The potential of natural enemies to suppress rice leaffolder populations

Promotoren: dr. J.C. van Lenteren
hoogleraar in de entomologie

dr. ir. R. Rabbinge
hoogleraar in de theoretische produktie-ecologie

Co-promotor: dr. ir. A. van Huis
universitair hoofddocent tropische entomologie

Joop de Kraker

The potential of natural enemies to suppress rice leaffolder populations

Proefschrift
ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van de Landbouwuniversiteit Wageningen,
dr. C.M. Karssen,
in het openbaar te verdedigen
op vrijdag 15 november 1996
des namiddags te half twee in de Aula.

This thesis contains the results of a collaborative research project of the Wageningen Agricultural University, Departments of Entomology and Theoretical Production Ecology, and the International Rice Research Institute in the Philippines. The project was financed by the Netherlands Ministry of International Co-operation (DGIS, Project WW/89/969), and supported by the Foundation for Biological Research (BION, now SLW, Project 436.991), which is subsidized by the Netherlands Organization for Scientific Research (NWO).

NWO

Kraker, Joop de

The potential of natural enemies to suppress rice leaffolder populations /
Joop de Kraker. - [S.1.:s.n.] -
Thesis Landbouwuniversiteit Wageningen. - With. ref. - With summary in Dutch.

ISBN 90-5485-601-7
Subject headings: rice pests / biological control / predation / crickets

The cover shows stylized drawings of a rice leaffolder moth and major natural enemies, against a background inspired by the typical whitish-striped leaffolder injury pattern.

Stellingen

1. Bladrollers en krekels zijn berekenbare beestjes.
   Dit proefschrift

2. Bij het vaststellen van de identiteit van predatoren en hun afzonderlijke aandeel in plaagmortaliteit, heeft, net als in de misdaadbestrijding, 'het op heterdaad betrappen' van de daders door middel van direkte observatie de meeste bewijskracht.
   Dit proefschrift

3. Produktiviteitsverhoging door stikstofbemesting en biologische beheersing van plagen *kunnen* in de rijstbouw goed samengaan.
   Dit proefschrift

4. Spraying for leaffolder ? That's not cricket !
   Dit proefschrift
   Bandong, J.P. & J.A. Litsinger, 1986. Int. Rice Research Newsl. 11(3):21.

5. Omdat bovenbazen nog steeds niet van 'bruine sluipers' houden, is de strijd voor een duurzame gewasbescherming meer gebaat bij een ragfijn politiek spel dan bij nijvere wetenschappelijke arbeid.
   Toonder, M.A., 1963. De Bovenbazen.

6. De geringe variabiliteit van tropische ecosystemen is bedrieglijk. Juist hierdoor zijn ze kwetsbaarder dan gematigde ecosystemen voor de verstoringen die het bedrijven van landbouw met zich mee brengt.
   Waage, J.K., 1991. In: D.L. Hawksworth (Ed.) The biodiversity of microorganisms and invertebrates: Its role in sustainable agriculture. CAB International.

7. De zeer optimistische voorpellingen (in bijvoorbeeld Gallagher 1992) over de 'zelfvermenigvuldiging' van IPM training door kennisverspreiding van boer tot boer berusten op een te naïef beeld van de sociale werkelijkheid.
   Gallagher, K.D., 1992. In: A.A.S.A. Kadir & H.S. Barlow (Eds.) Pest management and the environment in 2000.
   van de Fliert, E., 1993. Wageningen Agricultural University papers 93-3.

8. De eco-centrische stelling dat 'de aarde beter af zou zijn zonder de mens' is absurd, omdat met de afwezigheid van die laatste ook de inhoud van het begrip 'beter' verdwenen zal zijn.

9. Voortdurende twijfel als leidend principe in de wetenschap geldt met name andermans werk.

10. Naar het voorbeeld van Z.O. Azië zou ook in het Nederlandse beleid het vergroten van de ecologische geletterdheid in boerengroepen de voorkeur moeten genieten boven het persen van boeren in een keurslijf van eco-produktieregels.
    Reus, J.A.W.A., 1995. European Journal of Plant Pathology, Abstracts XIII International Plant Protection Congress, The Hague, the Netherlands, 2-7 July 1995.

11. Het 'missionaire' karakter van ontwikkelingssamenwerking maakt werkelijk 'vraaggestuurde' hulp onmogelijk.

12. Eenvoudigweg ontkennen dat Nederland vol is, verhult dat medemenselijkheid een prijs kent.

13. Het feit dat de Filippijnen slechts door rampen het nieuws halen doet velen ten onrechte veronderstellen dat een langdurig verblijf in dat land een daad van zelfopoffering is.

Stellingen, behorend bij het proefschrift
The potential of natural enemies to suppress rice leaffolder populations

Joop de Kraker
Wageningen, 15 november 1996

ABSTRACT

Rice leaffolders *Cnaphalocrocis medinalis* and *Marasmia* spp. (Lepidoptera: Pyralidae) are considered major pests in many Asian countries. Insecticide use against leaffolders is wide-spread, but may not be justified due to tolerance of the rice crop to leaffolder injury and a high level of natural biological control. This study was conducted to obtain more insight in the potential of indigenous natural enemies to suppress rice leaffolder populations and reduce the damage inflicted to the crop. The study started with a descriptive analysis of leaffolder population dynamics in Philippine rice fields, and then concentrated on experimental analysis of egg mortality and the impact of individual predator species. Models were used to integrate the experimental findings, to explain field observations, and to explore the consequences of varying biotic and abiotic conditions for leaffolder population dynamics and damage.

Rice leaffolder populations in eight unsprayed rice crops were characterized by an egg peak at maximum tillering and a broad larval peak around the booting stage, with peak larval densities ranging from 0.2 to 2.0 per hill. Variation in survival from egg to larval stages between crops was not correlated with the level of egg parasitism, natural enemy abundance, or predator-prey ratios. High levels of N-fertilization resulted in a strong increase in leaffolder larval density and injury, due to a positive effect on egg recruitment and survival of medium-sized larvae. The increase in larval survival was associated with lower predator-prey ratios. Egg mortality in the field averaged about 60%, and was mainly due to disappearance of eggs and to a lesser extent to parasitism by *Trichogramma* spp. Non-hatching was of minor importance. The level of egg disappearance was positively correlated with the densities of the predatory crickets *Metioche vittaticollis* and *Anaxipha longipennis*. Direct observations confirmed the major role of these crickets: in two crop seasons they were responsible for more than 90% of the observed egg predation. Minor predators were *Micraspis* sp., *Ophionea nigrofasciata*, and *Conocephalus longipennis*. The egg predation rate of the crickets in cages was described adequately with a linear functional response model, indicating that predation was limited only by the search rate. Increasing the predator density per cage led to a decrease in the egg predation rate per capita. Field testing of a model of predation of leaffolder eggs based on cage experiments showed that the observed trend in egg predation could be described as a function of cricket densities and crop leaf area. The evaluation also indicated that predator interference may limit the egg predation rate of the crickets, while the presence of alternative prey did not. A simulation study with a combined model of leaffolder population dynamics and rice crop growth highlighted the importance of natural enemies as well as crop growing conditions. The simulations indicated that larval densities as observed in the unsprayed fields would not cause significant yield loss in a well-fertilized crop. Yield losses simulated with an average leaffolder immigration pattern exceeded economic damage levels when no natural enemy action was included, while introduction of three field-observed natural mortality factors (egg predation, egg and larval parasitism) reduced losses to below these levels. Over their observed range in seasonal abundance, the predatory crickets could reduce leaffolder damage by 5 to 60% (average: 35%).

The identification of the major egg predators and quantification of their impact can serve as a starting point for research on strategies to conserve natural enemies of rice leaffolders, and as inputs to IPM training programs to stimulate farmers to reduce insecticide sprays against rice leaffolder. The study also indicated the importance of optimization of nitrogen fertilization to avoid reliance on chemical control, by maximizing the positive effects on yield formation and tolerance to injury, while minimizing the leaffolder density response. For this purpose, a combined leaffolder-rice simulation model is a useful, integrative tool, to study how interaction between these mechanisms affects rice yield.

Key words: *Cnaphalocrocis medinalis*, *Marasmia* spp., *Metioche vittaticollis*, *Anaxipha longipennis*, Philippines, rice, natural enemies, egg predation, population dynamics, simulation model, damage, fertilizer

Voorwoord Foreword

Zo'n 7 jaar geleden, op het vliegveld van Johannesburg, wachtte een tante me op met een telegram uit Nederland. In luttele woorden werd daarin m'n belangstelling gepeild voor een promotie-onderzoek aan de rijstbladroller in de Filippijnen. Dat ik die had, daarvan spreekt dit proefschrift inmiddels boekdelen. Zes jaar lang hebben de rijstbladroller en z'n vijanden me in hun greep gehouden, ruim drie jaar van intensief onderzoek in Zuidoost-Azië, gevolgd door nog eens bijna drie jaar van meer en minder ingespannen schrijfwerk in Wageningen. Een berg werk, maar gelukkig hoefde ik die niet in m'n eentje te verzetten.

De basis voor het projekt werd gelegd door Henk van den Berg tijdens een stage op het IRRI, maar toen het projektvoorstel uiteindelijk werd goedgekeurd had Henk allang een andere baan. Indirekt heeft hij toch nog invloed gehad op het onderzoek: als docent in een voor mij grondleggende cursus over biologische bestrijding in rijst op het IRRI, en als auteur van inspirerend onderzoek naar de rol van natuurlijke vijanden in Kenya en Sumatra.

De Wageningse begeleiding op het promotie-trajekt was maar liefst drie man sterk. De promotoren Joop van Lenteren en Rudy Rabbinge, en co-promotor Arnold van Huis bedank ik bij deze hartelijk voor het in mij gestelde vertrouwen en de tijd die ze voor mij hebben uitgetrokken. Arnold was als projektleider het meest direkt betrokken bij de voortgang van het onderzoek en zorgde er samen met Ineke Buunk voor dat aan de Nederlandse kant van de aardbol alles op rolletjes liep. Zowel Arnold als Joop hebben mij opgezocht in de Filippijnen en tijdens die bezoeken stimulerende feed-back gegeven. De kontakten met Rudy werden aanzienlijk frequenter na m'n verhuizing naar de vakgroep Theoretische Produktie-ecologie (TPE). Rudy, het is me een raadsel hoe je met zo'n overvolle agenda ook nog es mijn tijdschema in de gaten kon houden.
Een groot deel van de begeleiding bestond uit het kritisch doorlezen van de delen van het proefschrift. Arnold, je las de stukken nauwgezet en hebt daarbij tientallen overtollige woorden weggestreept. Je commentaar resulteerde altijd in een verbeterde presentatie en leesbaarheid. Joop, je gaf me alle ruimte voor eigen initiatief, inzicht en schrijfstijl. Je positieve benadering heeft me goed gedaan. Rudy, het was duidelijk dat je eerste, vaak kritische commentaren niet altijd even enthousiast door mij werden ontvangen. Je plaatste vraagtekens bij gedachtengangen die voor mij vanzelf spraken. Maar, doordat ik gedwongen werd de stukken weer grondig na te gaan, heeft dat toch vaak een grotere helderheid gebracht. Hoe verschillend ook in stijl van lezen, alle drie zijn jullie kampioenen van duidelijkheid. Alle slagen om de arm, hele en halve toespelingen, bedekte termen, vage suggesties, verontschuldigingen en omhaal van woorden die nu nog in de tekst te vinden zijn komen dus geheel voor mijn rekening.

At the International Rice Research Institute, I was based in the Entomology Division where the project was supervised by K.L. Heong. K.L., thanks for the freedom to pursue my research goals and for your help in establishing useful contacts. I found your 'farmer practice' perspective on the leaffolder problem quite inspiring and discussions with you have considerably broadened my insight into the socio-political aspects of rice IPM. Jim Litsinger, with his particular sense of humour and almost life-long experience in IPM, further enhanced my understanding of rice pest management. During most of my stay at IRRI Dale Bottrell was head of the Entomology Division. Dale, thanks for your interest in my research and your willingness to give support when needed.

By far the most important persons that have contributed to the success of the project were the ones assisting me in the actual work: Elpidio Hernandez, Florencio de Leon, Domingo Almario and Imelda Salon. Elpie, Boyet and Domeng, thanks for the many, many hours of concentrated work in field and lab. Your frank suggestions often helped to improve the quality and efficiency of the experiments. Meldz, apart from helping me out in data management, you were also good company in the office and an invaluable source of information on Philippine culture and folklore. It should be mentioned here also that the project did not only bear fruit in terms of research results. Indirectly it also 'made our tribe increase': three of us became first-time parents during the last year of the project !
Many other people in the Entomology Division provided help as well, some should be mentioned explicit: Ellen Genil gave secretarial support; Dong Arida helped me to get started with the field work and has often given useful advice; Bert Barrion's knowledge of the rice arthropod fauna is legendary and I was happy to profit from it; Mary Austria and her student assistants retrieved lots of references for me; Elsa Rubia shared her extensive knowledge on working with rice natural enemies; and finally, Tim Chancellor was always willing to lend me his equipment.
Many of the experiments were conducted outside IRRI in rice fields near Pila, owned by the Peñaranda family. I thank Mrs. Felisa and her sons for allowing me to use their land and for their kind hospitality.

Mijn onderzoeksprojekt was eigenlijk een klein zusje van het grote SARP (Simulation and Systems Analysis for Rice Production) projekt. Dankzij de steun van SARP projektleider Frits Penning de Vries en zijn opvolger Martin Kropff werd het leaffolder projekt stevig op IRRI-bodem verankerd. Met het werk en de inzichten van de 'pest & disease' coordinatoren Pieter de Jong, Lammert Bastiaans en Anne Elings heb ik m'n voordeel kunnen doen bij het modelleren van bladrollerschade. Mede-jonge-hond Prem Bindraban was goed voor vele kritische discussies over modelleren en nog veel meer, en SARP-sympathisant Marco van den Berg maakte het mogelijk dat ik op het IRRI van begin tot eind over goede computerfaciliteiten heb kunnen beschikken.

De titel van mijn projekt preciseerde de onderzoekslokatie als 'South and Southeast Asia', wat toch aanzienlijk meer omvat dan enkel de Filippijnen. Via stage-plekken voor Wageningse studenten op nationale onderzoeksinstituten in andere landen is geprobeerd het onderzoek toch de gewenste regionale breedte te geven. Cas de Roos in Thailand, en Muriel Klein Beekman en Angelique Lamour in Maleisië hebben onder niet zelden lastige omstandigheden veel veldwerk verzet. Hoewel hun proefresultaten uiteindelijk niet zijn opgenomen in dit proefschrift, heeft hun onderzoek wel geleid tot een beter en breder beeld van de ecologie van rijstbladrollers, iets waar ik vooral in de algemene discussie m'n voordeel mee heb kunnen doen.
Ook blikverruimend waren de plezierige kontakten met Koen den Braber, Marjon Fredrix en Jan Willem Ketelaar van het 'FAO Intercountry Programme in rice IPM'. Dankzij hen heb ik goed zicht kunnen krijgen op de huidige aanpak van IPM training en de mogelijke bijdrage van mijn onderzoek daaraan.

The field experiments conducted in Thailand and Malaysia were made possible and supervised by colleagues from national research institutes. Dr Somkid Disthaporn and Mr Raywat Pattrasudhi of the Thai Department of Agricultural Research, and Mr Chang Poon Min and Haji Muhamad bin Harun of the Malaysian Agricultural Research and Development Institute are gratefully acknowledged for their hospitality and pleasant collaboration.

Usually, reading the literature is the part of the work you can manage on your own. It's different, however, in case of rice leaffolder as a major part of past and current research is published in Chinese and Japanese. Yet, with the much appreciated help of Dr Guo Yu-jie, Dr Zhang Run-jie, Dr Yin Shin-you and Mr M. Nakai, I did have access to this rich source of leaffolder knowledge. Dr T. Wada provided me with a welcome translation of his thesis, in addition to his many excellent publications in English.

Terug in Nederland heb ik het eerste jaar voornamelijk thuis gewerkt. De vakgroep Entomologie werd bij voorkeur op hoogtijdagen, zoals uitstapjes, bezocht. Het bleek er overigens vol met aardige collega-promovendi te zitten, die de twee-wekelijkse PE-promovendi bijeenkomsten tot een leuke en nuttige bezigheid maakten.

Begin 1995 belandde ik op TPE als medewerker van het Nectar-projekt, onder de goede hoede van Kees Eveleens. Het bleek ook een prima omgeving te zijn om naast het werk het proefschrift af te ronden. Walter Rossing en Wopke van der Werf hebben delen van het proefschrift becommentariëerd en waren stimulerende discussie-partners. Gon van Laar weet altijd raad en daad, en Rob Dierkx hield de computer draaiend. Bij de ASK-bovenburen voorzag Daniel van Kraalingen me van de nieuwste simulatie software en liet Jaques Withagen zijn licht schijnen op statistische vraagstukken.

Both in IRRI-Entomology and at TPE I had to change office several times, allowing me to experience (and usually to enjoy) a wide variety in office mates. To mention the most 'persistent': manong Fil and manang Hermie at IRRI, and Holger Meinke, Doug Landis, Daniel Rodriguez and Paula Westerman at TPE, they were all good company. Maria Santos deserves special mentioning for her stable supply of cookies and the latest gossip from Los Baños. Outside the four walls of my office there were many more nice people to meet, both in IRRI-Entomology and at TPE, who made me feel at home at work. In particular I remember the friendship with Yoohan Song and Ken Schoenly.

Al doet het bovenstaande wellicht anders vermoeden, het werk heeft de laatste jaren niet het grootste deel van m'n leven gevuld. Dat is vooral te danken aan Baukje, Jelske en Marja. Baukje, tegelijkertijd heb je erg veel bijgedragen aan het tot stand komen van dit proefschrift, door indirekte steun, maar ook heel concreet door data- en tekstverwerking. Heit en mem wil ik bedanken voor hun bereidheid om de kinderen op te vangen, zowel om vakantie als om extra hard werken mogelijk te maken. Tenslotte bedank ik alle familie, vrienden en kennissen die ons met zoveel plezier in de Filippijnen en Nederland (hebben) doen wonen, en ook vaak meegeleefd hebben met het wel en wee van dit proefschrift. Johan Melse en Matthias Halwart zijn de record-houders in het aantal overnachtingen onder ons dak, en tijdens de promotie hoop ik ze weer aan mijn zijde te vinden.

Zes jaar bezig zijn met een onderwerp lijkt mogelijk wat veel, maar hoewel ik in de Filippijnen letterlijk allergisch voor rijst ben geworden, zijn er zoveel boeiende ontwikkelingen in rijst IPM dat ik er nog lang niet op uitgekeken ben. Bovendien, geen kleur ter wereld sprankelender en meer inspirerend dan van een jong rijst gewas !

Contents

General Introduction

Rice is the world's most important food crop second to wheat, feeding over 2 billion people in Asia alone. On this continent about 90% of the world's rice is grown, with more than 75% (360 million t of rough rice) being produced under irrigated conditions (IRRI 1993a). The rice crop not only provides food for people, it is also a host to over 800 species of insect herbivores. However, of this multitude less than 20 species are considered important pests in tropical Asia (Dale 1994). In irrigated rice cultivation in Asia the three major groups of insect pests are the lepidopterous stemborers, the homopterous leaf- and planthoppers, and a complex of leaf feeding insects. Of the latter group, rice leaffolders are the main species (Reissig et al. 1986, Dale 1994). In this introductory chapter, current knowledge on the biology, pest status and control of rice leaffolders is summarized to provide background information to the research described in this thesis. Subsequently, the research problem and objectives are defined and an outline of the thesis is presented.

