective in keeping the infestation levels below the damage threshold (Litsinger *et al.*, 1987; Barrion *et al.*, 1991; de Kraker, 1996). To meet the ever increasing demand for rice, however, the attainable yields will have to be raised, requiring higher nitrogenous-fertilizer inputs (Kropff *et al.*, 1994). As this increase in nitrogen input could stimulate leaffolder population growth or feeding rates, natural enemies may no longer be able to keep the pest below damaging levels. This would trigger more insecticide applications and the natural control of many other rice pests would then also be at risk (Way and Heong, 1994).

To optimize nitrogenous-fertilization for stable, high yields, not only agronomic effects, but also the effects of nitrogenous-fertilization on pest development should be accounted for. In the present field study, the effect of nitrogenous-fertilization on the dynamics of rice leaffolders and their natural enemies was investigated in detail by intensive sampling during one cropping season. The objective was to identify the major mechanisms leading to increased leaffolder infestation at high nitrogen levels. Knowledge of these mechanisms will be helpful to determine optimal nitrogen application levels in an integrated approach to crop management.

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*To whom correspondence should be addressed at: TPE, PO Box 430, 6700 AK Wageningen, The Netherlands. Fax: +31 317 484892; e-mail: joop.dekraker@staff.tpe.wau.nl

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2. Materials and methods

2.1. Location and lay-out of field experiment

The study was conducted during the wet season in a farmer's field in Pila, a municipality at about 20 km distance from the International Rice Research Institute (13° 14′ N, 121° 15′ E), Laguna Province, the Philippines. Laguna is a humid tropical lowland area where rice is grown year-round under irrigated conditions. The rice leaffolder population is a complex of three related species: *Cnaphalocrocis medinalis, Marasmia patnalis* Bradley, and *M. exigua* (Butler) (Arida and Shepard, 1986), the first two species being the most abundant in Laguna (Barrion *et al.*, 1991; de Kraker, 1996).

The experiment was laid out in a randomized complete block design, with three levels of nitrogenous-fertilizer in four replications. Blocks were located along a slope at increasing distance to the water inlet from the irrigation canal. The size of the treatment plots was 500 m^2. Treatment levels of nitrogenous-fertilization were 0, 75 and 150 kg N ha^{-1}, representing low, standard recommended, and high levels respectively. Nitrogenous-fertilizer was applied as ammonium sulphate in three split-doses over the season: 50% at 3 days after transplanting (d.a.t.), and twice 25% at 21 and 35 d.a.t.

The rice variety planted was IR70, a long-duration variety, which is susceptible to rice leaffolders, but (moderately) resistant to other common pests, like plant and leafhoppers and stemborers (IRRI, 1990). The field was planted with 2-week old seedlings in a 20 × 20 cm spacing on 31 August 1991. Weeding was done by hand and pesticides were not applied. The field was intermittently flooded.

2.2. Crop growth and yield

Crop growth was assessed by taking hill samples every 2 weeks, starting 1 month after transplanting. Sample size was three hills per plot. Plant height, number of tillers and leaves per hill, leaf colour and growth stage were recorded. Total leaf nitrogen content (%) was determined with the Kjeldahl method, at three crop growth stages: tillering (33 d.a.t.), panicle formation (58 d.a.t.), and flowering (86 d.a.t.). At maturity, yield was measured by harvesting 10 m^2 per plot. Grain yield was adjusted to 14% moisture content based on fresh weight.

Table 1. Effects of nitrogenous fertilization on bionomic parameters of rice leaffolders: (+)=significant increase, (—)=significant decrease, (0)=no significant effect, (?)=effect unknown

Parameter	*C. medinalis*		*M. patnalis*	
Larval survival	+	(4)	?	
Pupal survival	+	(4)	?	
Larval period	0	(4)	—	(6)
Pupal period	0	(4)	0^a	(3)
Leaf area consumed per larva	+	(5)	$+^a$	(3)
Relative consumption rate^b	—	(4)	?	
Pupal weight	+	(4)	$+^a$	(3)
Moth longevity	+	(4)	?	
Moth fecundity	+	(4)	?	
Oviposition (choice)	+	(1, 6)	?	
Oviposition (no-choice)	+	(2, 6)	?	

References: (1) Fukamachi, 1980; (2) Liang *et al.*, 1984; (3) Arida *et al.*, 1990; (4) Dan and Chen, 1990; (5) Fabellar and Heong, 1991; (6) de Kraker, unpublished.

^{a}Nitrogen-effect inferred from tested effect of leaf age and position, leaf nitrogen content was not measured.

^{b}Leaf biomass consumed per larval biomass.

2.3. Sampling of the arthropod fauna

The densities of rice leaffolder stages, their natural enemies, and other arthropods were estimated by a combination of sampling methods, starting 1 month after transplanting. Rice leaffolder moths and other mobile arthropods were sampled weekly with a suction sampler (D-Vac) in combination with a plastic bucket enclosure, covering four hills. On each sampling occasion, five D-Vac samples were taken per plot. Relative density estimates of highly mobile species, such as the larger hymenopterous parasitoids, were obtained by weekly sweepnet sampling. Four samples, of five sweeps each, were taken per plot. All suction and sweepnet samples were taken between 8.00 and 11.00 a.m. The collected arthropods were identified and classified as rice pests, predators, parasitoids, or 'other'. The 'other' category consisted of Diptera, mainly of families with aquatic larval stages (e.g. Ceratopogoniidae, Chironomidae, Tipulidae, Culicidae). Predators and parasitoids of rice leaffolders were classified according to Barrion *et al.* (1991). The efficiency of sweepnet samples decreased markedly as the crop grew denser, and therefore sweepnet results were only included in between-treatment comparisons for the insect taxa which are less efficiently sampled with D-Vac.