1. Biology of Rice Leaffolders

1.1 Distribution and host range

In Asia a complex of leaffolder species occurs in rice, of which three are of major importance: *Cnaphalocrocis medinalis* (Guenée), *Marasmia patnalis* Bradley and *M. exigua* (Butler). All three are lepidopterous species belonging to the Pyralidae family (Khan et al. 1988). As the species are morphologically related and overlap in geographic distribution and host plant range, taxonomic confusion is widespread in the older literature. Only fairly recent, in 1981, *M. patnalis* was discovered and described as a separate species (Bradley 1981). Before, it had been confused most often with *C. medinalis*, the principal leaffolder species in most areas in Asia (Khan et al. 1988). *C. medinalis* occurs throughout Asia from Pakistan to Japan, in Madagascar, in Australia and on the Pacific islands. *M. patnalis* is only reported from tropical parts of Asia, viz. the Philippines, Indonesia, Malaysia, India and Sri Lanka. This apparently limited distribution may just reflect its recent discovery. *M. exigua*, formerly known as *Susumia exigua*, is distributed throughout East, South-east and South Asia, and is the principal species on the Pacific islands. *C. medinalis* cannot overwinter in Korea, Japan, and the temperate areas of mainland China. Every year, the moth migrates over long distances to these areas from tropical regions (Chang et al. 1980, Hirao 1982, Miyahara 1981). For the other species such long distance dispersal is not known.

In tropical regions, rice leaffolders occur in all rice environments: in wet lowlands, as well as in dry uplands and in deepwater rice (Reissig et al. 1986, IRRI 1993b). They are present in rice throughout the year in areas with continuous irrigated rice cultivation (Barrion et al. 1991a, Velusamy & Subramaniam 1974). In areas with a rice fallow, leaffolders do not hibernate but are found feeding on other graminaceous crops, such as wheat and sorghum, during the off-season (Vyas et al. 1981, Bharati et al. 1990). Besides on these cultivated crops, *C. medinalis* can survive on more than 80 other plant species, mostly wild grasses (Khan et al. 1988). Both *Marasmia* species are more restricted in their host range (Abenes & Khan 1990, Barrion et al. 1991a).

Co-existence of the three leaffolder species in rice environments might be possible due to differential performance on non-rice hosts serving as a refuge (cf. Barrion et al. 1991a). They may also have specialized on different stages of the rice crop, as *C. medinalis* is often the first species to colonize a rice field, while *M. patnalis* dominates during the later crop stages (Barrion et al. 1991a). However, a comparison of the leaffolder species with regards to host-plant suitability at various ages has not been conducted. Natural enemies may play a role in creating different temporal niches on the shared host plant, but thus far there is no evidence that natural enemies prefer one leaffolder species above another.

1.2 Life cycle and bionomics

The life cycle of the three leaffolder species is very similar and differs only in bionomic details (Barrion et al. 1991a). The eggs are laid singly or in small rows parallel to the veins on either side of the leaves. After hatching, the first instar larvae crawls to the folded base of the youngest leaf or stays behind leaf sheaths (Ramachandran & Khan 1991a). Active folding of leaves, by stitching the edges together, starts from the late second instar onwards. The number of larval instars is usually 5 or 6, and occasionally 7. The proportion of larvae passing through more than five instars depends on temperature and host plant quality (Wada 1979, Chu et al. 1983, Cheng et al. 1987). After a pre-pupal period, the larvae pupate in a silk webbing, either inside a leaffold closed on both sides, or behind a leaf sheath (Vyas et al. 1980). The moths emerge in the evening, and mating and egg laying occurs at night (Lingappa 1972). During the day the moths stay in the rice canopy or on grassy weeds and only take short flights when disturbed (Velusamy & Subramaniam 1974).

C. medinalis eggs measure about 1.0 × 0.5 mm, the eggs of both *Marasmia* species are somewhat smaller. Full grown rice leaffolder larvae are about 2 cm long, while the moths have a wing span of c. 1.5 cm (Barrion et al. 1991a). Temperature and host plant species and condition are, in the absence of natural enemies, the major determinants of leaffolder survival and development (Rajamma & Das 1969, Yadava et al. 1972, Wada & Kobayashi 1980, Chu et al. 1983, Wu & Zhang 1984, Cheng 1987, Dan & Chen 1990). Under Philippine tropical lowland conditions, the developmental periods range from 3-5 days for the eggs, 15-25 days for the larval stage including the pre-pupal period, and 6-10 days for the pupae. The total period from egg to moth emergence thus takes 4-5 weeks (Joshi et al. 1985, Barrion et al. 1991a). The longevity of adult females is about one week, but varies greatly depending on humidity and the supply of a sugar-source (e.g. nectar or honeydew, Waldbauer et al. 1980). Egg laying starts 1-4 days after mating. During the oviposition period, the moths lay about 20-40 eggs per day, with maximum values of over 300 eggs during their entire life-span (Hirao 1982, Barrion et al. 1991a, Waldbauer et al. 1980).

1.3 Injury and damage

Prior to feeding, the larvae fold the leaves longitudinally by fastening the leaf margins with stitches of thread-like silk. Contraction of the silk strands results in a tubular structure open at both ends: the leaf roll or leaffold. Sometimes a feeding chamber is created by stitching two or three adjacent leaves together (Fraenkel & Fallil 1981). The larvae feed inside the folds by scraping off the green mesophyll tissue between the veins (Fraenkel et al. 1981). This results in leaves with linear, pale white striped injury symptoms, while heavily injured leaves may dry up completely (Velusamy & Subramaniam 1974). Generally, only one larva is found per fold and after feeding within a fold for several days, the larva moves to another leaf. In this way, a larva makes three to five leaffolds during its development (Barrion et al. 1991a, Hirao 1982, Cheng 1987).

Leaffolder larvae affect the growth of the rice crop in various ways. Consumption of mesophyll reduces the photosynthetically active area of the crop, while folding of leaves reduces light interception. Moreover, the rate of photosynthesis in the remaining green tissue in leaffolds may be reduced as well (de Jong 1992). The injured leaves might also serve as entry points for pathogens, but as yet there is no evidence of a correlation between the occurrence of leaffolders and foliar diseases. The effect of leaffolder injury on crop photosynthesis can result in yield loss, usually by a reduction of the number or percentage of filled grains (Hirao 1982, Bautista et al. 1984, Miyashita 1985, Murugesan & Chelliah 1983a,b). Heavy leaffolder infestation during the early vegetative stage can result in stunting and uneven ripening of the crop (Chang 1991).

Many empirical studies in various countries have been conducted to establish the relationship between leaffolder larval density or injury level and yield loss (see Chapter 8). The results of these studies depend on the specific experimental conditions and do not provide insight into the mechanisms that underlie the observed yield losses. Extrapolation of these descriptive damage relations to other situations is therefore inappropriate. Recently, dynamic simulation models of leaffolder damage have been developed to overcome these limitations (Graf et al. 1992, de Jong & Daamen 1992). These models calculate yield loss on the basis of the effect of leaffolders on crop growth processes. The general pattern emerging from the empirical and modelling studies is that the rice crop is most sensitive to leaffolder injury during the reproductive stage, i.e. between booting and grain filling. The crop is least sensitive during the vegetative, tillering stage, and is also less sensitive during the ripening period. The magnitude of yield loss as a function of injury depends strongly on the growing conditions of the crop (de Jong & Daamen 1992).

2. Pest status and control of Rice Leaffolders

2.1 Shift in pest status

Since the mid-1960s rice leaffolders have increased in abundance, and in many Asian countries they are now considered as important pests (Litsinger 1979, Reissig et al. 1986, Khan et al. 1988). The shift from minor to major pest has been attributed to the adoption of new rice growing practices that accompanied the introduction of high yielding varieties (Kulshreshta et al. 1970, Miyahara 1981, Dhaliwal et al. 1985, Litsinger 1989, Zhang 1991).

This 'Green Revolution rice technology' included increased cropping intensity (two to three crops per year), irrigation and a high input of nitrogenous fertilizers and pesticides (Loevinsohn et al. 1988). More recently, the change from transplanting to direct seeding appears to have increased leaffolder problems in some areas (Hirao & Ho 1987, Waibel & Meenakanit 1988, Chang 1991). In particular the effects of variety and N-fertilizer on rice leaffolder infestation have been the topic of numerous studies (e.g. Dhaliwal et al. 1979, Rajendran 1985, Saroja et al. 1987). The adoption of modern varieties *per se* does not seem to be the cause of increased leaffolder abundance. In general, they are not more favourable for leaffolder population development than traditional cultivars (Heinrichs et al. 1985, 1986). A large number of field trials, however, show that increased N-fertilization usually leads to higher leaffolder injury levels (see Chapter 2). Other crop management practices promoting leaffolder infestation in a rice field are high plant density and early or late planting (Saroja & Raju 1982, Thangamuthy et al. 1982, Suharto & Noch 1987, Dhaliwal et al. 1988, Chiranjeevi & Rao 1991).

Large-scale outbreaks of rice leaffolder have been reported from almost any rice-growing country in Asia from the 1960s onwards, most frequently from India (Khan et al. 1988). These outbreaks have been attributed to a reduced abundance of natural enemies, either as a consequence of extreme weather conditions such as severe drought (Mochida et al. 1987, Patel et al. 1987, Chatterjee 1987, Qadeer et al. 1988), or the indiscriminate use of broad-spectrum insecticides (Rajapakse & Kulasekare 1982, Litsinger 1989). However, evidence for this explanation is lacking.

2.2 Control measures

Farmers in South and South-east Asia predominantly use synthetic pesticides to control rice leaffolders (Uthamasamy 1985, Heong et al. 1994). To prevent unwarranted application of insecticides against rice leaffolders, past research has placed great emphasis on the establishment of economic injury levels and action thresholds for making spray decisions. For rice leaffolders such thresholds have been based either on injured leaves or on larval density. For example, in India thresholds of 1 to 2 injured leaves per hill have been recommended (Kalode 1985, Krishnaiah 1986), while in the Philippines recommended thresholds were 15%

damaged leaves or 1 larva per hill during the vegetative stage, and 5% injured leaves or 0.5 larva per hill during the reproductive and ripening stage (Bautista et al. 1984, Reissig et al. 1986, Bandong & Litsinger 1988). Similar threshold densities for larvae were recommended in China (Anonymous 1993). When field testing a range of action thresholds, Barrion et al. (1991) noted that spraying based on a threshold of injured leaves often produced no benefit, because the leaffolder population had pupated already when the threshold was reached. In addition to action thresholds, sampling methods to monitor leaffolder populations have been developed, based on the observed spatial distribution pattern within rice fields (Wada & Kobayashi 1985, Wu & Zhang 1985, Shepard et al. 1988, Heuel-Rolf & Vungsilabutr 1988). There are no published accounts on farmer adoption of these recommended thresholds and sampling procedures for leaffolders.

Control tactics other than broad-spectrum insecticides include microbial insecticides and inundative release of egg parasitoids. These agents have the advantage that they are harmless to naturally-occurring predators and parasitoids. Field trials showed promising results with commercial and local formulations of *Bacillus thuringiensis* against rice leaffolders (Peng et al. 1984, Barrion et al. 1991a, Tryon & Litsinger 1988). Other entomopathogens, such as *Beauveria bassiana* and *Nomuraea rileyi* have only been tested in the laboratory (Aguda & Rombach 1987). Mass-rearing and mass release of natural enemies to control rice leaffolders was successfully practised in China with *Trichogramma* egg parasitoids (Li 1982, Pu et al. 1988), while in India field evaluation of inundative releases of *T. japonicum* against *C. medinalis* is on-going (Bentur et al. 1994). However, according to Reissig et al. (1986) this practice is currently not economically feasible on a large scale throughout Asia.

Preventive, cultural control measures concern nitrogen fertilization and removal of alternative host plants (Uthamasamy 1985, Reissig et al. 1986, Litsinger 1994). To avoid rice leaffolder problems, farmers are recommended to reduce the amount of N-fertilizer and to apply it in splits at various growth stages. Removal of grassy weeds from rice fields and borders might also limit leaffolder infestations.

Growing a resistant variety is currently not an option to control rice leaffolders. All the IR and other popular high yielding rice varieties are susceptible, and resistant varieties are not commercially available (Reissig et al. 1986). Over 15,000 accessions of cultivated rice

(*Oryza sativa*) have been screened for resistance to *C. medinalis* at the International Rice Research Institute and in several national research centres, but sources of resistance were scarce and only moderate levels of resistance were found. High resistance levels were only identified in wild rice species (Heinrichs et al. 1985, Khan & Joshi 1990). Transfer of leaffolder resistance from wild rices to obtain highly resistant cultivated rice has not yet been attempted, and will be difficult because a multiplicity of resistance factors appears involved (Ramachandran & Khan 1991b). Moderate levels of varietal resistance to leaffolders have not received much attention, but may be very useful to enhance the ability of natural enemies to keep leaffolders below economic damage levels.

2.3 Natural biological control

The importance of natural biological control of rice pests (or short 'natural control'), the control exerted by naturally-occurring populations of predators, parasitoids and entomopathogens, has been largely neglected in rice pest management research until the late 1970s (Shepard 1989). Nowadays, the notion that most rice herbivores only rarely cause economic damage due to natural control is central in training and extension programs of integrated pest management (IPM) throughout Asia. Conservation of natural enemies is the primary control strategy advocated and applied in these programs (Gallagher 1992, Matteson et al. 1994).

2.3.1 Diversity of natural enemies

Rice leaffolders have a large and diverse complex of natural enemies, which includes more than 200 different species of parasitoids, predators and pathogens, recorded from all over Asia and the Pacific (Khan et al. 1988). Most of the records in the literature are associated with *C. medinalis* (Khan et al. 1988, Barrion et al. 1991a). Even at a smaller geographic scale the diversity is still large: in Philippine rice fields, where the arthropod foodweb has been studied intensively, about 80 predator species and over 50 parasitoids of rice leaffolders were identified (Barrion et al. 1991a). Most predator species are Coleoptera, notably Coccinellidae, Carabidae and Staphylinidae preying on larvae and pupae, and spiders preying on adults. In the Philippines, the rice leaffolder complex is host to 14 families of parasitoids.

All recorded egg parasitoids belong to the Trichogrammatidae family. Braconid and ichneumonid wasps are the dominant larval parasitoids. The composition of the leaffolder natural enemy complex differs between upland, rainfed lowland and irrigated lowland rice environments (Litsinger et al. 1987a). These differences are larger for the predator than for the parasitoid complex. The aquatic damselflies and dragonflies, and the sucking predatory bug *Cyrtorhinus lividipennis* are most common in flooded rice, while ground-dwelling predators, such as most ant and ground beetle species, can be important predators in dryland rice (Barrion & Litsinger 1980, Barrion & Litsinger 1985a, Litsinger et al. 1987a). The leaffolder predator species or genera that are most common in the Philippines occur throughout (sub-)tropical Asia (Ahmed et al. 1989, Bhardwaj & Pawar 1987; Kamal et al. 1987, Krishnasamy et al. 1984, Pang et al. 1984, Tan 1981, Upadhyay & Diwakar 1983, Yasumatsu et al. 1975, 1981). The species composition of the parasitoid complexes tends to be more location-specific.

2.3.2 Impact of natural enemies

The mortality inflicted by this diverse complex of natural enemies on rice leaffolders has been the topic of numerous studies. These can be divided in three categories: (1) field-based life table studies, (2) surveys of parasitism, and (3) inclusion studies with specific natural enemies.

Life table studies Many life table studies of *C. medinalis* were conducted in (sub-)tropical China (Gu et al. 1983, Pu et al. 1988, Zhang et al. 1988, Liang et al. 1993, You et al. 1993, Zhang et al. 1993). In a number of provinces and over a range of years the survival of leaffolders from egg to adult was studied, either by sampling of leaffolder populations, or by field exposure and recovery of cohorts of each stage. Mortality per stage was partitioned into disappearance and parasitism. In a few studies predation and pathogen infection were also recorded. Between locations and generations the long term averages of survival from egg to adult varied from 0.5 to 10%, while the overall average was below 5%. In South-China (Guangdong Province) survival was highest for the first generation after the rice fallow, and lower for subsequent generations (Gu et al. 1983, Liang et al. 1993). The factors causing the highest average mortality, as well as the factors correlating best with total generational mortality (key-factors) varied per location, but commonly concerned disappearance of pre-adult stages. This indicates that predators may play an important role in natural control of rice leaffolders. In South-Japan, life tables were based on stage-frequency analysis of sampling data and assessment of parasitism of the collected leaffolders (Wada 1989). The average survival from egg to adult was more than 15%, which is at least three times higher than found in South-China. Wada & Kobayashi (1991) attributed this high survival to the paucity of natural enemies in Japanese rice fields. In the Philippines, egg and larval mortality was studied with field exposure and recovery techniques (Kamal 1981, Arida & Shepard 1990). After two days exposure, egg disappearance averaged 50%, while 30% of the remaining eggs were parasitized (Arida & Shepard 1990). Larval disappearance was 75% in cages open to predators, compared with 35% in closed cages (Kamal 1981). Based on a census study of a series of leaffolder populations, Kamal (1981) estimated that survival from egg to pupa was less than 4%. All these studies indicate that natural enemies play an important role in suppressing rice leaffolder populations, in particular in tropical areas like South-China and the Philippines, where natural enemy abundance and diversity is high. A major shortcoming in these studies is that 'disappearance' remained mostly unspecified, and that quantitative relationships between mortality and predator abundance were not determined. Also, density dependence of mortality factors was not studied. This lack of understanding of the mechanisms underlying mortality makes extrapolation of the results to a different situation impossible.

Surveys of parasitism Reports on percentage parasitism based on field collection and rearing of leaffolders are available from a wider geographic range than the life tables. Most emphasis is on parasitism of the larval stage. Percentage parasitism is reported from Pakistan (Ahmed et al. 1989), India (Bharati & Kushwaha 1988, Bhatnagar 1989), Sri Lanka (Rajapakse & Kulasekare 1981), Malaysia (Yuen 1982), the Philippines (Kamal 1981, Litsinger et al. 1987a, Guo 1990, Arida & Shepard 1990), Taiwan (Chen & Chiu 1983), China (Guo & Zhao 1992) and Japan (Wada & Shimazu 1978, Kobayashi & Wada 1979). These reports are either based on a one-time survey over a large area, or on regular sampling of a leaffolder population at one location throughout a few cropping seasons. Reported rates of egg parasitism vary from 5 to 60%, while values reported for larval parasitism are commonly between 20 and 50%. Without more details on the rice leaffolder population dynamics over a range of seasons or locations, such reports are not very informative about the actual impact of the parasitoids (van Driesche 1983, Bellows et al. 1992). However, they are useful in revealing the occurrence and relative importance of parasitoid species, and their potential impact.

Inclusion studies The approach of the inclusion studies differs from life table studies and surveys of parasitism as mortality rates are not assessed in the open field. To study the relative importance or potential impact of naturally-occurring predator and parasitoid species their attack rates are determined in controlled experiments. Inclusion studies have been conducted at scales varying from test tubes to cages covering a few plants, with leaffolder eggs, larvae or adults as host or prey. These studies are useful to determine the acceptance of leaffolder prey by a large number of potential predator species, and to establish maximum daily consumption rates, provided the searching arena is sufficiently small (e.g. Yuen 1982). When experimental conditions are equal, inclusion studies can be used to compare the performance of natural enemy species (e.g. Bandong & Litsinger 1986, van den Berg et al. 1992). However, the attack rates cannot simply be extrapolated to field conditions, due to the artificial conditions in these studies, e.g. the unrealistic leaffolder and natural enemy densities, and possible changes in behaviour.