The densities of the immature leaffolder stages were estimated by random, destructive sampling of rice hills, twice a week. With a sample size of 15 hills per plot, less than 3% was removed from the plots by the end of the season. In the laboratory, the plants were examined for the presence of leaffolder eggs, larvae and pupae, and leaves with leaffolder injury. Larvae were classified in five size-classes, approximately corresponding with the five larval instars. The immature stages were kept in test tubes or petri-dishes until emergence of adults or parasitoids, or until premature death. Leaffolders could be identified to species only after moth emergence, because the immature stages of the three leaffolder species are very similar in appearance (Barrion *et al.*, 1991).

2.4. Parasitism and survival rates

As an indicator of parasitoid impact, a seasonal level of parasitism was calculated by dividing the number of hosts with clear symptoms of parasitism by the total number of hosts, after pooling all samples per plot. Leaffolders that died of unknown cause during rearing were excluded from the calculation on the assumption that healthy and parasitized hosts had similar chances of dying.

From the time series of leaffolder population samples, estimates were made of stage to stage survival rates using Southwood and Jepson's 'graphical method' (Southwood, 1978). The densities of the various leaffolder stages were adjusted according to their sampling efficiency. A previous experiment showed that relative to large larvae (L4, L5, L6), sampling eggs was ca 50% efficient, and sampling medium-sized larvae (L2, L3) ca 60%. Sampling efficiency of the cryptic and tiny first instar larvae is very low, and therefore this stage was excluded from the survival analysis. Survival rates were calculated from egg to larva, egg to medium-sized larva, and from medium-sized larva to large larva for each plot. Data on pupal densities were not sufficient to include in the analysis.

The calculated parasitism and survival rates are approximate values, meant for comparison between treatments and correlation with potential mortality factors. Further details on the calculation of parasitism and survival rates are given in de Kraker (1996).

2.5. *Statistical analysis*

All statistical tests were performed with the GLIM package (Crawley, 1993). Count data and ratios were log-transformed prior to analysis. Treatment effects on arthropod abundance, natural enemy to rice leaffolder ratios, rates of parasitism and survival ratios were assessed with an *F*-test in an ANOVA for completely randomized block designs. The effect of nitrogen application level and sampling method on rice leaffolder species composition in the samples was assessed with a *G*-test of independence (Poisson errors), with all samples pooled per treatment level. Simple linear correlation coefficients (r) were calculated to detect significant associations between rice leaffolder and natural enemy densities, natural enemy to leaffolder ratios, rates of parasitism, and survival ratios per plot ($n = 12$).

3. Results

3.1. *Impact of nitrogenous-fertilization on rice crop growth and arthropod abundance*

Nitrogenous-fertilization had a clear impact on rice crop growth (data not shown). Plants were taller and darker green at higher fertilization levels. Leaf nitrogen content was also positively correlated with nitrogenous-fertilization level, although differences were only significant during the active tillering stage. The average tiller and panicle number per hill increased with nitrogenous-fertilization level, but the effect was not significant due to large inter-plant variation. Grain yield per hill was highest in the medium nitrogen (75 kg ha^{-1}) treatment.

Nitrogenous-fertilization also had an impact on higher trophic levels. All four arthropod categories—pests, predators, parasitoids, and ‘others’—increased in abundance with nitrogenous-fertilization level (table 2). For the parasitoids this effect was highly significant when sampled with a sweepnet ($F_{2,6} = 13.88$, $P < 0.01$), but not with D-Vac sampling. Within the pest category, the abundance of Homoptera and Heteroptera did not increase significantly, in contrast to the Lepidoptera (adults) which increased about six times in average density (table 2). Within the Lepidoptera, the share of rice leaffolder moths increased with nitrogenous-fertilization level from 25 to 70%. Other common moths were green hairy caterpillar *Rivula atimeta* (Swinhoe) (Lepidoptera: Noctuidae), and yellow stemborer *Scirpophaga incertulas* (Walker) (Lepidoptera: Pyralidae). The temporal pattern of pest abundance was very similar for the three treatments. During the first part of the growing season sap-feeding homopteran pest species (plant- and leafhoppers) dominated, while after the flowering stage the seed-feeding hemipteran rice bugs (*Leptocorisa* spp.) were the most abundant.

3.2. *Population dynamics of rice leaffolders*

M. patnalis was the dominant leaffolder species, both for moths and larvae (table 3). The species composition of the samples differed per method: in the moth samples (D-Vac, sweepnet) *M. exigua* was practically absent, while this species constituted a considerable proportion of the larval samples. Nitrogenous-fertilization had no effect on the species composition of the sampled moths, but did affect the species composition of the sampled larvae, as the proportion of *M. patnalis* larvae increased with nitrogenous-fertilization level. The species composition of leaffolder larvae and moths differed significantly per crop growth stage. *C. medinalis* and *M. patnalis* were about equally abundant during the tillering stage, while *M. patnalis* was dominant from booting till maturity. *M. exigua* only made up a considerable part of the larval population (25%) after flowering.