In addition to these three categories of study on natural enemy impact on rice leaffolder, occasional reports of increased leaffolder infestation after insecticide applications also indicate the importance of natural enemies. Bandong & Litsinger (1986) observed high leaffolder injury levels in sprayed farmers' fields while injury was low in insecticide-free plots, and they suggest this difference was due to resurgence after spraying. In a number of studies, increased leaffolder infestation was correlated with the application of granular, systemic insecticides such as carbofuran and phorate (Velusamy & Chelliah 1985, Nadarajan & Skaria 1988, Panda & Shi 1989). It remains unclear, however, whether this is due to resurgence or whether a change in host plant quality or appearance, due to a growth-stimulating effect of the insecticide (Venugopal & Litsinger 1984, Litsinger et al. 1987b), resulted in higher leaffolder infestation. Positive effects on leaffolder fitness of sub-lethal dosages of three commonly used insecticides were dismissed as a possible cause of resurgence (Tevapuchom & Heong 1991).

In conclusion, a diverse complex of natural enemies of rice leaffolders is present in tropical rice fields in Asia, and numerous studies indicate that these naturally-occurring predators, parasitoids and pathogens can cause high mortality to rice leaffolders. A quantification of the impact of natural enemies in relation to their abundance is generally lacking, however. Such quantitative knowledge is needed for the development of leaffolder management strategies that make optimal use of natural control.

3. Problem definition and research objectives

Rice leaffolders are common in rice fields throughout Asia, causing conspicuous injury to the leaves. Rice farmers perceive foliar pests as serious threats and generally apply insecticides in response to leaffolder symptoms, even at very low infestation levels (Heong 1991, Heong et al. 1994, IRRI 1993c, Rola & Pingali 1993). Surveys in the Philippines and Vietnam have shown that a major part (30-40%) of all insecticide applications is targeted at leaf-feeding insects of which rice leaffolders are the main species (Heong et al. 1994). These sprays are usually applied during the first month after crop establishment (Escalada et al. 1992, Vo Mai et al. 1993). This pattern of widespread early insecticide use in tropical rice is a cause of concern because it may disrupt the natural control of rice pests, which is the cornerstone of integrated management of rice pests (Kenmore 1991, Gallagher 1992). The type of insecticides used and time of spraying enhance in particular the risk of outbreaks of the brown planthopper *Nilaparvata lugens* (Heong 1991, Holt et al. 1992). Outbreaks of this pest following insecticide applications against leaffolders have been reported from the Solomon Islands (Stapley 1978). Recent large-scale brown planthopper outbreaks in Vietnam's Mekong delta have also been partly attributed to early and frequent applications of broad-spectrum insecticides against leaffolders and thrips (Vo Mai 1992, Heong et al. 1994). Insecticides applied to control rice leaffolder kill its natural enemies as well, and in some cases may thus even lead to higher leaffolder injury than in untreated fields (Bandong & Litsinger 1986, Wu et al. 1986).

Considering these problems, a critical assessment of the need for chemical control of rice leaffolders is required. It is likely that farmers overestimate leaffolder injury and consequently overuse insecticides, because under favourable growing conditions a rice crop can tolerate substantial defoliation without suffering yield loss (e.g. Hu et al. 1993, IRRI 1993c). Mortality inflicted by the numerous naturally-occurring predators and parasitoids may therefore be sufficient to keep the leaffolder population below economic damage levels most of the time. When the negative effects on farmer health are considered, the economic justification for insecticide use against leaffolders becomes even more questionable (cf. Rola & Pingali 1993).

To assess whether natural enemies can suppress rice leaffolder populations to below economic damage levels, the relationship between leaffolder population dynamics and yield loss should be defined, as well as the impact of natural enemies on leaffolder densities. The literature review in the previous sections indicated that both relationships have already been studied to some extent, but mostly in an empirical, descriptive way. Leaffolder damage relations and the impact of natural enemies varied considerably within and between these studies, and thus lack general applicability. A quantitative understanding of the mechanisms that underlie the (system-level) relationships between the populations of natural enemies and leaffolders, and the rice crop, will be needed to explain and predict how these relationships change under different conditions. In the present study such a systems analytical approach was followed, with the objectives:

(1) to quantify the impact of natural enemies on rice leaffolder populations, and

(2) to assess the potential of natural enemies to prevent rice leaffolder damage,

on the basis of the underlying ecological and crop physiological mechanisms.

The ultimate aim of this study was to contribute to the development of a management strategy for rice leaffolder in tropical Asia, that maximizes the natural control potentials and minimizes yield losses. Both the development and the implementation of such a leaffolder management strategy require a quantitative insight into the interactions between natural enemies, leaffolders and the crop in the rice field ecosystem. Once the major factors contributing to effective natural control of rice leaffolders are identified, management options for leaffolder can be determined, such as conservation measures for major natural enemy species, or crop management practices that reduce crop sensitivity to leaffolder injury. Implementation of IPM in Asia is currently achieved by providing farmers with a framework to analyze and monitor the ecosystem of their own fields to fine tune decisions to their objectives and constraints, rather then by trying to transfer centrally developed decision rules (Gallagher 1992, Matteson et al. 1994). Research can contribute to that development by providing new ecological knowledge and insights concerning the role and potential of natural enemy species in leaffolder control. These insights may stimulate farmers to apply insecticide sprays against rice leaffolder only as a last resort.

4. Methodology and outline of the thesis

The methodology of the study is schematically represented in Figure 1. Experimentation and modelling was conducted at various levels of integration and complexity. The experiments served to describe the system (rice leaffolder field population dynamics), and to analyze the components (egg mortality, egg predation), and underlying processes (predator behaviour). With the models the experimental results at lower levels were integrated to explain observations and explore relations at the higher level. Experimental results at the same level served to validate the model, or to provide input data for descriptive parts. This approach resulted in a simulation model of leaffolder population dynamics, that included the effect of several natural enemies, and which was coupled with a crop growth model for rice. The modelling of rice leaffolder damage with the crop growth model followed the same explanatory approach as for the impact of natural enemies. However, experimental work focused on natural enemies, and most data on leaffolder injury and its effects on crop growth processes were obtained from the literature.

The combined model can be used to assess to what extent natural enemies can suppress rice leaffolder infestations, and, consequently, prevent yield loss. Due to its mechanistic, quantitative nature, the model can provide insight in the relative importance of variables and in the impact of changing biotic and abiotic conditions on the effects of natural enemies on leaffolder population dynamics and damage.

To study natural enemy impact, a combination of sampling and life table studies, experimental and observational methods, and modelling techniques was used (Table 1). As

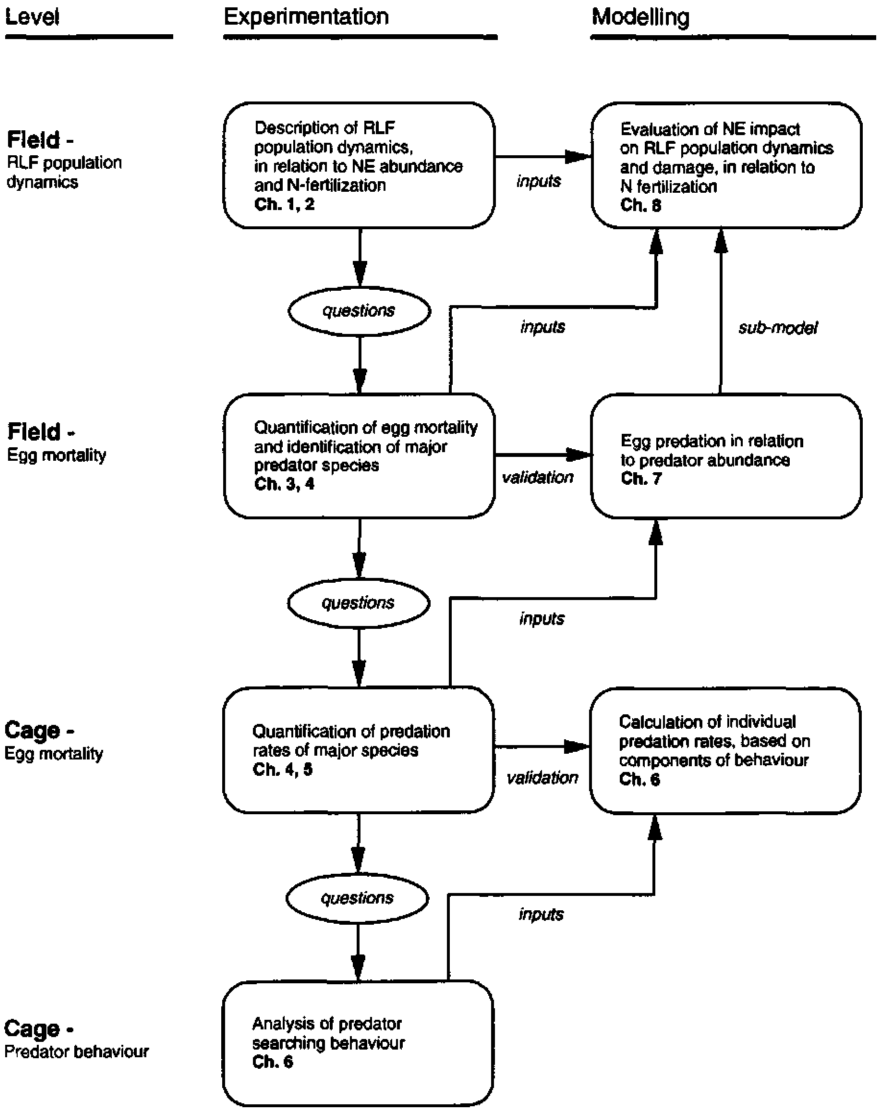


Figure 1. Outline of the approach taken to evaluate the impact of natural enemies (NE) on rice leaffolder (RLF) populations and damage.

has been stressed in a number of reviews dealing with the evaluation of indigenous natural enemy impact (Bellows et al. 1992, Luck et al. 1988, Shepard & Ooi 1991), no single method is without limitations, and the use of various techniques served to complement and cross-check the results.

Table 1. Methods used to evaluate the impact of natural enemies (NE) on rice leaffolder populations.

Methods	Chapter	Objectives		
		Determine impact NE community	*Determine identity (major) NE species*	*Determine impact (major) NE species*
- sampling of pest and natural enemy populations	1,2,3,4	X	.	.
- field exposure of lab-laid egg cohorts	3,4	X	X	X
- monitoring of natural egg cohorts	3	X	X	X
- direct observation of egg predation	4	.	X	X
- egg predation studies in cages	4,5	.	.	X
- behavioural observations of egg predators	6	.	.	X
- modelling of egg predation	7	.	.	X
- modelling of RLF population dynamics and damage	8	X	.	X

For a descriptive analysis of pest population dynamics and the natural enemy complex, populations of rice leaffolders and their natural enemies were sampled in unsprayed rice fields in Laguna Province, the Philippines (Chapter 1). To explore the impact of the natural enemy complex, correlations between leaffolder abundance, leaffolder survival, parasitism rates, and natural enemy density were investigated. During one season, N-fertilizer was applied at three levels to study its effects on the population dynamics of rice leaffolders and their natural enemies (Chapter 2). Further studies concentrated on egg stage mortality, which was measured by field exposure and recovery of laboratory-laid egg cohorts and by monitoring naturally-laid eggs (Chapter 3). Egg mortality was partitioned into parasitism, disappearance due to unidentified causes, and non-hatching. Multiple regression was applied to identify potentially important mortality factors. To unambiguously identify the major egg predator species, exposure of leaffolder eggs was combined with direct observation of egg predation in the fields during two crop seasons (Chapter 4). These direct observations were complemented with laboratory assessments of egg acceptance, consumption rate and prey preference of a range of predator species (Chapter 4). A series of cage experiments was conducted to quantify the predation rates of the major predator species of leaffolder eggs (Chapter 5). Their searching behaviour was studied in detail to check the assumptions and results of the cage predation experiments (Chapter 6). The results of the cage predation experiments were used to construct a model of field predation of leaffolder eggs, which was evaluated with independent field data (Chapter 7). Finally, a combined pest-crop model of leaffolders in rice was developed and used to test the hypothesis that in unsprayed rice fields in Laguna Province natural enemies can suppress leaffolder populations to below economic damage levels (Chapter 8). Data on leaffolder population densities and mortality factors from the field studies were used as input to the model to assess their effect on rice yields under different levels of fertilization. The contribution of the major egg predator species was evaluated by incorporation of the sub-model for egg predation into the combined pest-crop model.

The thesis concludes with a discussion of the methodology, the implications for research and implementation of rice leaffolder management, and the possible impact of changes in rice cultivation on the natural control of rice leaffolders (General Discussion).

Chapter 1

Population dynamics of rice leaffolders and their natural enemies in irrigated rice in the Philippines

Abstract Populations of rice leaffolders (Lepidoptera: Pyralidae) and their natural enemies were studied in eight irrigated rice crops in Laguna Province, the Philippines. The rice leaffolder complex consisted of three species: *Cnaphalocrocis medinalis*, *Marasmia patnalis*, and *Marasmia exigua* (in order of appearance during the crop season). Either *C. medinalis*, or *M. patnalis* was dominant, or both were equally abundant. Leaffolder population dynamics were characterized by an egg peak at maximum tillering and a broad larval peak around booting stage. Peak densities ranged from 0.2 to 2.0 larvae per hill. Leaf injury was highest around flowering with 1 to 10 injured leaves per hill. During the first month after transplanting leaffolder populations were always very low. Most larvae originated from immigrant moths and there was no substantial second generation. This pattern can be explained by leaffolder ovipositional preference for the maximum tillering stage.

Eleven species of hymenopterous parasitoids were reared from the field-collected leaffolder eggs, larvae and pupae. The seasonal percentage egg parasitism by *Trichogramma* sp. (Hymenoptera: Trichogrammatidae) ranged from 0 to 50%, and percentage larval parasitism from 14 to 56%. *Macrocentrus philippinensis* (Hymenoptera: Ichneumonidae) was the most commonly reared larval parasitoid. Forty natural enemy taxa that may attack rice leaffolders were identified from the suction and sweepnet samples: 24 predator taxa and 16 parasitoid taxa. The number of taxa found per crop ranged from 28 to 36. Predator populations were numerically dominated by hemipteran species. The most common taxa of parasitoids were *Cotesia* spp., *Opius* spp., and *Tetrastichus* spp. The estimated survival rates from leaffolder egg to larval stages and between larval stages showed large variation between crops, but were not correlated with the level of egg parasitism, predator abundance, or predator-prey ratios. Survival of medium-sized larva was negatively correlated with parasitism of young larvae.

The generally low densities of rice leaffolders in Philippine transplanted rice may be caused by their ovipositional preference, allowing for only one generation, and high immature mortality caused by the abundant and diverse complex of natural enemies.

Introduction

Since the mid-sixties rice leaffolders *Cnaphalocrocis medinalis* 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). The shift from minor to major pest has been attributed to the adoption of new rice growing practices that accompanied the introduction of high yielding varieties (Kulshreshtha et al. 1970, Dhaliwal et al. 1985, Litsinger 1989). Rice leaffolder larvae cause conspicuous injury by folding leaves and scraping off the green mesophyll tissue (Fraenkel & Fallil 1981, Fraenkel et al. 1981), and farmers respond usually by applying insecticides, even at very low infestation levels (Heong et al. 1994). However, in many cases it is questionable whether chemical control of rice leaffolder is justified, despite its increased abundance. Modern rice varieties have a high tolerance to defoliation (e.g. Hu et al. 1993, IRRI 1993c), and tropical rice fields harbour a large complex of natural enemies, that may keep rice leaffolder populations below damaging levels most of the time (Khan et al. 1988, Barrion et al. 1991a). Apart from negative side effects on health and environment, insecticides may even promote leaffolder infestations (Bandong & Litsinger 1986, Nadarajan & Skaria 1988, Panda & Shi 1989).

Knowledge of rice leaffolder population dynamics, and insight in the factors determining leaffolder abundance, such as natural enemies, is essential as a basis for a more rational pest management. Rice leaffolder population dynamics have been studied well in China and Japan, where the pest is mainly migratory and has distinct generations (Liang & Pang 1987, Zhang et al. 1988, Wada & Kobayashi 1991). However, in tropical Asia, where leaffolders are breeding year-round, their population dynamics have rarely been studied in detail. Infestation levels are usually reported only as percentage injured leaves, and few studies deal with factors affecting population densities. Most reports on the impact of natural enemies concern percentages of larval parasitism, while relations between natural enemy abundance and leaffolder infestation levels have not been established.

In this chapter a study is presented of the population dynamics of rice leaffolders and their natural enemies during eight crop seasons in the Philippines. The objective was to analyze the population dynamics of the leaffolder complex, and to obtain insight in the factors determining their temporal abundance and survival during a crop season. The specific interest of this study concerned the role of natural enemies in leaffolder population dynamics. Therefore, the dynamics of leaffolder natural enemies and leaffolder parasitism rates were determined as well, and related to leaffolder abundance and survival rates. The results of the study are discussed in view of leaffolder pest management.

Materials and Methods

Description of study area and fields

The study was conducted in Laguna Province, the Philippines, a humid tropical lowland area where rice is grown year-round under irrigated conditions. The rice leaffolder population in Laguna is a complex of three related species: *Cnaphalocrocis medinalis* (Guenee), *Marasmia patnalis* Bradley, and *M. exigua* (Butler) (Arida & Shepard 1986). The first two species are the most abundant in Laguna, and dominance by any one species can vary during a cropping season (Barrion et al. 1991a).

Fieldwork was carried out in eight rice crops, covering three sites and six seasons (Table 1). One of the sites was a field at the experimental farm of the International Rice Research Institute (IRRI) in Los Baños (13°14'N, 121°15'E). The two other sites (Pila and Victoria) were farmers' fields at 15-20 km distance from IRRI. The fields were transplanted in a 20 × 20 cm spacing with 2-week old seedlings of a variety susceptible to leaffolder. The crops received fertilizer at a rate of about 90 kg N ha^{-1}, according standard recommendations. Weeding was done by hand and pesticides were not applied. The IRRI field was kept permanently flooded until a week before harvest, while the farmers' fields in Pila and Victoria were intermittently flooded. Rice yields were between 4 and 7 tons per hectare.

Arthropod sampling

The densities of rice leaffolder stages and their natural enemies were estimated by a combination of sampling methods (Table 1). Rice leaffolder moths and arthropod natural enemies were sampled with a suction sampler (D-Vac or Blower-Vac, Arida & Heong 1992) in combination with a plastic bucket enclosure, covering four hills. To include fast-moving insects like orthopterans, the enclosure was placed abruptly over the hills. Relative density estimates of highly mobile species, such as the larger hymenopterous parasitoids and Odonata, were obtained by sweepnet sampling in five of the crops. Suction and sweepnet samples were taken between 8.00 and 11.00 a.m. Predators and parasitoids of rice leaffolders were counted using a checklist based on the Philippine rice leaffolder foodweb (Barrion et

Table 1. Details of field studies of the population dynamics of rice leaffolders and their natural enemies, Laguna, Philippines. Given for the three sampling methods: size (*no. of sample units per sample*), no. (number of sampling dates), period (period during which samples were taken, in weeks after transplanting). Sampling units for each method: hill, 1 hill; suction, enclosure covering 4 hills; sweepnet, 5 sweeps.

Location	Area (ha)	Variety	Year-season	Transplanting date	Hill samples			Suction samples			Sweepnet samples		
					Size	No.	Period	Size	No.	Period	Size	No.	Period
Victoria	0.49	R-10	1991 dry	12 January	50	5	(4–12)	25	6	(2–12)	20	6	(2–12)
Pila	0.62	C-4	1991 dry	4 January	50	5	(5–13)	25	7	(3–15)	20	7	(3–15)
Pila	0.20	IR70	1991 wet	31 August	60	22	(4–16)	20	12	(4–15)	16	12	(5–16)
Pila	0.34	C-4	1992 dry	27 January	100	9	(5–14)	24	3	(6–10)	20	6	(5–14)
Pila	0.34	IR72	1993 dry	4 February	100	8	(3–13)	25	10	(3–13)	–		–
Pila	0.34	IR72	1993 wet	16 August	50	4	(4–12)	30	4	(4–12)	–		–
IRRI	0.25	IR72	1992 wet	23 June	30	7	(3–14)	15	6	(3–14)	10	5	(4–12)
IRRI	0.25	IR72	1993 wet	17 July	50	3	(7– 9)	30	3	(7– 9)	–		–

al. 1991a, Cohen et al. 1994). The densities of the immature leaffolder stages were estimated by random sampling of rice hills. In the laboratory the plants were checked for the presence of leaffolder eggs, larvae and pupae and leaves injured by leaffolder larvae. 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 were identified to species only after moth emergence, because the immature stages of *C. medinalis* and *Marasmia* spp. are very similar in appearance and difficult to distinguish morphologically (Barrion et al. 1991a). The moths can be easily identified to species by their wing markings (Barrion & Litsinger 1985b).

Ratios of natural enemy to rice leaffolder density were calculated for moths, immatures, and larvae separately, using counts from hill and suction samples. Within the natural enemy complex attacking leaffolders, Odonata and Araneae were classified as moth predators, while Coleoptera, Orthoptera and Hemiptera were classified as predators of leaffolder immatures. For each crop, natural enemy to leaffolder ratios were calculated over three consecutive periods of five weeks, representing the vegetative, reproductive and ripening stage (Yoshida 1981). Also the seasonal averages of these ratios were calculated.

Parasitism

Reliable estimates of parasitoid impact on a host population are difficult to obtain and usually require recruitment data in addition to host population samples (van Driesche 1983, van Driesche et al. 1991). In this study such additional data were not collected and therefore a seasonal level of parasitism was calculated only as an indicator of parasitoid impact. This was done by dividing the number of hosts with clear symptoms of parasitism by the total number of hosts, after pooling the samples per crop season. Leaffolders that died of unknown cause were excluded from the calculation on the assumption that healthy and parasitized hosts had similar chances of dying. This indicator of parasitoid impact can be improved by correction for differences between healthy and parasitized hosts in development time, mortality rate, and sampling efficiency (van Driesche 1983).

Egg parasitism To calculate the seasonal percentage egg parasitism, a correction has to be made for differences in development time. Healthy eggs hatch in about 4 days (Barrion et al. 1991a), while parasitoids emerge from the parasitized eggs in about 10 days (own observations). Parasitism becomes visible after 4 days, when parasitized eggs change in colour from whitish-yellow to black. Egg parasitism was calculated using two methods. In the first case (method A), only apparently healthy, white eggs were included. The percentage parasitism was determined by rearing the collected eggs in the laboratory. As the time till hatching of healthy eggs is the same as till turning black, no correction for duration has to be made, while sampling efficiency and disappearance rate are likely to be similar. However, because the eggs are protected from parasitoids during the remaining period of development by taking them out of the field, this method underestimates the potential parasitoid impact (van Driesche 1983). In the other case (method B), black parasitized eggs were included in the calculation, but their numbers were corrected for the longer development time. As they remain longer in the field, they will be overrepresented in the samples. The correction factor lies between 1 and 2.5 (=duration parasitized egg/healthy egg), depending on the egg mortality rate. Taking into account the relatively lower disappearance rate of black eggs (own observations), and assuming a similar sampling efficiency, a correction factor of 2 was used. Including the black eggs reduces the underestimation due to protection inherent to method A. It may even overestimate parasitism, because parasitoid emergence from black eggs was not checked and may be well below 100%, thus increasing the 'duration' of parasitized eggs.

Larval parasitism Corrections of the percentage larval parasitism were not possible, due to a lack of detailed knowledge on the large number of parasitoid species that were reared from the larval samples. The susceptible host stage for each species could not be defined as the majority of the parasitoids may attack most larval stages, but can have preferences for a certain stage or size (Guo 1990). Host development rate appears usually unaffected until the larvae are killed by the parasitoid (Rurkviree 1981, Guo 1990). Whether parasitism changes the probability of death due to other factors is not known, nor whether sampling efficiency is affected. Therefore the seasonal percentage larval parasitism was simply calculated as the total number of parasitized larvae, divided by the total number of collected larvae of all stages, without further corrections. Percentage parasitism for each larval stage separately was calculated in a similar way.

Survival rates

From the time series of leaffolder population samples per crop, estimates were made of stage to stage survival rates. A large number of methods has been developed to calculate stage-specific survival rates from stage-frequency data (Manly 1989). However, most of these methods require additional data on the initial recruitment, or make the - usually unrealistic - assumption that the daily or stage-specific survival rate is constant. A simple and well-known method that does not have these limitations, is Southwood and Jepson's 'graphical method' (Southwood 1978). Per stage, the number alive mid-way is calculated by dividing the area under the density curve by the stage-specific development time. As this method implies that all mortality occurs at the end of the stage, no truly stage-specific survival rates can be obtained. The survival from mid-way stage i till mid-way stage $i+1$ is estimated by dividing the number in stage $i+1$ by those in stage i.

For seven leaffolder populations survival rates were calculated from egg to larva, egg to medium-sized larva (L2, L3), and from medium-sized larva to large larva (L4, L5, L6). Data on pupal densities were insufficient to include in the analysis. An average duration of 4 days was taken for the egg stage, 5 days for the medium-sized larvae and 11 days for the large larvae. The three leaffolder species differ only slightly in stage durations (Barrion et al. 1991a). Duration depends primarily on temperature, and in case of larvae also on host plant quality (Wada & Kobayashi 1980). However, ambient temperature was fairly constant under the conditions studied, and host-plant effects on larval development are relatively small (Wada 1979, de Kraker unpublished), justifying the use of standard durations.

The densities of the various leaffolder stages were adjusted according to their sampling efficiency. A previous experiment showed that relative to large larvae (L4-L6), the sampling efficiency of eggs was about 50%, and of medium-sized larvae (L2, L3) about 60%. Sampling efficiency of the cryptic and tiny first instar larvae is very low, and therefore this stage was excluded from the survival analysis.

The calculated stage to stage survival rates are only approximate values, primarily meant for comparison between crops and correlation with other variables.

Correlation analysis

A correlation analysis was applied to identify significant associations between the observed or derived variables of the leaffolder - natural enemy system. Such correlations can indicate potentially important factors in the natural control of leaffolders, and serve to guide more detailed research into the underlying causal mechanisms. For example, a significant positive correlation between leaffolder egg or larval abundance and the level of parasitism would indicate the presence of density-dependent mechanisms, and correlations between leaffolder stage survival rates and the abundance of natural enemy groups can help to identify natural enemies with a major impact. Simple linear correlation coefficients were computed between the following variables (using one seasonal value for each crop) in a matrix: abundance of leaffolder stages (average density, area under the density curve, recruitment per hill), eggs-moth ratio, stage to stage survival rates, percentages egg and larval parasitism, abundance of natural enemy groups, and natural enemy-leaffolder ratios. In addition, x-y plots of the correlated variables were inspected to check for obvious non-linear relationships.

Results

Rice leaffolder population dynamics and injury

Species composition Two leaffolder species, *C. medinalis* and *M. patnalis*, were found in all eight rice crops, while a third species, *M. exigua*, was found in five crops. In most crops, *C. medinalis* appeared first, soon followed by *M. patnalis*, while *M. exigua* was usually last. The percentage of the seasonal total made up by any of the three species was quite variable (Table 2). Either *C. medinalis* or *M. patnalis* was dominant, or both were equally abundant. Species composition per crop was significantly dependent on sampling method in two out of seven times (Table 2). In both cases the share of *M. exigua* in the larval samples (hill samples) was larger than in the moth samples (sweepnet or suction sampler).

Table 2. Species composition of rice leaffolder complex in eight rice crops, Laguna, Philippines, as a percentage of seasonal totals (N), determined with three sampling methods (suction, sweepnet, and hill samples).

Location	Year-season	Species	Percentage of total			Effect of sampling method [a]
			Suction	Sweepnet	Hill	
Victoria	1991 - DS	*C. medinalis*	81.5	89.4	–	
		M. patnalis	18.5	10.6	–	
		M. exigua	0.0	0.0	–	
		(N)	(27)	(47)		n.s.
Pila	1991 - DS	*C. medinalis*	66.7	72.4	–	
		M. patnalis	33.3	27.6	–	
		M. exigua	0.0	0.0	–	
		(N)	(9)	(29)		n.s.
Pila	1992 - DS	*C. medinalis*	54.7	49.5	43.8	
		M. patnalis	43.0	47.0	46.6	
		M. exigua	2.3	3.5	9.6	
		(N)	(42)	(202)	(73)	n.s.
Pila	1993 - DS	*C. medinalis*	11.1	–	–	
		M. patnalis	88.9	–	–	
		M. exigua	0.0	–	–	
		(N)	(8)			–
Pila	1991 - WS	*C. medinalis*	38.4	45.3	21.1	
		M. patnalis	61.6	54.7	57.2	
		M. exigua	0.0	0.0	21.7	
		(N)	(30)	(71)	(180)	***
Pila	1993 - WS	*C. medinalis*	33.3	–	6.4	
		M. patnalis	33.3	–	63.8	
		M. exigua	33.3	–	29.8	
		(N)	(6)		(47)	n.s.
IRRI	1992 - WS	*C. medinalis*	76.3	51.9	50.0	
		M. patnalis	23.7	37.0	33.3	
		M. exigua	0.0	11.1	16.7	
		(N)	(21)	(27)	(12)	n.s.
IRRI	1993 - WS	*C. medinalis*	83.3	–	40.6	
		M. patnalis	16.7	–	43.8	
		M. exigua	0.0	–	15.6	
		(N)	(65)		(32)	***

[a] X^2−test: n.s. = non-significant, $p>0.05$; *** = $p<0.001$

Figure 1 (opposite page). Mean densities of rice leaffolder stages in four wet season rice crops (□ Victoria 1991; △ Pila 1991; ○ Pila 1992; + Pila 1993), and four wet season crops (□ Pila 1991; △ Pila 1993; ○ IRRI 1992; + IRRI 1993), Laguna, Philippines. Arrow indicates rice flowering stage. Moths: suction samples; standard errors (S.E.) were about 40% of the sample means. Eggs (healthy and parasitized): hill samples; S.E. about 20%. Larvae (healthy and parasitized): hill samples; S.E. about 20%. Dotted line indicates the conservative action threshold (see text). Leaves with rice leaffolder injury: hill samples; S.E. about 10%.

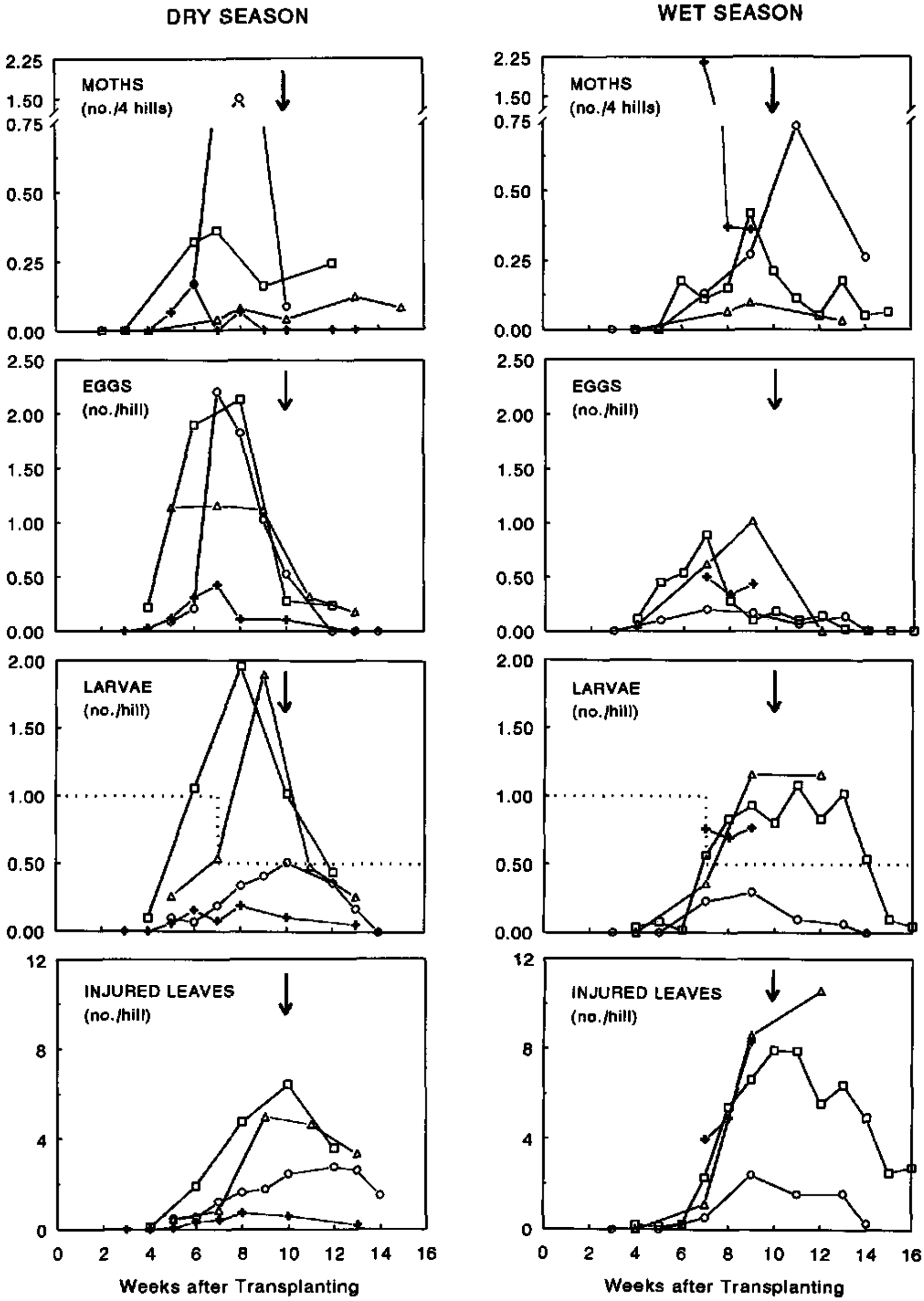
Abundance and injury Rice leaffolder moths appeared usually four weeks after transplanting (WT), but the timing of the peak densities did not follow a consistent pattern (Fig. 1). Eggs peaked around maximum tillering stage (7 WT), with a broad larval peak following one or two weeks later, at booting stage (Fig. 1). After the flowering stage only few eggs were found. Peak larval densities ranged from 0.2 to 2.0 hill^{-1}. Only few pupae and pupal cases were found in the samples, and peak densities were below 0.2 hill^{-1}. Pupae are difficult to find, because leaffolder larvae often pupate behind leaf sheaths.

Leaf injury due to rice leaffolder larvae became visible after 4 WT. The number of injured leaves per hill peaked around flowering, and decreased towards maturity due to leaf senescence (Fig. 1). Peak levels of injured leaves per hill ranged from 0.7 to 10.6, and were higher in the wet season than in the dry season. The percentage of injured leaves per hill was approximately the same as the number, as there were about 100 leaves per hill.

Leaf injury per crop was positively correlated with larval infestation level ($r=0.8$, $p<0.05$), both calculated as area under the density curve. The ratio of injured leaf-days to larva-days was significantly lower for the dry season crops than for the wet season crops (t-test, $p<0.01$).

Composition and abundance of leaffolder natural enemy complex

Species diversity Forty leaffolder natural enemy taxa were identified from the arthropod samples: 24 predator and 16 parasitoid taxa (Appendix). The differences between the eight rice crops were only moderate in terms of number of taxa found per crop. This number ranged from 24 (IRRI 1992-WS), to 36 (Pila 1993-DS) in the suction samples, and from 24 (IRRI 1992-WS) to 31 (Pila 1991-DS) in the sweepnet samples. Combining both methods usually resulted in more taxa per crop, as the sampling methods are partly complementary and a larger sampling effort also increases the number of taxa collected. During a crop


DRY SEASON
WET SEASON
MOTHS
(no./4 hills)
EGGS
(no./hill)
LARVAE
(no./hill)
INJURED LEAVES
(no./hill)
2.25
1.50
0.75
0.50
0.25
0.00
2.50
2.00
1.50
1.00
0.50
0.00
2.00
1.50
1.00
0.50
0.00
12
8
4
0
0
2
4
6
8
10
12
14
16
Weeks after Transplanting
Weeks after Transplanting

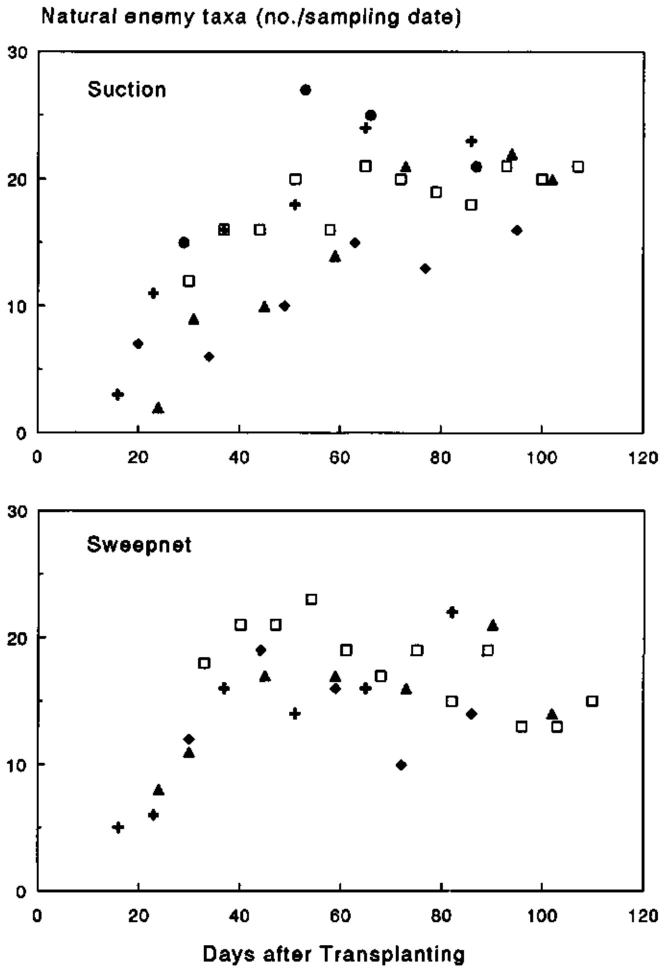


Figure 2. Total number of leaffolder natural enemy taxa per sampling date for suction sampler and sweepnet: + Victoria 1991-DS; ▲ Pila 1991-DS; ● Pila 1993-DS; □ Pila 1991-WS; ◆ IRRI 1992-WS.

season, the number of leaffolder natural enemy taxa rose to a peak level at about 50 days after transplanting, and then stabilized or decreased slowly towards maturity (Fig. 2).