Densities of leaffolder moths, eggs and larvae increased strongly with nitrogenous-fertilization level (table 4, figure 1). The average larval density in the high nitrogen treatment was

Table 2. Effect of nitrogenous fertilization on the abundance of rice arthropod groups (no. per four hills, seasonal average of D-Vac samples). Ratio high/low is the quotient of abundance at 150 N and 0 N treatment levels

	Treatment level (kg N ha^{-1})					
Arthropod group	0	75	150	Ratio high/low	Treatment effect[a]	
Pests	3.4	3.8	4.7	1.4	$F = 5.29$	*
Homoptera	2.3	2.1	2.6	1.1	$F = 3.40$	n.s.
Heteroptera	0.5	0.9	1.0	2.0	$F = 2.54$	n.s.
Lepidoptera	0.1	0.2	0.6	6.0	$F = 19.36$	**
Predators	5.0	6.6	8.2	1.6	$F = 26.83$	**
Parasitoids	3.0	3.9	4.2	1.4	$F = 2.88$	n.s.
Others	12.0	15.7	21.7	1.8	$F = 43.42$	**

[a] df=2, 6; n.s.=non-significant; *=$P<0.05$; **=$P<0.01$; ***=$P<0.001$.

Table 3. Species composition of the rice leaffolder complex, as a percentage of seasonal totals (N), determined with three sampling methods (D-Vac, sweepnet, and hill samples)

		Treatment level (kg N ha^{-1})				
Sampling method	Species	0	75	150	Treatment effect[a]	
D-VAC (moths)	*C. medinalis*	67	38	34		
	M. patnalis	33	62	65		
	M. exigua	0	0	1		
	(N)	(6)	(26)	(107)	G=3.10	n.s.
Sweepnet (moths)	*C. medinalis*	30	46	40		
	M. patnalis	70	54	60		
	M. exigua	0	0	0		
	(N)	(30)	(63)	(184)	G=2.25	n.s.
Hill sample (larvae)	*C. medinalis*	27	21	13		
	M. patnalis	44	57	76		
	M. exigua	29	22	11		
	(N)	(66)	(180)	(886)	G=48.05	***
Effect of sampling method[a]		G=21.69 ***	G=41.86 ***	G=115.73 ***		

[a]Effect on species composition: df=4; n.s.=non-significant, P>0.05; ***=P<0.001.

Table 4. Effect of nitrogeneous-fertilization on abundance of rice leaffolder stages and injured leaves (seasonal average of samples). Ratio high/low is the quotient of abundance at 150 N and 0 N treatment levels

		Treatment level (kg N ha^{-1})					
Leaffolder stage	(units)	0	75	150	Ratio high/low	Treatment effect[a]	
Moths	(no. per five sweeps)	0.18	0.33	0.96	5.3	F=10.37	*
Moths	(no. per four hills)	0.03	0.11	0.46	15.3	F=8.88	*
Eggs	(no. per hill)	0.13	0.25	0.60	4.6	F=31.40	**
Larvae	(no. per hill)	0.24	0.57	1.92	8.0	F=11.44	**
Pupae	(no. per hill)	0.01	0.02	0.06	6.0	F=4.56	n.s.
Injured leaves	(no. per hill)	2.0	4.3	13.3	6.7	F=10.92	**

[a]df=2, 6; n.s.= non-significant, $P>0.05$; *=$P<0.05$; **=P=<0.01.

eight times the density in the zero nitrogen treatment. The average number of injured leaves per hill was positively correlated with larval density (r = 0.99, df = 10, $P<0.001$), and increased with nitrogenous-fertilization level. While the percentage of injured leaves did not exceed 10% in the zero and medium nitrogen treatment, it reached as high as 30–35% in the high nitrogen treatment during the ripening stage (figure 1).

3.3. Diversity and abundance of leaffolder natural enemies

A total of 33 leaffolder natural enemy taxa were identified from the arthropod samples: 21 predator and 12 parasitoid taxa. This seasonal total of taxa was the same for each treatment, although the number of taxa per sampling date was usually lower in the zero nitrogen treatment. This is most probably a result of the lower natural enemy density in this treatment.

The abundance of most natural enemies of rice leaffolder increased with nitrogenous-fertilization level (table 5). The increase of the tettigoniid *Conocephalus longipennis* (de Haan) (Orthoptera) was not significant in the D-Vac samples, but highly significant in the sweepnet samples ($F_{2,6}$ = 99.30, $P<0.01$). A sweepnet is more suitable to sample this large and fast-moving species. Of all groups of leaffolder natural enemies only the Coccinellidae and Araneae did not increase significantly with nitrogenous-fertilization level, neither in the D-Vac nor in the sweepnet samples. Natural enemies increased less in abundance with nitrogenous-fertilization level than leaffolders. This is illustrated by the curvilinear relationship between the seasonal total D-Vac catches per plot of the gryllid and carabid predators and their leaffolder prey stages, eggs and larvae respectively (figure 2). As a consequence, the natural enemy to leaffolder ratios decreased with nitrogenous-fertilization level (table 6). Differences between treatments in natural enemies to leaffolder ratio were smallest for the group of major leaffolder parasitoids.

The temporal pattern of predator abundance was similar for the three treatments: the first half of the growing season spiders and hemipterans were most abundant, while during the second half coleopterans and orthopterans dominated. In addition to the natural enemy to leaffolder abundance ratios, the degree of overlap in temporal occurrence between these natural enemies and their leaffolder prey was also calculated (see Van den Berg and Cock, 1993). Overlap in phenology ranged from 35 to 75%, and was lowest for the Coccinellidae and Tettigoniidae. These species were present mainly around or after flowering, when the leaffolder population was declining already. Between the treatments, the differences in the percentage temporal overlap were small (5–10%).

3.4. *Parasitism and survival of leaffolders in relation to nitrogenous-fertilization level*

Ten species of hymenopterous parasitoids were reared from the field-collected rice leaffolder eggs, larvae, and pupae (for details, see de Kraker, 1996). Eggs were parasitized by *Trichogramma* sp. (probably *T. japonicum* Ashmead), while the braconids *Macrocentrus philippinensis* Ashmead and *Cardiochiles philippinensis* Ashmead were the most common parasitoids in the larval samples. Seasonal percentages of parasitism of leaffolder eggs and larvae were independent of nitrogenous-fertilization level (table 7). Both egg and larval parasitism (%) decreased with crop age, but were independent of rice leaffolder density. The seasonal percentage larval parasitism per plot was not correlated with average parasitoid abundance, nor with the parasitoid to larva ratio.