Species abundance The most common predator species, both in terms of incidence and abundance, were the spiders *Pardosa pseudoannulata* (Lycosidae) and *Tetragnatha* spp. (Tetragnathidae), the beetles *Ophionea nigrofasciata* and *Micraspis* sp., the orthopterans *Conocephalus longipennis*, *Anaxipha longipennis* and *Metioche vittaticollis*, and the hemipterans *Cyrtorhinus lividipennis*, *Microvelia douglasi atrolineata*, *Mesovelia vittigera* and *Polytoxus fuscovittatis*. Predator populations were numerically dominated by the hemipteran species (Fig. 3). *C. lividipennis* dominated during the dry season, and *M. d. atrolineata* in the wet season crops. In terms of predator biomass this picture would be very different, as the individual weight of the dominant hemipterans is only 5-10% of the weight of the spiders, beetles or orthopterans. Temporal trends in abundance varied per crop for spiders and hemipterans, while the numbers of coleopteran and orthopteran predators were always highest during the last part of the crop season (Fig. 3). The ratio of predators (Odonata, Araneae) to leaffolder moths ranged from 3 to 19, while the number of predators (Coleoptera, Orthoptera, Hemiptera) per leaffolder immature varied from 2 to 16 between crops. Excluding the hemipterans resulted in ratios of 0.4 to 2.4. Predator-prey ratios were usually lowest during the reproductive crop stage, mainly because then leaffolder densities were highest.

The abundance of the hymenopterous parasitoids is represented by counts from the sweepnet samples (Fig. 4), because for these species this sampling method is the more efficient. The parasitoids did not show a consistent pattern in abundance during the crop season. The most common taxa of larval parasitoids were *Cotesia* spp., *Opius* spp., and *Tetrastichus* spp. Six parasitoid species that accounted for 90% of parasitism of collected rice leaffolder larvae (*Macrocentrus philippinensis*, *Cardiochiles philippinensis*, *Copidosomopsis nacoleiae*, *Temelucha philippinensis*, *Trichomma cnaphalocrocis*, and *Goniozus* sp.), only made up a minor percentage (7-26%) of the population of potential parasitoids (Fig. 4). The parasitoid-leaffolder host ratio for these major species ranged from 0.05 to 0.32 per crop.

The variation between crops in natural enemy to leaffolder ratios was large, but the average densities of leaffolder stages were not negatively correlated with the abundance of their natural enemies.

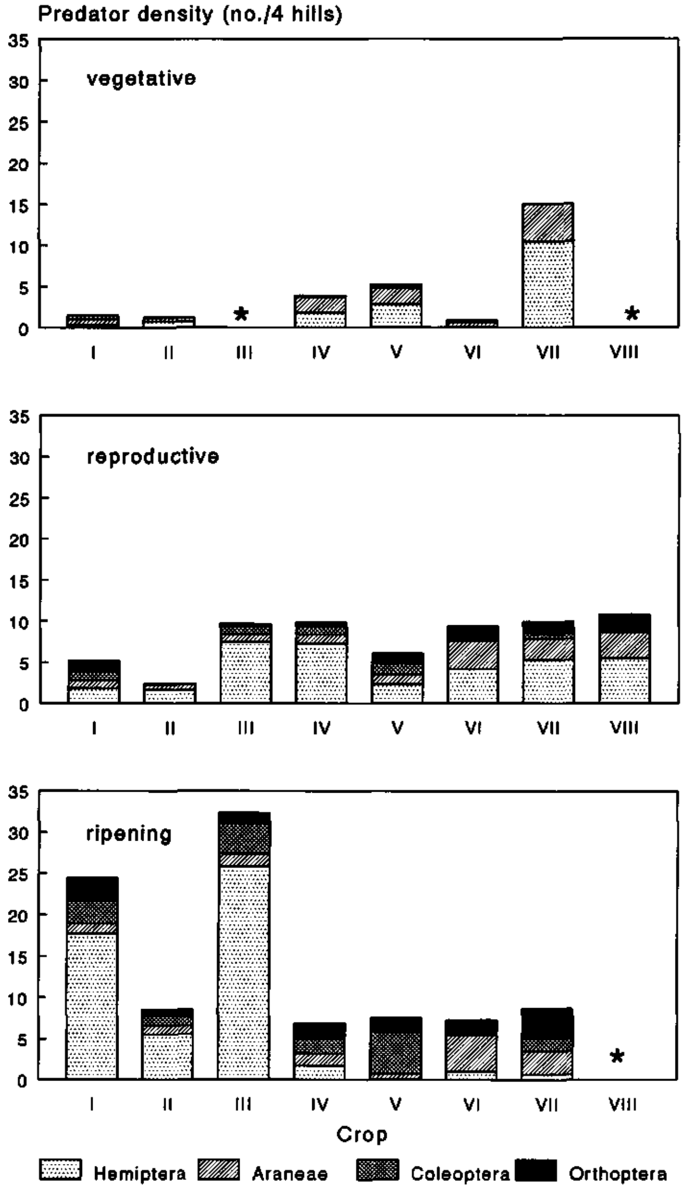


Figure 3. Mean density of major predator groups of rice leaffolders during the three crop growth stages in four dry season crops (I = Victoria 1991, II = Pila 1991, III = Pila 1992, IV = Pila 1993), and four wet season crops (V = Pila 1991, VI = Pila 1993, VII = IRRI 1992, VIII = IRRI 1993), Laguna, Philippines. Predators were sampled with a suction sampler. Asterix: no samples collected.

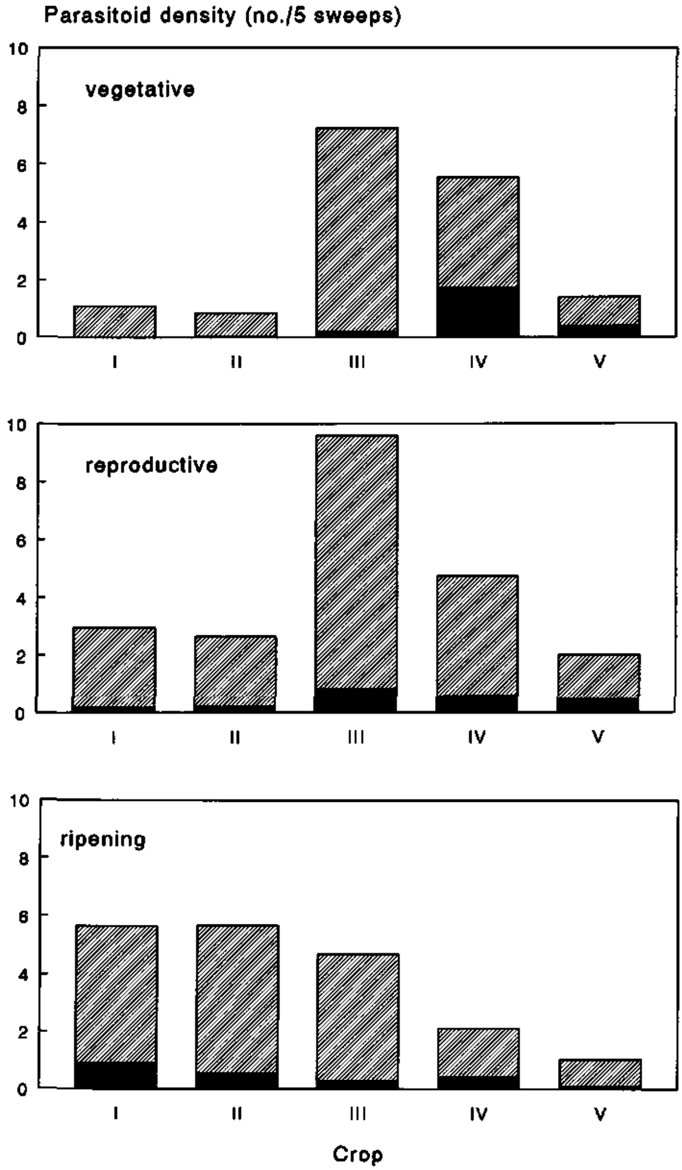


Figure 4. Mean density of hymenopterous parasitoids of rice leaffolders during the three crop growth stages in five rice crops (I = Victoria 1991-DS, II = Pila 1991-DS, III = Pila 1991-WS, IV = Pila 1992-DS, V = IRRI 1992-WS), Laguna, Philippines. Filled area in bar indicates the density of six parasitoid species, accounting for 90% of parasitism in larval samples. Parasitoids were sampled with a sweepnet.

Parasitism

Eleven species of hymenopterous parasitoids were reared from the field-collected rice leaffolders: one from the eggs, ten from larvae and two from pupae (Table 3). The two species reared from pupae, *Tetrastichus* sp. and *T. cnaphalocrocis*, were also reared from larvae. It could not be determined from which leaffolder species parasitoids emerged, as the immature stages are morphologically very difficult to distinguish.

Leaffolder larvae infected by entomopathogens were rarely observed in the samples or in the fields.

Egg parasitism The seasonal percentage of eggs parasitized by *Trichogramma* sp. (probably *T. japonicum*), varied from 0 to 50% (Table 4). This variation was independent of the average egg density per crop. Parasitism was consistently lower during the wet season, probably due to the negative impact of wind and rain on parasitoid activity (Keller et al. 1985). During a growing season, the percentage parasitism of apparently healthy eggs decreased steadily towards crop maturity.

The two calculation methods of seasonal percentage egg parasitism showed the same trend in variation between crops. However, inclusion of 'black' parasitized eggs (method B) yielded estimates that were about twice as high as calculated from apparently healthy eggs (method A). The 'true value' lies probably somewhere in between.

Larval parasitism Percentage larval parasitism ranged from 14 to 56% per crop (Table 4). The level of parasitism was independent of the average larval density. There was no correlation between adult parasitoid abundance or parasitoid-host ratio and the level of parasitism. Percentage parasitism was usually highest in the last larval instars. Larval parasitism was relatively low at the start and the end of the crop season. The species composition of the reared parasitoids was not related with crop stage.

The ranking of larval parasitoids according to their share in parasitism varied from crop to crop. *M. philippinensis* was the most commonly reared parasitoid, followed by *C. nacoleiae*, and *T. cnaphalocrocis*. However, the last two species were probably overrepresented, because *C. nacoleiae* has a longer development time than the other parasitoids, while *T. cnaphalocrocis* occurs primarily in late larval instars. These instars were sampled more efficiently and survived better in the laboratory.

Table 3. Parasitoid species reared from samples of rice leaffolder eggs, larvae, and pupae, Laguna, Philippines: (−)=absent, (+)=present, (*)=most common parasitoid in that crop. Locations: VI=Victoria, PI=Pila, IR=IRRI; seasons: DS=dry season, WS=wet season.

Family	Species	Host stage [a]	Crop						
			VI 91 DS	PI 91 DS	PI 92 DS	PI 91 WS	PI 93 WS	IR 92 WS	IR 93 WS
Bethylidae	*Goniozus* sp.	larva	−	+	+	+	+	−	−
Braconidae	*Cardiochiles philippinensis*	larva	−	*	−	+	+	−	+
	Cotesia spp.	larva	*	+	+	+	−	−	+
	Macrocentrus philippinensis	larva	+	−	*	*	+	*	+
Chalcididae	*Brachymeria* sp.	larva	−	−	−	−	−	−	+
Elasmidae	*Elasmus* sp.	larva	+	+	−	+	−	−	−
Encyrtidae	*Copidosomopsis nacoleia*	larva	−	−	+	+	+	−	*
Eulophidae	*Tetrastichus* sp.	larva,pupa	−	−	−	+	−	−	+
Ichneumonidae	*Temelucha philippinensis*	larva	+	+	+	+	+	−	+
	Trichomma cnaphalocrocis	larva,pupa	−	−	+	+	*	−	+
Trichogrammatidae	*Trichogramma* sp.	egg	+	+	+	+	+	−	+

[a] stage collected in the field, host stage of attack or emergence may differ

Table 4. Percentage parasitism of rice leaffolder eggs and larvae, pooled over a crop season, or at peak density, Laguna, Philippines. Egg parasitism was calculated in two ways: A = % parasitism of apparently healthy eggs; B = % parasitism of all eggs, including black parasitized eggs.

Location	Year-season	Egg parasitism			Larval parasitism		
		Season		Peak	Season		Peak
		A	B	B	L1-3	L1-5	L1-5
Victoria	1991-DS	–	>50.2	>34.9	–	26.7	46.7
Pila	1991-DS	–	>49.3	>49.7	–	38.8	53.8
Pila	1992-DS	27.3	44.5	48.1	46.4	43.8	35.0
Pila	1992-DS	26.9	40.4	62.3	–	–	–
Pila	1991-WS	17.6	31.1	29.7	27.4	31.6	15.9
Pila	1993-WS	1.6	14.9	4.3	29.8	40.5	41.0
IRRI	1992-WS	0.0	0.0	0.0	0.0	14.3	0.0
IRRI	1993-WS	5.5	12.6	8.3	52.8	55.6	76.0

Table 5. Estimated recruitment per hill of rice leaffolder stages, and stage to stage survival rates. Stages: E=egg; L=larva; ML=medium–sized larva; LL=large larva.

Location	Year-season	Recruitment per hill					Survival rates			
		Moth	Egg	Larva	Medium	Large	E-L	E-ML	ML-LL	E-LL
Victoria	1991-DS	0.7	9.2	4.2	–	–	0.46	–	–	–
Pila	1991-DS	0.2	9.1	3.1	–	–	0.34	–	–	–
Pila	1992-DS	1.3	13.9	1.3	4.4	0.4	0.09	0.31	0.09	0.03
Pila	1993-DS	0.1	3.1	0.5	1.9	0.1	0.16	0.63	0.05	0.03
Pila	1991-WS	0.5	6.7	3.4	7.5	2.1	0.50	1.12	0.28	0.30
Pila	1993-WS	0.2	11.2	3.5	8.0	2.0	0.31	0.72	0.25	0.18
IRRI	1992-WS	1.0	4.6	0.7	0.7	0.7	0.15	0.16	0.90	0.14

Recruitment and survival rates

The estimated seasonal recruitment of apparently healthy eggs ranged from 3 to 14 hill^{-1} (Table 5). Egg recruitment was not correlated with the abundance of leaffolders moths, and the number of eggs per moth ranged from less than 10 to more than 140. This variation was independent of predator-prey ratio or abundance of moth predators and predators of immatures.

The recruitment levels of eggs and larvae were statistically independent. The estimated survival rates from egg to larval stage, or from egg to medium-sized larvae and from medium-sized larvae to large larvae, varied considerably between crops (Table 5). The survival rates were not correlated with egg or larval recruitment, nor with percentage egg parasitism, predator abundance or predator-prey ratio. Survival from medium-sized to large larvae was higher in the wet season than in the dry season (Table 5). These larval survival rates were negatively correlated with the percentage parasitism of the first three larval instars ($r=0.98$, $p<0.05$).The survival rate from mid egg stage to mid large larval stage (E-LL) averaged 0.14 for five rice crops (range: 0.03 - 0.30, Table 5). The sampling efficiency of eggs may have been lower than the value used for the calculations (0.5), because the survival rate from egg to medium-sized larvae was larger than one in one crop (Pila 1991-WS). This implies that the level of egg recruitment was generally underestimated, and that as a result survival rates were overestimated.

Discussion

Abundance of rice leaffolders during a crop season

Rice leaffolders may complete two to three generations on a single rice crop, considering their generation time of five weeks (Khan et al. 1988, Barrion et al. 1991a), and their ability to feed and survive on each stage of the rice plant (Wada 1979, Chu et al. 1983, Arida et al. 1990, Telvapuchom 1990). However, the observed pattern (Fig. 1) indicates the presence of only one, or two overlapping generations. Leaffolder moths emerging from early laid eggs (around 5 WT), may contribute to the tail of the egg peak (around 10 WT), but moths emerging from the egg peak around 7 WT usually do not reproduce in the same crop. Only in two wet season crops (Pila 91-WS, IRRI 92-WS) a small second egg peak was observed. This means that the majority of the leaffolder larvae originates from immigrant moths, and that population build-up is not expected to occur on a single crop.

The consistent occurrence of the egg peak around the maximum tillering stage suggest that this stage is the most preferred by rice leaffolders for oviposition. In a choice situation, *C. medinalis* moths indeed laid most eggs in the tillering crop (Fukamachi 1980,1983, de Kraker unpublished). In Japan, *C. medinalis* moths emerging after flowering did not oviposit in the same crop and emigrated (Wada et al. 1980, Wada & Kobayashi 1982). The oviposition preference is probably related to the quality of the host plant, as rice plants in the ripening stage are less suitable for development and survival of leaffolder larvae (Wada 1979, Cheng 1987, Heong 1990, Telvapuchom 1990). *M. patnalis* and *M. exigua* may have a different oviposition preference, as they usually occur later during the crop season. However, only few eggs of either leaffolder species were found in the ripening stage, so all three species appear to avoid oviposition on a host plant of decreasing quality.

Moth and egg density will probably be poor indicators of larval density and injury, as no correlations were found between the recruitment levels of moths, eggs and larvae. The absence of these correlations is apparently due to the large variation in survival rates between the crops. Bandong & Litsinger (1988) tested the use of moth density as a basis for leaffolder control decisions, but concluded that it did not perform well. They suggested that this was caused by the activity of egg predators. However, the variability in the number of eggs per leaffolder moth may also be explained by moth behaviour. Rice leaffolder moths, being very sensitive to low humidity (Waldbauer & Marciano 1979, Wada & Kobayashi 1980), are shade-loving species (Lingappa 1972, Barrion et al. 1991a). While crops in the tillering stage are favoured for oviposition, the moths prefer a more developed crop or a weed vegetation as a habitat during daytime (Fukamachi 1983, Wada & Kobayashi 1991, Miyahara 1992, de Kraker unpublished). In an area of continuous and a-synchronous rice growing as in Laguna, moths may thus move between crops in different growth stages during a 24 h period. Observations in a comparable rice growing area in Malaysia support this view (Wada & Nik 1991). In case of such behaviour, moth density sampled during daytime will be poorly correlated with egg density in the same field.

Species composition of rice leaffolder complex

The rice leaffolder complex was composed of three species (*C. medinalis*, *M. patnalis*, *M. exigua*), varying in dominance. This is in line with earlier studies in Laguna Province (Arida & Shepard 1986, Barrion et al. 1991a). Separate analysis of the population dynamics of the three species is hampered by difficulties in the identification of immature stages. As the three species inflict similar injury and share the same natural enemy complex, there seems to be no urgent need for differentiation. However, to predict the effect of changes in rice growing practices, such as the introduction of resistant varieties, knowledge about their differential effect per species would be needed.

Need for chemical control?

The question whether the rice leaffolder populations in these untreated fields caused yield losses that justify chemical control cannot be answered directly, because yield loss studies were not included. In the Philippines, recommended action thresholds for rice leaffolder control are 5-15% injured leaves, or 0.5-1.0 larvae per hill (Bautista et al. 1984, Bandong & Litsinger 1988, Reissig et al. 1986). The higher and lower values represent the thresholds during the vegetative and reproductive stage respectively. However, these thresholds have been questioned on empirical and theoretical grounds, and values of 2, and even 5 larvae per hill have been suggested (Smith et al. 1989, Heong 1993). Counts of larvae are preferred over injured leaves as a basis for control decisions, as the leaffolds may not contain larvae any more and the injury cannot be reversed by spraying (Bandong & Litsinger 1988).

The larval population stayed below the conservative threshold of 0.5-1.0 larvae per hill in three out of eight crops (Fig. 3). In the other crops, this threshold was exceeded during the reproductive stage. However, in all crops the larval population peak stayed below the level of 2 $hill^{-1}$. Moreover, a considerable proportion of these larvae was parasitized (Table 4) and may have caused less injury than healthy larvae. In this study, parasitism of young larvae affected the survival to large larvae, thus decreasing the proportion of older larvae in the population. Parasitism of young larvae might therefore be the cause of the lower 'injured leaves to larvae ratio' in the dry season crops, as the major part of the injury is caused by the older larvae (Heong 1990).

Why are rice leaffolder densities so low in the Philippines?

The observations of the present study are consistent with the general pattern that emerges from studies over the last 15 years in insecticide-free rice fields from many different locations and seasons in the Philippines, both in terms of larval phenology and abundance (Kamal 1981, Guo 1990, Randriamananoro 1990, Barrion et al. 1991a). The time course and level of the percentage injured leaves was within the range determined by Litsinger et al. (1987a,b) in a large-scale yield loss study covering 60 rice crops. The observed levels of larval parasitism and the major species involved also correspond with earlier findings in the Philippines (Kamal 1981, Guo 1990, Arida & Shepard 1990, Barrion et al. 1991a).

Thus, rice leaffolder populations in Philippine rice fields rarely exceed larval densities of 2 hill^{-1}, while the percentage of injured leaves is almost always below 10-15%. A major explanatory factor for these low population levels might be the relatively late colonization of the transplanted rice fields. With an oviposition peak at maximum tillering and avoidance of oviposition after flowering, there is no time for a substantial second generation. Late colonization also implies that most generalist natural enemies are already present and relatively abundant, and may thus cause more mortality. The result is a relatively low carry-over to other crops (Loevinsohn 1984). According to this hypothesis, leaffolders could become more damaging when the attractive period for oviposition starts earlier or continues longer. For example when leaffolders would colonize the crop earlier, they might partly escape their natural enemies, and there would also be time for a second generation. This could be the case in direct seeded rice, where oviposition occurs at a much earlier crop stage compared with transplanted rice, probably due to the higher plant density (Chang 1993, de Kraker unpublished). Other examples are rice crops with a long growth duration, prolonging the period for leaffolder oviposition as well. In a long-duration variety with high inputs of N-fertilizer two egg peaks were observed before flowering and substantial leaf injury occurred (>30%, Chapter 2).

Leaffolder survival and the role of natural enemies

The average survival rate from egg to large larvae was 14% for five crops. The three crops with the lowest survival rates were also those in which leaffolders did not exceed the economic threshold level of 0.5 larvae per hill during the reproductive stage. The observed levels correlate well with the results of a survival analysis conducted by Kamal (1981) in eleven rice crops at IRRI, who found that survival from eggs to large larvae was between 12 and 20%. No other field studies on leaffolder survival in tropical Asia have been published. There are strong indications that a large part of the mortality is caused by natural enemies. The estimated survival rates for the field populations were much lower than for leaffolders reared on susceptible varieties when natural enemies were excluded: in greenhouse and field cages larval survival rates were 70-90% (Waldbauer & Marciano 1979, Kamal 1981, Barrion et al. 1991a). The difference in survival between the open field and the cages will mainly be caused by natural enemies, although a-biotic factors, like strong wind and rainfall in the wet season or low humidity in the dry season, may have caused some additional mortality in the field.

Rice leaffolder management can be improved when the effect of natural enemy densities on leaffolder infestations is known. Natural enemy abundance might be accounted for in the threshold for chemical control, or conservation measures could be taken to sustain natural control (Shepard & Ooi 1991). However, although the presented data set covers a fairly wide range in leaffolder densities and survival rates, and in levels of parasitism and natural enemy abundance, no clear relationships between these variables were found. This may be due to the generalist nature of most of the predators included in this study, rice leaffolders being only a minor part of their diet. The causes and effects of the diversity and abundance of these generalists will be primarily related to the numerically dominant prey or host species, as has been shown for spider and hemipteran predators and their homopteran prey species (Kenmore et al. 1984, Heong et al. 1991, Cohen et al. 1994). Not only most predators are generalists, also two of the most abundant parasitoid taxa (*Cotesia* spp. and *Tetrastichus* spp.) probably included species that have a fairly wide host range. Furthermore, parasitoid species that are not linked to rice leaffolder, but to other, more abundant hosts, may have been included in taxa that were only identified at genus level. This probably occurred with *Opius barrioni*, a common parasitoid of the abundant rice whorl maggot *Hydrellia philippina*.

Even in case of percentage parasitism, which is a more direct approximation of a mortality factor, relationships with leaffolder survival were not always clear. Parasitism of young larvae was correlated with survival from medium-sized to large larva, but egg parasitism was not correlated with survival from egg to medium-sized larva. Probably the impact of egg predation was relatively more important, and thus determining the variation in survival rates.

This study indicates that natural enemies inflict high levels of mortality on leaffolder immatures, but a different approach is needed to answer the question whether and which natural enemies can keep rice leaffolder populations below damaging levels at a given level of egg recruitment. To determine quantitative relationships between natural enemy abundance and leaffolder mortality, more experimental methods are required that study stage survival with known recruitment, and that separate the effects of various mortality factors (van Driesche 1983, Luck et al. 1988, Bellows et al. 1992). It will also be necessary to identify the major species within the large complex of leaffolder natural enemies, as for these species a relationship between abundance and impact on leaffolder survival can be expected.

Chapter 2

Impact of N-fertilization on the population dynamics and natural control of rice leaffolders

Abstract The effect of N-fertilization on the population dynamics and natural control of rice leaffolders was studied during the 1991 wet season in Laguna Province, the Philippines. Nitrogen was applied at three levels (0, 75 and 150 kg N ha^{-1}), and its impact on crop performance, arthropod abundance, and rates of leaffolder parasitism and survival was assessed with weekly samples.

Rice plants were taller and had a higher leaf N-content with increasing N-fertilization, but grain yield was highest at the medium N level. Herbivores, predators, and parasitoids increased in abundance with N-fertilization level. The average density of rice leaffolder larvae at the highest N level was eight times the density at zero N 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 N-fertilization on egg recruitment and survival of medium-sized larvae. The percentage parasitism of eggs and larvae was not affected by N-fertilization. The increase in survival of medium-sized larvae with N levels is probably due to the lower predator to leaffolder ratios. The generalist predators increased less in abundance with N-fertilizer level than did leaffolder immatures, resulting in lower levels of natural control.

The strong increase in infestation of rice leaffolders and other pests with N-fertilization level is probably the cause of the lower yield at the highest N level, as compared with the medium N level. In optimization of N inputs the effects on pest infestation should thus be taken into account. An increase in N-fertilization level over a wide area will not necessarily lead to a rise in leaffolder infestation, as the large increase in leaffolder larval densities in the present small-scale experiment was mainly due to oviposition preference for heavily fertilized plots.

Introduction

Since the mid-sixties rice leaffolders (*Cnaphalocrocis medinalis* 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). The shift from minor to major pest has been attributed to the adoption of new rice growing practices that accompanied the introduction of high yielding varieties (Kulshreshtha et al. 1970, Dhaliwal et al. 1985, 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 N-fertilizer on rice leaffolder infestation have been the topic of numerous studies. Rice variety *per se* seems an unlikely cause of increased leaffolder infestations, as only very few varieties have resistance against rice leaffolder, and modern varieties are generally not more favourable for population development than traditional cultivars (Heinrichs et al. 1985, 1986, Khan & Joshi 1990). A large number of field trials, however, show that increased N-fertilization usually leads to higher leaffolder injury levels (Fig. 1). The effects of N-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 N-fertilization affects fitness and feeding parameters of rice leaffolders (Table 1). As usual for herbivores (Mattson 1980), N appears to be a limiting factor for growth, reproduction and survival. The reported increase in leaffolder injury with N-fertilization level may thus have various causes, but the relative importance of these factors under field conditions is not known.

In insecticide-free fields with current farmer crop management practices, rice leaffolder infestations in the Philippines are generally low and natural control seems effective in keeping the infestation levels below the damage threshold (Litsinger et al. 1987a,b, Barrion et al. 1991a, Chapter 8). To meet the ever increasing demand for rice, however, the attainable yields will have to be raised, requiring higher N-fertilizer inputs (Kropff et al. 1994). As this increase in N 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 & Heong 1994).

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

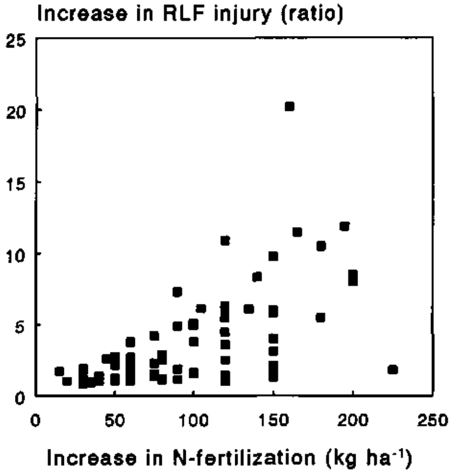


Figure 1. Relative increase in rice leaffolder injury as a function of the increase in N-fertilization: x-variable calculated as the difference between fertilizer treatment level *n* and the lowest fertilizer level in the trial, y-variable calculated as the ratio of the injury at treatment level *n* to the injury at the lowest level. Compiled from 15 published field trials (Balasubramanian et al. 1983, Chandragiri et al. 1974, Chandramohan & Jayaraj 1977, Chantaraprapha 1980, Dhaliwal et al. 1979, Michael Raj & Morachan 1973, Rajendran 1985, Rekhi et al. 1985, Saroja et al. 1981, Saroja & Raju 1982, Saroja et al. 1987, Subbaih & Morachan 1974, Swaminathan et al. 1985, Thakur & Mishra 1989, Upadhyay et al. 1981).

Table 1. Effects of N-fertilization on performance of rice leaffolders: (+) = significant increase, (−) = significant decrease, (0) = no significant effect, (?) = effect unknown. References: (1) Fukamachi 1980, (2) Liang et al. 1984, (3) Arida et al. 1990, (4) Dan & Chen 1990, (5) Fabellar & Heong 1991, (6) de Kraker unpublished.

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)	?	

[a] N effect inferred from tested effect of leaf age and position, leaf N-content leaves was not measured

[b] leaf biomass consumed per larval biomass

Materials and Methods

Location and lay-out of field experiment

The study was conducted during the 1991 wet season in a farmers' 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* (Guenée), *Marasmia patnalis* Bradley, and *M. exigua* (Butler) (Arida & Shepard 1986). The first two species are the most abundant in Laguna, and dominance by any one species can vary during a cropping season (Barrion et al. 1991a).

The experiment was laid out in a randomized complete block design, with three levels of N-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 nitrogen fertilization were 0, 75 and 150 kg N ha^{-1}, representing low, standard recommended, and high levels respectively. N-fertilizer was applied as ammonium sulphate in three split-doses over the season: 50% at 3 days after transplanting (DAT), and twice 25% at 21 and 35 DAT.

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 transplanted with 2-week old seedlings in a 20 × 20 cm spacing on August 31, 1991. Weeding was done by hand and pesticides were not applied. The field was intermittently flooded.

Crop growth, development and yield

Crop growth and development was assessed by taking hill samples every two weeks, starting one month after transplanting. Sample size was 12 hills per treatment. Plant height, number of tillers and leaves per hill, leaf colour and plant growth stage were recorded. Total leaf N-content (%) was determined with the Kjeldahl method, at three crop stages: tillering (33

DAT), panicle formation (58 DAT), and flowering (86 DAT). At maturity, yield was measured by harvesting 10 m^2 per plot. Grain yield was adjusted to 14% moisture content based on fresh weight.

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 one 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. 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 were taken per plot, with five sweeps as sampling unit. 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 the Philippine rice leaffolder foodweb (Barrion et al. 1991a, Cohen et al. 1994). The efficiency of sweepnet samples decreases markedly as the crop grows 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 checked 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. 1991a).

Parasitism

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. Calculation of the percentage egg parasitism was based on parasitism of apparently healthy eggs, excluding black parasitized eggs. No correction for a difference in duration of healthy and parasitized eggs has to be made, because the time till hatching of healthy eggs or turning black of parasitized eggs is the same. The seasonal percentage larval parasitism was calculated as the total number of parasitized larvae, divided by the total number of collected larvae of all stages, without further corrections. Percentage parasitism of eggs and larvae was calculated over the entire crop season, as well as over the first and second leaffolder population peak separately.

Survival rates

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. The sampling efficiency of the cryptic and tiny first instar larvae is very low, and so this stage was excluded from the survival analysis. Survival rates were calculated from egg to larva, egg to medium-sized larva (L2, L3), and from medium-sized larva to large larva (L4, L5, L6) for each plot and population peak separately. Data on pupal densities were not sufficient to include in the analysis.

The calculated stage to stage survival rates are only approximate values, primarily meant for comparison between treatments and correlation with potential mortality factors. Further details on the calculation of parasitism and survival rates are given in Chapter 1.

Results

Impact of N-fertilization on rice crop growth and arthropod abundance

Nitrogen fertilization had a clear impact on rice crop growth and development (Table 2). Plants were taller and darker green at higher fertilization levels. Leaf N-content was also positively correlated with N-fertilization level, although differences were only significant during the active tillering stage. The average tiller and panicle number per hill increased with N-fertilization level, but the effect was not significant due to large inter-plant variation. Grain yield per hill was highest in the medium N (75 kg ha^{-1}) treatment. Due to better water supply, the plants in the upper blocks near the irrigation canal were generally taller, had fewer tillers, a lower leaf N-content and a higher grain yield per hill, these last two block effects being significant.

Table 2. Effect of N-fertilization on rice crop characteristics: leaf N-content, tiller number, plant height and grain yield.

Crop parameter	Treatment level (kg N ha^{-1})			% change low-high	Significance [a]	
	0	75	150		treatment	block
Leaf N-content (% dwt)						
- active tillering	3.8	4.1	4.7	+24	**	*
- panicle initiation	3.0	3.2	3.5	+16	n.s.	n.s.
- heading	2.0	2.5	2.6	+30	n.s.	n.s.
Tiller number (no. per hill)						
- maximum	42	52	54	+29	n.s.	n.s.
- final	20	21	26	+30	n.s.	n.s.
Final plant height (cm)	78	87	91	+17	***	n.s.
Grain yield (g per hill)	15.1	17.5	16.4	+9	*	**

[a] n.s.=non-significant; *=$p<0.05$; **=$p<0.01$; ***=$p<0.001$ (ANOVA, count data log-transformed)

N-fertilization also had an impact on higher trophic levels. All four arthropod categories - pests, predators, parasitoids, and 'others' - increased in abundance with N-fertilization level (Table 3). For the parasitoids this effect was highly significant when sampled with sweepnet, but not significant with D-Vac sampling. Within the pest category, Homoptera and Heteroptera did not increase significantly, in contrast to Lepidoptera (adults) which increased about six times in average density (Table 3). Rice leaffolder moths comprised a large proportion of all Lepidoptera, which increased with N-fertilization level from 25 to 70%. Other common moths were *Rivula atimeta* (green hairy caterpillar), and *Scirpophaga incertulas* (yellow stemborer). The block effect on the number of Lepidoptera per sweepnet sample was highly significant: more moths were sampled in the upper blocks, where the plants were taller, and which were flooded longer.

The temporal pattern of pest abundance was very similar for the three treatments. During the first part of the crop season homopteran pest species (plant- and leafhoppers) dominated, while after the heading stage the hemipteran rice bugs (*Leptocorisa* spp.) were most abundant.

Table 3. Effect of N-fertilization on the abundance of rice arthropod groups. Seasonal average of D-Vac samples (no. per 4 hills).

Arthropod group	Treatment level (kg N ha^{-1})			% change low-high	Significance [a]	
	0	75	150		treatment	block
Pests	3.4	3.8	4.7	+38	*	n.s.
Homoptera	2.3	2.1	2.6	+13	n.s.	n.s.
Heteroptera	0.5	0.9	1.0	+100	n.s.	n.s.
Lepidoptera	0.1	0.2	0.6	+600	**	n.s.
Predators	5.0	6.6	8.2	+64	**	n.s.
Parasitoids	3.0	3.9	4.2	+40	n.s.	n.s.
Others	12.0	15.7	21.7	+81	**	n.s.

[a] n.s.=not-significant; *=$p<0.05$; **=$p<0.01$; ***=$p<0.001$ (ANOVA, count data log-transformed)

Population dynamics of rice leaffolders

Species composition *M. patnalis* was the dominant leaffolder species, both for moths and larvae (Table 4). Species composition depended on sampling method: in the moth samples (D-Vac, sweepnet) *M. exigua* was practically absent, while this species constituted a considerable proportion of the larval samples. N-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 N-fertilization level.

Table 4. 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).

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

[a] Effects on species composition with X^2-test: n.s. = non-significant, $p>0.05$; ** = $p<0.01$; *** = $p<0.001$

The species composition of leaffolder larvae and moths differed significantly per crop 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. The effect of N-fertilization on the species composition of leaffolder larvae was related to these differences in phenology. In all treatments *M. patnalis* was the dominant species during the later crop stages. As N-fertilization increased leaffolder density in particular during this period (Fig. 2), the overall seasonal species composition changed in favour of *M. patnalis*.

Table 5. Effect of N-fertilization on abundance of rice leaffolder stages and injured leaves, seasonal average of samples.

Leaffolder stage	(units)	Treatment level (kg N ha^{-1})			% change low-high	Significance [a]	
		0	75	150		treatment	block
Moths	(no. per 5 sweeps)	0.18	0.33	0.96	+433	*	n.s.
Moths	(no. per 4 hills)	0.03	0.11	0.46	+1433	*	n.s.
Eggs	(no. per hill)	0.13	0.25	0.60	+362	**	*
Larvae	(")	0.24	0.57	1.92	+700	**	*
Pupae	(")	0.01	0.02	0.06	+500	n.s.	n.s.
Injured leaves	(")	2.0	4.3	13.3	+565	**	n.s.

[a] n.s. = non-significant, $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$ (ANOVA, count data log-transformed)

Abundance and injury Densities of leaffolder moths, eggs and larvae increased strongly with N-fertilization level (Table 5, Fig. 2). The average larval density in the high N treatment was eight times the density in the zero N treatment. The average number of injured leaves per hill was positively correlated with larval density ($r = 0.99$, $df = 10$, $p < 0.001$), and leaf injury also increased with N-fertilization level. While the percentage of injured leaves did not exceed 10% in the zero and medium N treatment, it reached as high as 30-35% in the high N treatment during the ripening stage (Fig. 2).

Moth density peaked around 9 weeks after transplanting (WT), but the temporal pattern of moth abundance was not clearly linked to the phenology of the immature stages (Fig. 2). Based on the stage density data separated per treatment plot, the temporal abundance of leaffolder egg and larval stages was divided into two broad peaks, each lasting 30 to 35 days.