Survival from egg to medium-sized larva was similar for all nitrogenous-fertilization levels, but survival from medium-sized to large larva increased markedly with nitrogenous-fertilization level (table 7). Survival rates from egg to medium-sized larvae were larger than 1.0, indicating that the sampling efficiency of leaffolder eggs was probably lower than assumed. The survival from egg to medium-sized larva was not correlated with the seasonal percentage egg parasitism. Neither was the survival from medium-sized to large larva correlated with percentage larval parasitism. However, larval

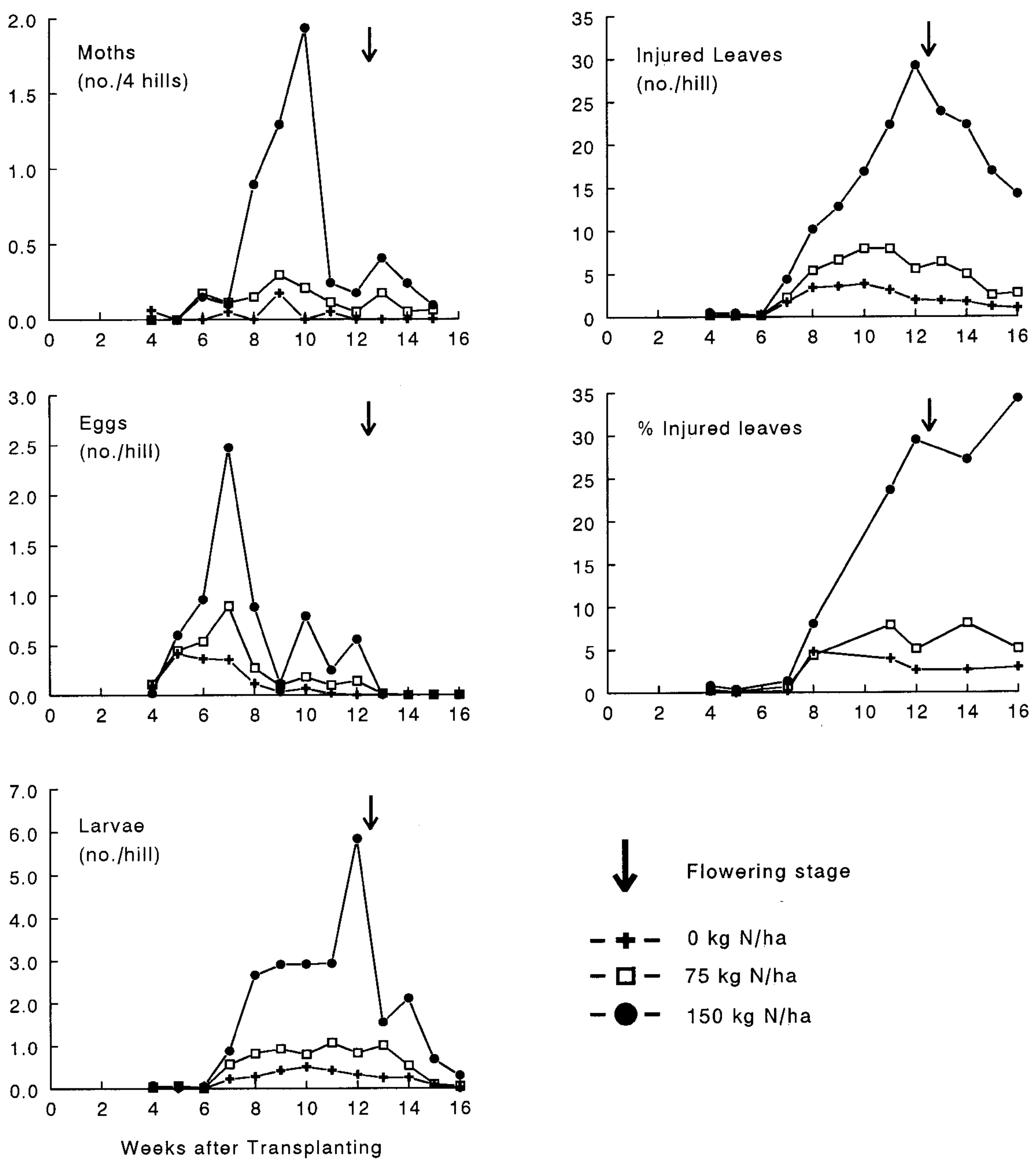

Figure 1. Mean densities of rice leaffolder moths, eggs, larvae, injured leaves and percentage injured leaves, at three levels of nitrogenous-fertilization: 0, 75 and 150 kg N ha^{-1}. Standard errors were ca 20% of sample means.