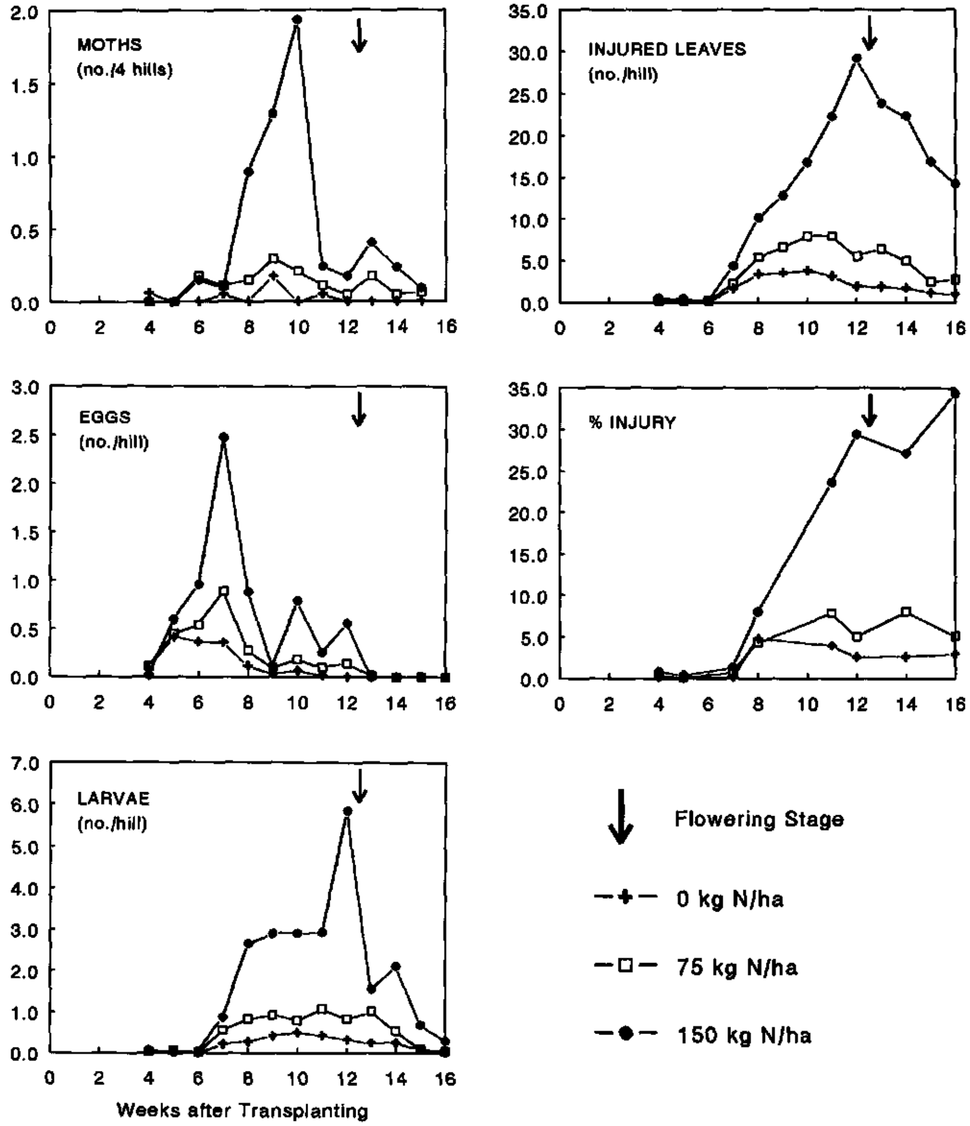


Figure 2. Mean densities of rice leaffolder moths, eggs, larvae, injured leaves and percentage injured leaves, at three levels of N-fertilization: 0, 75 and 150 kg N ha^{-1}. Standard errors were about 20% of sample means.

The larval peaks follow the peaks in egg abundance, the first occurring around 7 WT (maximum tillering) and the second around 11 WT (booting). The size of these peaks increased with N-fertilization level. These two larval peaks are difficult to distinguish in Figure 2, due to averaging of replicates and pooling of larval instars.

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 N treatment. This is most probably a result of the lower natural enemy density in this treatment.

Table 6. Effect of N-fertilization on abundance of natural enemies of rice leaffolders. Seasonal average of D-Vac samples (no. per 4 hills).

Natural enemy taxon	Treatment level (kg N ha^{-1})			% change low-high	Significance [a]	
	0	75	150		treatment	block
Predators:						
Coleoptera	1.81	2.35	2.92	+61	*	n.s.
Coccinellidae	1.18	1.40	1.36	+13	n.s.	*
Carabidae	0.35	0.49	0.85	+143	**	n.s.
Staphylinidae	0.28	0.46	0.73	+161	*	*
Orthoptera	0.66	1.14	1.48	+124	**	n.s.
Gryllidae	0.49	0.89	1.02	+108	**	n.s.
Tettigoniidae	0.16	0.25	0.48	+200	n.s.	n.s.
Hemiptera	1.14	1.74	2.35	+106	**	*
Araneae	1.17	1.16	1.10	−6	n.s.	n.s.
Parasitoids: [b]						
Hymenoptera - potential	1.48	2.18	2.41	+63	*	n.s.
Hymenoptera - major	0.12	0.24	0.43	+258	*	n.s.

[a] n.s. = non-significant, $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$ (ANOVA, count data log-transformed)

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

The abundance of most natural enemies of rice leaffolder increased with N-fertilization level (Table 6). The increase of the tettigoniid *Conocephalus longipennis* was not significant in the D-Vac samples, but highly significant in the sweepnet samples. 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 N-fertilization level, neither in the D-Vac nor in the sweepnet samples. Natural enemies increased less in abundance with N-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 (Fig. 3). As a consequence the natural enemy to leaffolder ratios decreased with N-fertilization level (Table 7). This effect was more pronounced during the second leaffolder population peak thanduring the first, in particular for the predators. Differences between treatments were smallest in case of specialist leaffolder parasitoids.

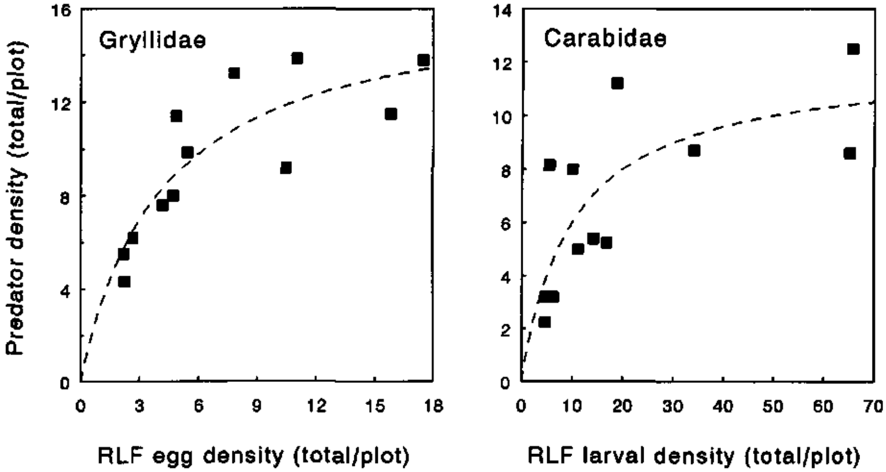


Figure 3. Seasonal total catch per treatment plot of predators (D-Vac samples) versus their rice leaffolder prey stage (hill samples): Gryllidae vs. leaffolder eggs and Carabidae vs. leaffolder larvae. Dotted lines are eye-fitted curves to indicate general trend.

Table 7. Effect of N-fertilization on the natural enemy to rice leaffolder (RLF) ratio, calculated over the entire season, as well as over the two population peaks separately. Ratios of average density per hill (D-Vac and hill samples).

Natural enemy:Leaffolder ratio		Treatment level (kg N ha^{-1})			% change low-high	Significance [a]	
		0	75	150		treatment	block
Predators [b]:RLF Moths	- season	45.74	11.11	2.94	−94	**	*
Predators [c]:RLF Immature	- season	2.39	1.57	0.67	−72	**	n.s.
	- 1st peak	1.51	1.19	0.62			
	- 2nd peak	4.12	2.15	0.74			
Predators [d]:RLF Immatures	- season	1.64	1.05	0.44	−73	**	n.s.
	- 1st peak	0.50	0.43	0.20			
	- 2nd peak	3.86	1.96	0.69			
Parasitoids [e]:RLF Larvae	- season	1.54	0.97	0.31	−80	**	n.s.
(Potential)	- 1st peak	1.63	1.08	0.40			
	- 2nd peak	1.46	0.88	0.26			
Parasitoids [f]:RLF Larvae	- season	0.12	0.10	0.06	−50	*	**
(Major)	- 1st peak	0.14	0.11	0.08			
	- 2nd peak	0.10	0.10	0.04			

[a] n.s. = non-significant, $p>0.05$; * = $p<0.05$; ** = $p<0.01$ (ANOVA, ratios log-transformed);
[b] Coleoptera, Orthoptera, Hemiptera; [c] Coleoptera, Orthoptera; [d] Araneae, Odonata;
[e] Hymenoptera recorded as RLF larval parasitoids; [f] Species accounting for 85% of observed parasitism

The temporal pattern of predator abundance was similar for the three treatments: the first two months after transplanting spiders and hemipterans were most abundant, after that coleopterans and orthopterans dominated. In addition to the natural enemy to leaffolder abundance ratios, also the degree of overlap in temporal occurrence between these natural enemies and their leaffolder prey was calculated (cf. van den Berg 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%).

Parasitism and survival of leaffolders in relation to N-fertilization level

Parasitism of leaffolder eggs and larvae Ten species of hymenopterous parasitoids were reared from the field-collected rice leaffolder eggs, larvae, and pupae (Table 8). Eggs were parasitized by *Trichogramma* sp. (probably *T. japonicum*), and *Copidosomopsis nacoleiae*. As the latter species only kills its host during the last larval stage, it is classified here as a larval parasitoid. The leaffolder larvae were parasitized by eight species. The braconids *Macrocentrus philippinensis* and *Cardiochiles philippinensis* were the most common parasitoids in the larval samples. Other common species were *Temelucha philippinensis*, *C. nacoleia* and *Trichomma cnaphalocrocis*. Notable differences between the three treatments concerning the distribution of parasitized larvae over the various parasitoid species, were the decreasing share of *T. philippinensis* with N-fertilization level, and the large share of *C. philippinensis* in the high N treatment (Table 8). This is related to their phenology:

Table 8. Parasitoid species reared from samples of rice leaffolder eggs, larvae, and pupae: (−)=absent, (+)=present. In brackets: percentage per species of total emerged larval parasitoids.

Family	Species	Host stage	Treatment level (kg N ha^{-1})		
			0	75	150
Trichogrammatidae	*Trichogramma* sp.	egg	+	+	+
Bethylidae	*Goniozus* sp.	larva	+ (3)	+ (4)	+ (2)
Braconidae	*Cardiochiles philippinensis*	larva	+(17)	+(17)	+(36)
	Cotesia spp.	larva	+ (7)	+(10)	+ (3)
	Macrocentrus philippinensis	larva	+(30)	+(32)	+(34)
Elasmidae	*Elasmus* sp.	larva	−	+ (2)	+(<1)
Encyrtidae	*Copidosomopsis nacoleiae*	egg-larva	+(13)	+(13)	+(12)
Ichneumonidae	*Temelucha philippinensis*	larva	+(23)	+(11)	+ (5)
	Trichomma cnaphalocrocis	larva-pupa	+(7)	+(11)	+ (8)
Eulophidae	*Tetrastichus* sp.	pupa	−	−	+
			(100)	(100)	(100)

T. philippinensis was practically absent during the second larval peak, when the differences in density between the treatments increased, while *C. philippinensis* was then the dominant parasitoid.

Seasonal percentages of parasitism of leaffolder eggs and larvae were independent of N-fertilization level (Table 9). Both egg and larval parasitism (%) decreased with crop age, and thus parasitism was usually lower during the second population peak than during the first (Table 9). Percentage egg and larval parasitism was 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.

Table 9. Effect of N-fertilization on parasitism and stage survival of leaffolder eggs and larvae, calculated over the entire season as well as over the two population peaks separately. Effect on %parasitism of separate population peaks was not tested because of low numbers.

		Treatment level (kg N ha^{-1})			Significance [a]	
		0	75	150	treatment	block
Percentage parasitism						
Egg parasitism	- season	16.1	20.2	13.1	n.s.	n.s.
	- 1st peak	17.1	21.8	13.0		
	- 2nd peak	0.0	0.0	14.3		
Larval parasitism	- season	33.7	31.3	37.9	n.s.	n.s.
	- 1st peak	50.0	46.5	48.8		
	- 2nd peak	11.9	10.0	30.2		
Stage to stage survival rate						
Egg - Medium Larva	- season	1.08	1.08	0.97	n.s.	n.s.
	- 1st peak	0.54	0.56	0.55	n.s.	n.s.
	- 2nd peak	4.53	5.13	3.32	n.s.	n.s.
Medium - Large Larva	- season	0.23	0.29	0.66	*	n.s.
	- 1st peak	0.29	0.33	0.55	*	n.s.
	- 2nd peak	0.20	0.25	0.77	*	n.s.

[a] n.s. = non-significant, $p>0.05$; * = $p<0.05$; ** = $p<0.01$ (ANOVA, ratios log-transformed)

Stage to stage survival Survival from egg to medium-sized larva was similar for all N-fertilization levels, both for the first and second leaffolder population peak (Table 9). Survival from medium-sized to large larva increased markedly with N-fertilization level. Separate survival analysis of the two population peaks shows that this increase was highest in the second period. Survival rates from egg to medium-sized larvae were much larger than one during the second peak, indicating that the sampling efficiency of leaffolder eggs on older, taller plants was 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 survival rates were negatively correlated with natural enemy to leaffolder (immature or larvae) ratios, and positively correlated with average density of eggs and medium-sized larvae.

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:

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

Figure 4 shows the values of log (N_{LL}) and the three terms of the equation for all twelve treatment plots. To determine which of the three terms alone explains most of observed variation in abundance of large larvae, correlation coefficients were calculated between $\log(N_{LL})$ and each of the terms, for both leaffolder population peaks separately and combined. In none of the three cases the survival from egg to medium-sized larva explained a significant part of the variation. During the first population peak, abundance of large larvae was best correlated with egg recruitment (r^2=0.92), and during the second peak with survival from medium-sized to large larva (r^2=0.89). The overall variation in abundance of large larvae was best explained by egg recruitment (r^2=0.93). 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, the major determinant of the density of large larvae during both population peaks appears to be egg recruitment.

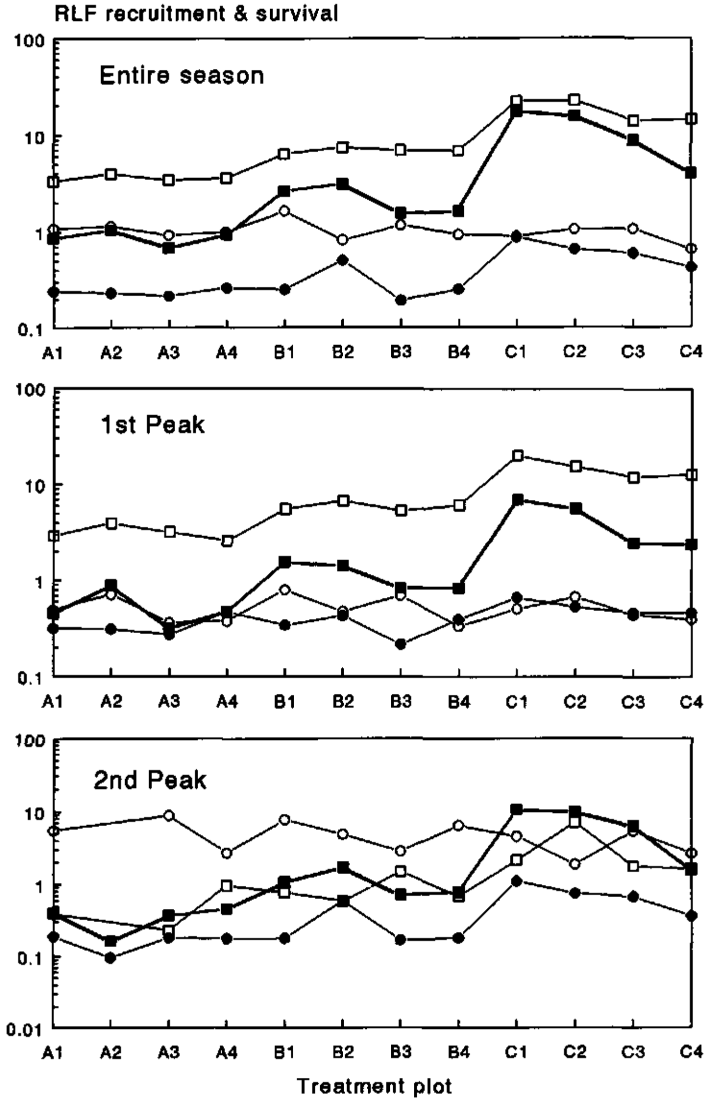


Figure 4. Levels of egg recruitment N_{EGG} (□), large larval recruitment N_{LL} (■), survival from egg to medium-sized larva S_{EGG} (○), and survival from medium-sized to large larva S_{ML} (●) per treatment plot. Treatment levels A, B, C represent 0, 75, 150 kg N ha^{-1} respectively, with four replicates per treatment (1-4).

Discussion

Impact of N-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 (Table 2 and 3), suggesting that the system is N-limited (White 1979). N-fertilization increased the production of rice plant biomass and enhanced leaf N-content, thus forming the basis for the increase in rice pest herbivore abundance (Table 3). The additional N-supply probably also led to increased production of algae and other microflora in the floodwater and on the soil surface (Craswell & Vlek 1979), supporting higher populations of Diptera with aquatic larval stages, comprising most of the 'other' category (Roger et al. 1994). In turn, predators and parasitoids, the third trophic level, responded numerically to the increased abundance of their herbivore prey. The relatively limited increase in Homopteran pest species with N-fertilization level (Table 3), might be due to host plant resistance of IR70 to several of these species. In all treatments their average densities were relatively low (cf. Heong et al. 1992). This may, however, also indicate the effectiveness of natural control of homopteran rice pests in insecticide-free rice fields, even at high fertilization levels. Fredrix et al. (cited in: Kenmore 1991) showed that the initially high egg recruitment of planthoppers in fields with a high fertilization level did not result in increased densities of nymphs, probably due to the numerical response of the predator *Cyrtorhinus lividipennis*. In the present study, the densities of *C. lividipennis* increased with N-fertilizer level, suggesting a similar numerical response.

Response of rice leaffolder populations to N-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. Chapter 1), and about six times higher than the peak density in the plots with a standard (medium) fertilization level (Fig. 2). Recommended economic thresholds (Bautista et al. 1984, Bandong & Litsinger 1988, Smith et al. 1989, Heong 1993) for rice leaffolder control were all exceeded in the high N treatment, both in terms of percentage injured leaves and larval densities.

A number of possible explanations for the increase in rice leaffolder injury with N-fertilization level can be discarded in the present study. As the number of injured leaves was linearly correlated with larval density, the effect of fertilization 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 N-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 the leaffolder moths and the proximity of the treatment plots. The major effects of N-fertilization on rice leaffolder 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 (Fig. 4), the most injurious stage of rice leaffolder.

Rice leaffolder egg recruitment Egg recruitment explained most of the overall variation in large larval abundance between the treatment plots. N-fertilization level had a strong positive effect on average egg density (Table 5). This phenomenon has been observed before, both in small and large-scale experiments with *C. medinalis* (Fukamachi 1980, de Kraker unpublished). *M. patnalis* and *M. exigua* apparently have a similar oviposition response, as larval densities of all three species increased with N-fertilization level. Increased egg recruitment is probably a result of an aggregation of ovipositing females in well-fertilized plots (preference), as well as an increase in the number of eggs laid per female. Oviposition experiments with small plots fertilized with different levels of N, indicated that preference was the major cause of the increase in egg density from medium to high N levels (de Kraker unpublished).