Table 5. Effect of nitrogenous-fertilization on abundance of natural enemies of rice leaffolders (no. per four hills, seasonal average of D-Vac samples). Ratio high/low is the quotient of abundance at 150 N and 0 N treatment levels

	Treatment level (kg N ha^{-1})					
Natural enemy taxon	0	75	150	Ratio high/low	Treatment effect[a]	
Predators:						
Coleoptera	1.81	2.35	2.92	1.6	$F = 9.77$	*
Coccinellidae	1.18	1.40	1.36	1.2	$F = 2.69$	n.s.
Carabidae	0.35	0.49	0.85	2.4	$F = 14.55$	**
Staphylinidae	0.28	0.46	0.73	2.6	$F = 9.92$	*
Orthoptera	0.66	1.14	1.48	2.2	$F = 13.10$	**
Gryllidae	0.49	0.89	1.02	2.1	$F = 16.28$	**
Tettigoniidae	0.16	0.25	0.48	3.0	$F = 4.64$	n.s.
Hemiptera	1.14	1.74	2.35	2.1	$F = 40.98$	**
Araneae	1.17	1.16	1.10	0.9	$F = 0.08$	n.s.
Parasitoids:[b]						
Hymenoptera — potential	1.48	2.18	2.41	1.6	$F = 6.05$	*
Hymenoptera — major	0.12	0.24	0.43	3.6	$F = 9.69$	*

[a] df = 2, 6; n.s. = non-significant, $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$.

[b] Potential: species recorded as RLF larval parasitoids; major: species accounting for 85% of observed parasitism.

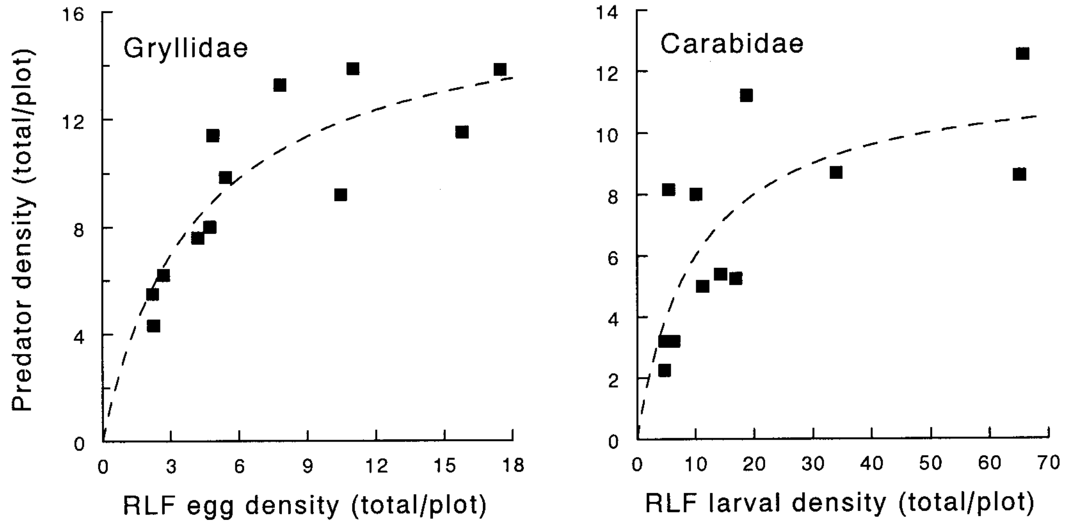

Figure 2. Seasonal total catch of predators (D-Vac samples) versus their rice leaffolder prey stage (hill samples) per treatment plot: Gryllidae vs leaffolder eggs and Carabidae vs leaffolder larvae. Dashed lines are eye-fitted curves to indicate general trend.

survival rates were negatively correlated with predator to leaffolder immature and parasitoid to larvae ratios (df = 10, $r = -0.82$, $P < 0.01$ and $r = -0.83$, $P < 0.001$, respectively) and positively correlated with average density of eggs and medium-sized larvae (df = 10, $r = 0.80$, $P < 0.01$ and $r = 0.77$, $P < 0.01$, respectively).

The last larval instars of rice leaffolders are responsible for more than 90% of the total leaf area consumed during the larval stage (Heong, 1990), and leaf injury is thus mainly dependent on the density of these instars. The abundance of large leaffolder larvae (N_{LL}) depends on egg recruitment (N_{EGG}), and subsequent survival from eggs to medium-sized larva (S_{EGG}), and from medium-sized to large larva (S_{ML}). By taking the log-values the equation for N_{LL} becomes additive:

$$\log(N_{LL}) = \log(N_{EGG}) + \log(S_{EGG}) + \log(S_{ML})$$

To determine which of the three terms alone explained most of observed variation in abundance of large larvae per plot, correlation coefficients were calculated between log (N_{LL}) and each of the terms. Survival from egg to medium-sized larva did not explain a significant part of the variation ($r = 0.14$, df = 10, $P < 0.1$). Abundance of large larvae was best correlated with egg recruitment ($r = 0.97$, df = 10, $P < 0.001$), and, somewhat less, with survival from medium-sized to large larva ($r = 0.92$, df = 10, $P < 0.001$). In fact, survival from medium-sized to large larva cannot be viewed completely separate from egg recruitment, as this survival rate was positively dependent on egg recruitment. Thus, egg recruitment is probably the major factor determining the density of large larvae.

Table 6. Effect of nitrogenous-fertilization on the natural enemy to rice leaffolder (RLF) ratio, calculated over the entire season (ratios of average density per hill, D-Vac and hill samples)

	Treatment level (kg N ha^{-1})				
Natural enemy: Leaffolder ratio	0	75	150	Treatment effect[a]	
Predators[b]: RLF moths	45.74	11.11	2.94	$F = 33.63$	**
Predators[c]: RLF immatures	2.39	1.57	0.67	$F = 30.93$	**
Predators[d]: RLF immatures	1.64	1.05	0.44	$F = 33.93$	**
Potential parasitoids[e]: RLF larvae	1.54	0.97	0.31	$F = 35.77$	**
Major parasitoids[f]: RLF larvae	0.12	0.10	0.06	$F = 5.74$	*

[a] df = 2, 6; n.s. = non-significant, $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$.

[b] Araneae, Odonata; [c] Coleoptera, Orthoptera, Hemiptera; [d] Coleoptera, Orthoptera.

[e] Hymenoptera recorded as RLF larval parasitoids; [f] Species accounting for 85% of observed parasitism.

Table 7. Effect of nitrogeneous-fertilization on parasitism and stage survival of leaffolder eggs and larvae, calculated over the entire season

	Treatment level (kg N ha^{-1})				
Parameter	0	75	150	Treatment effect[a]	
Egg parasitism (%)	16.1	20.2	13.1	$F = 0.88$	n.s.
Larval parasitism (%)	33.7	31.3	37.9	$F = 1.16$	n.s.
Egg—medium larva (survival ratio)	1.08	1.08	0.97	$F = 0.76$	n.s.
Medium—large larva (survival ratio)	0.23	0.29	0.66	$F = 14.98$	**

[a] df = 2, 6; n.s. = non-significant, $P > 0.05$; ** = $P < 0.01$.

4. Discussion

4.1. *Impact of nitrogenous-fertilization on the rice ecosystem*

The input of additional nitrogen to the irrigated rice ecosystem led to an increase in biomass at three trophic levels, suggesting that the system is nitrogen-limited (White, 1978). Nitrogenous-fertilization increased the production of rice plant biomass and enhanced leaf nitrogen content, thus forming the basis for the increase in rice pest herbivore abundance (table 2). The additional nitrogen supply probably also led to increased production of algae and other microflora in the floodwater and on the soil surface (Craswell and Vlek, 1979), supporting higher populations of Diptera with aquatic larval stages, comprising most of the 'other' category in table 2 (Roger *et al.*, 1994). In turn, predators and parasitoids at the third trophic level responded numerically to the increased abundance of their herbivore prey.

4.2. *Response of rice leaffolder populations to nitrogenous-fertilization*

Application of 150 kg N ha^{-1} resulted in larval peak densities that were at least three times higher than densities commonly observed in Laguna Province (cf. de Kraker, 1996), and about six times higher than the peak density in the plots with a standard (medium) fertilization level (figure 1). Recommended economic thresholds (Bautista *et al.*, 1984; Bandong and Litsinger, 1988; Smith et al., 1989; Heong, 1993) for rice leaffolder control were all exceeded in the high nitrogen treatment, both in terms of percentage injured leaves and larval densities.

A number of possible explanations for the increase in rice leaffolder injury with nitrogenous-fertilization level (see table 1) can be discarded in the present study. As the number of injured leaves was linearly correlated with larval density and the ratio of injured leaves to larvae even tended to decline with nitrogenous-fertilization level (cf. table 4), the effect on leaf injury cannot be due to increased larval feeding rates. The phenology of immature leaffolder stages was similar for all treatments, indicating that the duration of immature stages was not markedly affected. Differences in leaf nitrogen content between the treatments may have led to better larval growth, heavier pupae, and increased female fecundity. However, this could only have affected the size of the second generation, but was even then probably unimportant considering the mobility of leaffolder moths and the proximity of the treatment plots. The major effects of nitrogenous-fertilization on rice leaffolder identified in the present study were increased egg recruitment (i.e. total number of eggs laid in the crop), and subsequently higher larval survival rates, both leading to a strong increase in the abundance of large larvae, the most injurious stage of rice leaffolder (figure 3).

4.2.1. Effect of nitrogenous-fertilization on rice leaffolder egg recruitment. The strong positive effect of nitrogenous-fertilization on leaffolder egg density (table 4) has been observed before, both in small and large-scale experiments with *C. medinalis* (Fukamachi, 1980; de Kraker, unpublished). *Marasmia patnalis* and *M. exigua* apparently have a similar oviposition response, reflected in the increase of their larval densities with nitrogenous-fertilization level. Among the three species, *M. patnalis* probably responded most strongly, as its share in the larval samples increased from 44 % in the zero nitrogen to 76% in the high nitrogen level (table 3). Increased egg recruitment is probably a result of aggregation of ovipositing females in well-fertilized plots (preference), as well as an increase in the number of eggs deposited per female. Oviposition experiments with small plots fertilized with different levels of nitrogen with either a confined or a free-moving moth population indicated that

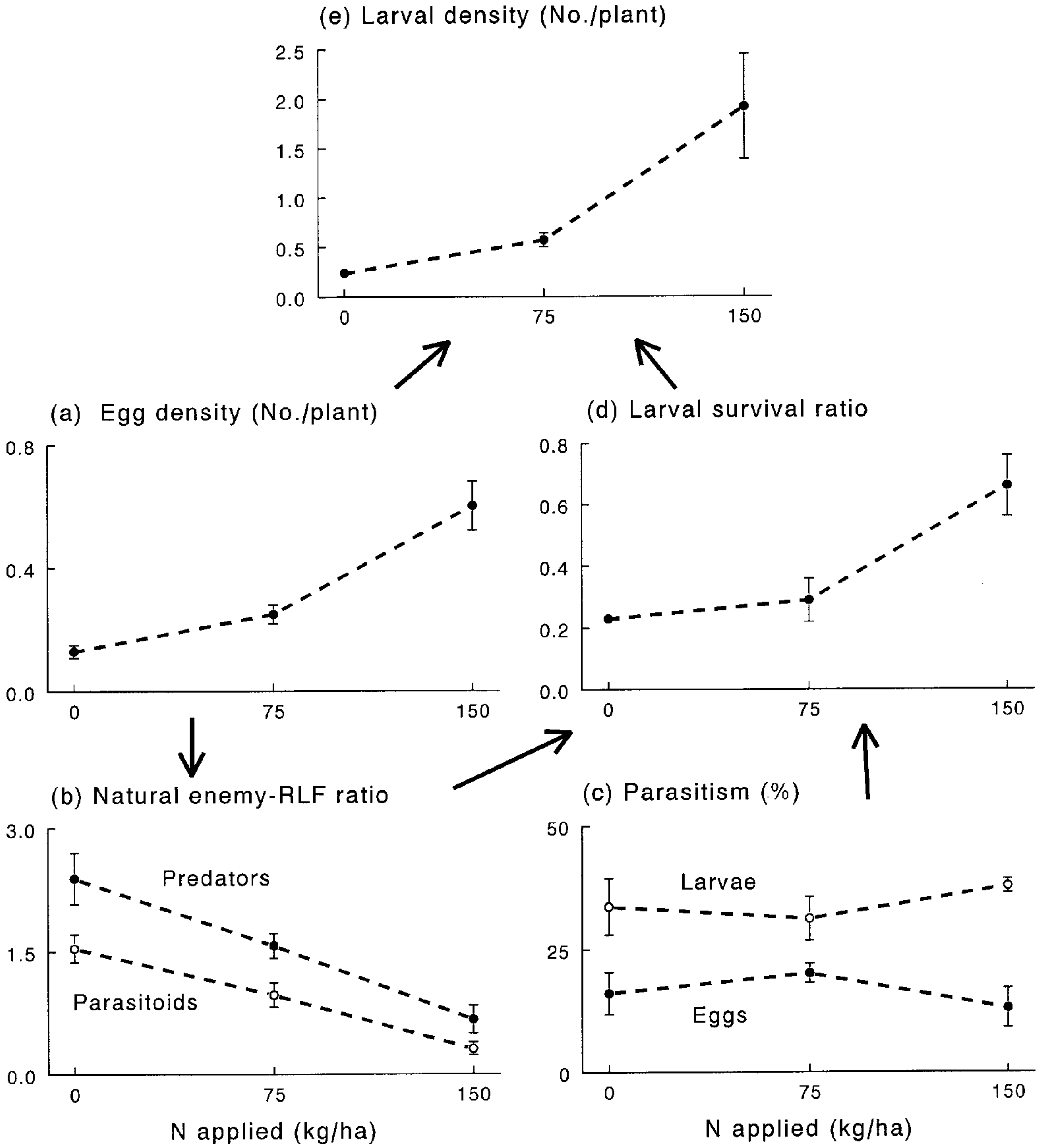

Figure 3. Effects of nitrogenous-fertilization on the density of rice leaffolder (RLF) larvae: RLF moths lay many more eggs in plots receiving a high level of nitrogenous-fertilizer (a, cf. table 4), resulting in fewer predators and parasitoids per rice leaffolder egg or larvae (b, cf. table 6). The level of egg and larval parasitism is not affected (c, cf. table 7), but the survival of medium-sized larvae increases with nitrogenous-fertilization level (d, cf. table 7), probably as a result of the lower predator to RLF ratios (b). More eggs (a) and better larval survival (d) result in a steep increase in larval density with nitrogen application level (e, cf. table 4). Error bars indicate standard errors of the treatment means.

preference was the major cause of the increase in egg density from medium to high nitrogen levels (de Kraker, unpublished).

4.2.2. Effect of nitrogenous-fertilization on rice leaffolder larval survival. Survival rates were also significantly affected by the level of nitrogenous-fertilization, notably the survival from medium-sized to large larva (table 7). This effect might be either direct, by enhancing larval survival through improved host plant quality, or indirect, through the impact of natural enemies. Dan and Chen (1990) reported a direct effect of nitrogenous-fertilization on *C. medinalis* larval survival in pot experiments, but they did not specify the magnitude of this effect. Our own observations suggest that this effect is small within the range in leaf nitrogen content of the present study. A closer look at the field data also indicates that a direct effect of host plant quality is unlikely: while leaf nitrogen content tended to be higher in the lower blocks, larval survival was generally lower. Indirectly, nitrogenous-fertilization may lead to better nutrition and reduce the larval development period, thus decreasing the risk of attack (Price *et al.*, 1980). However, the effect of leaf nitrogen content on the larval development period of leaffolders is small (Dan and Chen, 1990; de Kraker, unpublished), and the phenology of immature leaffolder stages was similar for all treatments. Another possible indirect effect is a reduced searching efficiency of leaffolder natural enemies at higher nitrogenous-fertilization levels, due to the higher crop density and larger leaf area (e.g.

de Kraker, 1996). This might indeed have contributed to the increased larval survival in the high nitrogen treatment, but does not explain the large difference with the medium nitrogen treatment, as differences in crop density and plant height between these treatments were relatively small.

The increase in survival of medium-sized larvae with nitrogen level is most likely due to the less-than-proportional increase in leaffolder natural enemies, reflected in the decrease in the natural enemy to leaffolder ratios (table 6). Leaffolder egg density increased more than 4.5 times from the zero nitrogen to the high nitrogen level, while the density of most natural enemy groups increased less than three times (tables 4 and 5). The less-than-proportional numerical response of the leaffolder natural enemies may be due to their predominantly generalist nature. Their numerical response is then expected to be based on overall prey density (table 2: Pests and Others), which increased less dramatically with nitrogen level than leaffolder density. The relatively high numerical response of the more specialized leaffolder enemies, the major larval parasitoids (tables 5 and 6), confirms this relationship between specialization and numerical response. A less-than-proportional numerical response could be compensated by a functional response to leaffolder density, resulting in similar levels of mortality at high and low leaffolder densities. Egg and larval parasitoids probably displayed such a functional response, as percentages of egg and larval parasitism were independent of leaffolder density and fertilization level while parasitoid to leaffolder ratios declined (table 7). In the more generalist predators, such a compensatory functional response may well have been absent or insufficient, resulting in the observed increase in leaffolder larval survival.

The question remains why survival from egg to medium-sized larva was not affected by the changes in predator-prey ratio, while survival from medium-sized to large larva was. It could be that predation is not a major factor in survival from egg to medium-sized larva, unlike in medium-sized to large larval survival. The effect of abiotic factors, such as heavy rainfall, on successful settling of young larvae might be a more important, density-independent factor (de Kraker, unpublished). Another possible explanation concerns the functional response of the larval predators. These predators can consume large numbers of small larvae per day, but only a few medium-sized or large larvae (Yuen, 1982; Win, 1989). Therefore their functional response to changes in young larval density may have been much stronger. In a choice situation, they also might have a preference for young larvae, resulting in switching to these stages when total prey abundance is high, as in the high nitrogen treatment.

4.3. *Implications for integrated crop management*

Modern rice varieties are highly responsive to nitrogenous-fertilization (Yoshida, 1981). Apart from raising the attainable yield level, increased nitrogen supply can make the crop less sensitive to pest injury (Peng, 1993). However, high fertilizer inputs may also lead to increased pest infestation levels, which reduce the expected gains in rice yield. Several reports demonstrate this effect (Hu *et al.*, 1986; Saroja *et al.*, 1987; Inoue and Fukamachi, 1990). In the present study, grain yield per hill was highest in the medium nitrogen treatment, although crop biomass and nitrogen content were higher in the high nitrogen treatment. The high pest infestation levels in the latter treatment may well be the cause of this discrepancy.

In an integrated crop management approach, optimization of nitrogenous-fertilization should take these effects on pest infestation into account, in particular when reliance on chemical pest control is to be reduced. This does not necessarily imply that the recommended fertilization levels will be agronomically sub-optimal. Although higher nitrogenous-fertilization levels generally cause an increase in rice leaffolder infestation, this effect may be (partly) avoided by adapting application method and timing. In particular early application of all fertilizer leads to high infestation levels (Saroja *et al.*, 1981), but this timing is also unfavourable from an agronomic viewpoint, as it leads to inefficient uptake and use of nitrogen for yield formation (Thiyagarajan *et al.*, 1995).

4.4. *Effect of large-scale nitrogenous-fertilization on rice leaffolder infestation*

The present study and numerous others were all small-scale, one-season experiments (for a compilation of 15 published field trials, see de Kraker, 1996). What would the effect on rice leaffolder infestation be, if the nitrogenous-fertilization level was raised over a large spatial and temporal scale? The strong effect of nitrogenous-fertilization in small-scale experiments appears primarily due to the preference of ovipositing females for a well-fertilized crop, relative to other rice crops and perhaps also to surrounding grassy vegetation. Increasing nitrogenous-fertilization over a large spatial scale would diminish this form of 'associated susceptibility', and probably have a far less pronounced effect on leaffolder infestation levels. The relationship between spatial scale of enhanced fertilization and egg deposition rate could be quantified with knowledge of the dispersal range of ovipositing leaffolder moths (cf. Kareiva, 1982).

The importance of other effects of nitrogenous-fertilization on rice leaffolder performance (table 1) appeared to be small in the present one-season study. However, on a larger scale their combined effect may result in higher intrinsic rates of increase of rice leaffolders. Leaffolders will then become more abundant when their mortality factors, such as natural enemies, are not proportionally and positively density-dependent. An increased potential for population growth also implies that leaffolder outbreaks may occur more frequently (McNeill and Southwood, 1978), especially when natural enemies suffer relatively more from the use of broad-spectrum insecticides or from adverse weather conditions (e.g. Rajapakse and Kulasekare, 1982; Patel *et al.*, 1987; Qadeer, 1988). In this way, the widespread adoption of chemical nitrogenous fertilizers has probably contributed to the reported increase in leaffolder abundance and outbreak frequency since the mid-1960s (Khan *et al.*, 1988). In unsprayed fields, however, current levels of nitrogenous-fertilization do generally not result in leaffolder population levels causing economic damage (de Kraker, 1996). Way and Heong (1994) postulate that even in intensified irrigated rice systems, natural controls are adequate for most insect pests, if not upset by insecticide use. The question is whether natural control would still be sufficient with a further major increase in nitrogenous-fertilization level. In the present study, the abrupt nitrogen-induced rise in leaffolder egg recruitment was not compensated by a response of the natural enemies, as in the case of brown planthopper (Kenmore, 1991). Natural enemies might respond better to the more gradual and general increase in leaffolder density resulting from a large-scale increase in nitrogenous-fertilization, but ecological theory does not permit a simple prediction regarding this matter (Crawley, 1992). Interactions among three trophic levels are highly complex, and can work in opposite directions (Price *et al.*, 1980).

5. Concluding remarks

The present experiment confirms the finding of previous research that in a choice situation leaffolder infestations increase with the level of nitrogenous-fertilization. In our study, the increase in infestation was primarily a result of higher egg recruitment, probably due to ovipositional preference. As the increase in natural enemy abundance was less than the increase in leaffolder egg and larval density, natural enemy to leaffolder ratios decreased with nitrogen level, while larval survival increased. At a single field scale, the effect of relatively high nitrogen levels on leaffolder infestations may be reduced by adapting the timing and method of nitrogen application. An increase in the spatial scale over which high levels of nitrogen are applied will probably also reduce the leaffolder density response, which appears mainly based on preference. Both aspects indicate options to optimize nitrogenous-fertilization in an integrated approach to crop management, at individual as well as community levels of decision making.

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