Rice leaffolder larval survival Not only egg recruitment, but also survival rates were significantly affected by the level of N-fertilization, notably the survival from medium-sized to large larva (Table 9). This effect might be either direct, by enhancing larval survival through improved host plant quality, or indirect, through the impact of natural enemies. Without a more experimental approach it will be difficult to separate direct and indirect effects. Dan & Chen (1990) reported a direct effect of N-fertilization on *C. medinalis* larval survival in pot experiments, but they did not specify the magnitude of this effect. Own observations suggest that this effect is small within the range in leaf N-content of the present study. A closer look at the field data indicates that a direct effect of host plant quality is unlikely. Around heading, differences in leaf N-content were not significant anymore, while differences in larval survival were greatest. Furthermore, while leaf N-content tended to be higher in the lower blocks, larval survival was generally lower.

N-fertilization may also have indirect effects on larval survival through the impact of natural enemies (Price et al. 1980). Better nutrition can reduce the larval development period, and thus decrease the risk of attack. However, the effect of N-level on the larval development period of leaffolders is small (Dan & Chen 1990, de Kraker unpublished), and, as mentioned before, 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 N-fertilization levels, due to the higher crop density and larger leaf area (e.g. Chapter 3 and 5). This might indeed have contributed to the increased larval survival in the high N treatment, but does not explain the large difference with the medium N treatment, as differences in crop density and height between these treatments were relatively small (Table 2).

Most likely, the increase in survival of medium-sized larvae with N-level is due to the less-than-proportional increase in leaffolder natural enemies, reflected in the decrease in the natural enemy to leaffolder ratios (Table 7). Leaffolder egg density increased more than 350% from the zero N to the high N level, while the density of most natural enemy groups increased less than 200% (Table 3 and 4). 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 primarily dependent on general prey density, which increased less dramatically with N-level than leaffolder density (Table 2). As expected, the numerical response of specialists, such as the major larval parasitoids, was relatively high (Table 6). 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 egg and larval parasitism were independent of leaffolder density and fertilization level (Table 9). 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 might 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 on successful settling of young larvae might be a more important, density independent factor, especially during periods of heavy rainfall (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 larva (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 N treatment.

Implications for integrated crop management

Modern rice varieties are highly responsive to N-fertilization (Yoshida 1981). Apart from raising the attainable yield level, increased N-supply can make the crop more tolerant 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) reported that the percentage yield loss due to insect pests (planthoppers, stemborers and leaffolders) was positively correlated with N-fertilizer level. Inoue & Fukamachi (1990) found that in unsprayed plots the infestations of planthoppers and leaffolder increased with N-level, while the yields were the same for both low and high N-level. In insecticide-protected plots yields were significantly higher in the high N treatment. Also Saroja et al. (1987) noted that in untreated plots rice leaffolder infestation rose sharply at high N-levels, while yields were not significantly different. In the present study, grain yield per hill was highest in the medium N treatment, although crop biomass and N-content were higher in the high N treatment (Table 2). The high pest infestation levels in the latter treatment may well be the cause of this discrepancy (Chapter 8).

In an integrated crop management approach, optimization of N-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 N-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). Crop growth models can be very helpful to optimize nitrogen management. Such models can incorporate not only the effect of level and timing of N-fertilization on crop yields (Thiyagarajan et al. 1995), but also the effect of different pest infestation levels on yield (Rossing et al. 1993, Chapter 8).

Effect of large-scale N-fertilization on rice leaffolder infestation

The present study and the others summarized in Figure 1 were all small-scale, one-season experiments. What would the effect on rice leaffolder infestation be, if the N-fertilization level was raised over a large spatial and temporal scale ? The strong effect of N-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 N-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 importance of other effects of N-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 will probably result in higher intrinsic rates of increase of rice leaffolders. Whether these rates can be realized depends on the nature of the mortality factors, such as natural enemies. When mortality factors are not proportionally and positively density dependent, leaffolders will become more abundant. Their increased potential for population growth may also lift them more easily above the 'natural enemy ravine' (Southwood & Comins 1976, McNeill & Southwood 1978, Price et al. 1980). This implies that leaffolder outbreaks may occur more frequently, especially when natural enemies suffer relatively more from the use of broad-spectrum insecticides or from adverse weather conditions (e.g. Rajapakse & Kulasekare 1982, Patel et al. 1987, Qadeer 1988). In this way, the wide-spread adoption of chemical nitrogenous fertilizers has probably contributed to the reported increase in leaffolder abundance and outbreak frequency since the mid-sixties (Khan et al. 1988). In unsprayed fields, however, current levels of N-fertilization do generally not result in leaffolder population levels causing economic damage (Chapter 1 and 8). Way & 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 N-fertilization level. In the present study, the abrupt N-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 N-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).

Concluding remarks

The present experiment confirms the finding of previous research that in a choice situation leaffolder infestations increase with the level of N-fertilization. In this experiment, 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 N-level, while larval survival increased. At a single field scale, the effect of relatively high N-levels on leaffolder infestations may be reduced by adapting the timing and method of N-application. An increase in the spatial scale over which high levels of N are applied will probably also reduce the leaffolder density response, which appears mainly based on preference. Both aspects indicate options to optimize N-fertilization for agronomic as well as pest management objectives in an integrated approach to crop management.

Chapter 3

Rice leaffolder egg mortality in irrigated rice fields

Abstract Egg mortality of rice leaffolders *Cnaphalocrocis medinalis* and *Marasmia patnalis* was studied in unsprayed irrigated rice fields in Laguna Province, Philippines. Mortality was assessed by field exposure of laboratory-laid eggs for two days and by monitoring of naturally-laid eggs. Egg disappearance, the major mortality factor, was low in the first four weeks after transplanting and then increased. Eggs were parasitized by *Trichogramma japonicum* (Hymenoptera: Trichogrammatidae). Parasitism was highest at the start of the crop and decreased to a low level towards maturity. Non-hatching was of minor importance. Over the total duration of the egg stage, the average disappearance of exposed laboratory-laid eggs was 40% (6 crops), and of naturally-laid eggs 46% (4 crops). Egg mortality due to parasitism averaged 15% and 18% respectively. The potential impact of egg parasitism is probably partly obscured by the disappearance of parasitized eggs.

A high level of egg disappearance was correlated with high densities of predatory crickets *Metioche vittaticollis* and *Anaxipha longipennis* (Orthoptera: Gryllidae). Disappearance of exposed laboratory-laid eggs was in addition negatively correlated with the egg density on exposed hills, while disappearance of naturally-laid eggs was also positively correlated with average leaffolder egg density and total rainfall. Percentage parasitism of exposed leaffolder eggs was positively correlated with the density of *Trichogramma* host eggs in the field, and negatively correlated with crop leaf area and wind speed. The possible causal mechanisms underlying these correlations are discussed.

Introduction

Since the mid-sixties rice leaffolders *Cnaphalocrocis medinalis* and *Marasmia* spp. (Lepidoptera: Pyralidae) have increased in abundance in intensified rice growing areas, and in many Asian countries they are now considered as important pests (Reissig et al. 1986, Khan et al. 1988). Rice leaffolder larvae cause conspicuous injury by folding leaves and scraping off the green mesophyll tissue (Fraenkel & Fallil 1981, Fraenkel et al. 1981). In Asia, a major part of early-season insecticide applications in rice is targeted against leaf-feeding insects, of which rice leaffolders are the main species (Heong et al. 1994). However, most sprays may not be justified as modern rice varieties can tolerate a substantial amount of defoliation without suffering yield loss (e.g. Hu et al. 1993, IRRI 1993). Moreover, leaffolders have a large natural enemy complex which may keep them below economic damage levels most of the time (Khan et al. 1988). For example, in Philippine rice fields more than 80 predator species and over 50 parasitoids of rice leaffolders have been recorded (Barrion et al. 1991a). Studies of rice leaffolder population dynamics in Philippine rice fields indicated that a large proportion of immature mortality could be attributed to natural enemies (Kamal 1981, Chapter 1). To develop leaffolder management strategies that make optimal use of the naturally-occurring predators and parasitoids, more insight is needed in how leaffolder mortality relates to the abundance of natural enemy groups or species (Shepard & Ooi 1992). Field sampling of rice leaffolders and their natural enemies did not provide sufficient data to determine such relationships (Chapter 1). More experimental methods are required that study stage survival with known recruitment, and that separate the effects of various mortality factors (van Driesche 1983, Luck et al. 1988, Bellows et al. 1992). It will also be necessary to identify those species within the large complex of natural enemies, that cause the major part of the mortality, as for these species a relationship between abundance and impact on leaffolder survival can be expected (Shepard 1989).

Egg mortality can play an important role in suppressing rice leaffolders to below damaging levels, because it acts before the larval stages that cause the damage. Research by Arida and Shepard (1990) showed that mortality of leaffolder eggs can be quite high: in transplanted rice they found maxima of 90% disappearance and 85% parasitism during two days of field exposure. The mortality levels due to both factors were quite variable throughout the year, but factors explaining this variability were not identified.

This chapter reports on a study of field mortality of rice leaffolder eggs under a wide range of conditions, by exposure of laboratory-laid eggs and by monitoring naturally-laid eggs. The objective was to assess the levels of egg mortality inflicted by various factors, and to analyze variation in these mortality levels in relation to weather conditions and the density of eggs and various predator groups. The results of such a mortality analysis at field level can be used to provide hypotheses for further research on the causal factors and underlying mechanisms.

Materials and Methods

Field sites

The study was conducted in Laguna Province, the Philippines, a humid tropical lowland area where rice is grown year-round under irrigated conditions. The rice leaffolder population in Laguna Province is a complex of three related species: *Cnaphalocrocis medinalis* (Guénee), *Marasmia patnalis* Bradley, and *M. exigua* (Butler). The first two species are the most abundant in Laguna, and dominance by any one species can vary during a cropping season (Barrion et al. 1991a, Chapter 1).

Fieldwork was carried out in three lowland rice fields. One field was located at the experimental farm of the International Rice Research Institute (IRRI) in Los Baños (13°14'N, 121°15'E). The two other sites (Pila and Victoria) were farmers' fields at 15-20 km distance from IRRI. The fields were transplanted in a 20 × 20 cm spacing with 2-week old seedlings of a variety susceptible to rice leaffolder. The crops were fertilized with about 90 kg N ha^{-1}, according to standard recommendations. Weeding was done by hand and no pesticides were applied. The IRRI field was kept permanently flooded until a week before harvest, while the farmers' fields in Pila and Victoria were intermittently flooded. Further details on the field studies are given in Table 1.

Insect sampling and collection of crop and weather data

The densities of potential predators and insect eggs were estimated by sampling on the day before or after assessment of egg mortality (Table 1). Predator populations were sampled with a suction sampler (D-Vac or Blower-Vac, Arida & Heong 1992) in combination with a plastic bucket enclosure, covering four hills. To include fast-moving insects like orthopterans, the enclosure was placed abruptly over the hills. Suction samples were taken between 8.00 and 11.00 a.m. The samples were sorted using a dissecting microscope and predators were identified to genera or species. Egg densities were estimated by random sampling of rice hills. In the laboratory the plants were checked for the presence of eggs of leaffolders and other lepidopteran or dipteran hosts of *Trichogramma* spp. (Table 2).

Table 1. Rice leaffolder egg mortality studies in irrigated rice fields, Laguna, Philippines. Units of sampling methods: hill samples = 1 hill, suction samples = enclosure covering 4 hills.

Location	Area (ha)	Variety	Season – year	Transplanting date	Time of exposure/marking (week after transplanting)	Exclusion cages	Sample size	
							Hill	Suction
(a) Exposure of laboratory-laid eggs								
Victoria	0.49	R-10	1991 dry	12 January	3, 6, 9, 12	yes	50	25
Pila	0.62	C-4	1991 dry	4 January	4, 7, 10, 13, 15	yes	50	25
Pila	0.34	IR72	1993 dry	4 February	4, 5, 6, 7, 8, 10, 13	yes+insecticide	65	25
Pila	0.34	IR72	1993 wet	16 August	4, 7, 9, 12	no	50	30
IRRI	0.25	IR72	1992 wet	23 June	3, 5, 7, 9, 11, 13	yes+insecticide	30	15
IRRI	0.25	IR72	1993 wet	17 July	8, 9	no	50	30
(b) Monitoring naturally-laid eggs								
Pila	0.08	IR70	1991 wet	31 August	5, 7, 10, 12	–	15	6
Pila	0.34	C-4	1992 dry	27 January	5, 6, 7, 8, 9	–	100	24
Pila	0.14	IR72	1993 dry	4 February	6, 7, 8	–	35	15
IRRI	0.12	IR72	1993 wet	17 July	7, 8	–	25	15

Concurrently with sampling for insect eggs, 15-20 hills per field were randomly collected and the leaf area per hill was measured with an electronic leaf area meter (LI-COR LC3100). Daily weather data, viz. total rainfall, average temperature and average wind speed, were obtained from the wetland weather station at IRRI.

Field assessment of egg mortality

Two methods were applied to assess mortality of leaffolder eggs in the field (Table 1): field exposure of laboratory-laid eggs in six rice crops (14,600 eggs exposed in 28 cohorts) and monitoring of naturally-laid eggs in four rice crops (2,000 eggs in 14 cohorts). The latter, less manipulative method was used as check and alternative to the first method, but could not be applied when leaffolder egg density was very low (< 0.05 eggs per hill).

Exposure of laboratory-laid eggs Plants with leaffolder eggs were obtained by caging field-collected female moths with potted rice plants overnight in the laboratory. The following day the newly-laid eggs were counted and marked. The field-collected leaffolder moths used for oviposition were a mixture of *C. medinalis* and *M. patnalis*. The exposed rice plants were always of the same age and variety as the plants in the field. The number of eggs on the exposed plants ranged from 1 to 60, and between cohorts the average egg density varied from 3.5 to 28.4 per plant. The number of exposed rice plants ranged from 11 to 55 per exposure. Both the number of plants per exposure and the average egg density depended on the availability of female leaffolder moths and their oviposition rate. The egg-bearing plants were usually taken to the field inside a closed van, but in the 1991 dry season they were transported in a semi-open pick-up truck. The majority of the potted plants was randomly distributed over the rice field. The remaining part, representing 20-50% of all exposed leaffolder eggs, was placed in exclusion cages. These predator exclusion cages (1.5 × 1.5 × 1.5 m), made from nylon or fibreglass mesh, had been placed in the fields right after transplanting with their sides sealed in the mud. During the 1992 wet season (WS) at IRRI and the 1993 dry season (DS) in Pila, a broad-spectrum insecticide was sprayed inside the cages in between the exposures.

After two days of field exposure all plants were retrieved and the fate of the eggs was checked in the laboratory. The recovered eggs were held in test tubes to check for parasitism and non-hatching. Parasitism by the egg-larval parasitoid *Copidosomopsis nacoleiae* was not recorded as egg mortality, because the parasitized eggs still hatch and the parasitoid kills its host not before the last larval stage. According to Arida & Shepard (1990), this parasitoid accounts for less than 5% of leaffolder egg parasitism in Laguna.

Monitoring naturally-laid eggs In randomly selected parts of the field, the rice hills were searched for leaffolder eggs. The position of the eggs on the leaf was marked using a waterproof felt-tip pen. A hanging label was put around the stem and the position of the hill was marked with a numbered bamboo stick. In this way individual records could be kept for each egg. Marked eggs were checked daily to record their fate: disappeared, unhatched, hatched, or coloured black (= parasitized). Observations were continued for seven days. Eggs still unhatched at that time were considered not viable.

A reliable visual estimation of the age of the leaffolder eggs was not possible in the field until the blackhead stage, i.e. less than 12 hours before hatching. Consequently, the marked eggs did not represent a cohort of eggs laid on the same day, but differed in age from newly-laid to more than three days old. Yet, for convenience they will be referred to as egg cohorts, laid in the same week. The number of marked eggs ranged from about 50 to 300 per cohort, depending on egg density in the field and available labour.

Calculation of egg mortality rates

Before the mortality rates of the laboratory-laid or naturally-laid cohorts can be compared and included in a single analysis, several biases inherent to the methodology must be removed. This involved: correction of the percentage disappearance of laboratory-laid eggs for egg loss during handling and transport, calculating the percentage parasitism of laboratory-laid eggs independent of egg disappearance, and correcting the egg mortality rates of naturally-laid eggs for the variation in average age at marking. These calculations were based on the assumptions that (1) the egg disappearance rate, either due to predators or abiotic factors, was the same for healthy and parasitized eggs, until the latter turn black, and (2) daily rates of disappearance or parasitism were constant during the entire egg stage, which takes about four days for both *C. medinalis* and *M. patnalis* (Barrion et al. 1991a).

Disappearance of laboratory-laid eggs Egg disappearance on field-exposed plants may be overestimated due to dislodgement of the laboratory-laid eggs during handling and transport. On plants placed inside the insecticide-treated exclusion cages egg disappearance was only 0-4%, and was always lower than disappearance on field-exposed plants. The cages protected the eggs not only from predators, but also from the impact of strong wind and rain. Thus, egg disappearance on these caged plants was probably exclusively due to transport and handling. Per crop, the percentage disappearance on field-exposed plants was corrected for this effect by subtracting the average percentage lost on the caged plants. During the exposures in Pila 1993-WS and IRRI 1993-WS no cages were used, therefore the values of the preceding seasons were taken. In 1991-DS (Victoria and Pila), when the plants were transported in a pick-up truck, the exclusion cages were not sprayed with insecticide and therefore not effective in excluding all the predators. For this season, egg loss due to transportation was therefore estimated by taking egg-bearing plants at different growth stages back and forth to the field with the pick-up truck. Probably due to mechanical abrasion by wind-blown leaves, the egg loss during transport in the pick-up was considerably higher than in the closed van, and ranged from about 5% before flowering to 25% at maturity.

Parasitism of laboratory-laid eggs The percentage parasitism on exposed plants used in the regression analysis was based on the number of recovered eggs. Due to disappearance of parasitized eggs during field exposure, calculation of the percentage parasitism with the total number of exposed eggs would underestimate the potential importance of egg parasitism, and make its value dependent on the percentage egg disappearance. Yet, for the 4-day egg mortality levels, the percentage parasitism was based on the total number of exposed eggs, so that egg parasitism and disappearance were calculated as additive values.

Mortality of naturally-laid eggs To compare egg mortality across cohorts, the rates should be corrected for the differences in exposure period resulting from the variation in average age at marking. The average age of the egg cohorts at marking (T_m) was calculated from the mean duration until hatching of the survivors (T_h, Table 3b), and the total mean duration of the egg stage (T_d):

$$T_m = T_d - T_h$$

A daily rate of egg disappearance (r_{dis}) per cohort was calculated as a weighted average of the daily disappearance of unhatched eggs during the first three days after marking. For each cohort a hypothetical 'original' cohort size (N_0) could then be computed, based on the number of marked eggs (N_m), the age of the cohort (T_m), and the daily egg disappearance rate (r_{dis}):

$$N_0 = N_m / (1 - r_{dis})^{Tm}$$

The adjusted mortality rates over the total egg stage duration were based on N_0. This resulted in lower rates of parasitism and non-hatching and in higher rates of disappearance, because the eggs of the cohort that disappeared before marking (N_0 - N_m) were now included.

Correlation and regression analysis

The observed leaffolder egg mortality was correlated with other measured variables, such as egg and predator densities, and weather variables. Identification of variables that statistically explain a significant part of the observed variation in mortality can be helpful to provide hypotheses for research on the underlying causal mechanisms.

(1) For exposed laboratory-laid egg cohorts, simple linear correlation coefficients were computed between the number of disappeared or parasitized eggs, and the number of exposed or recovered eggs per hill. The same was done with the percentage disappeared or parasitized eggs per hill. Exposed cohorts with very low rates of disappearance or parasitism (<5%) were excluded from the analysis.

(2) The variation in egg mortality rates of the laboratory and naturally-laid cohorts was analyzed with multiple linear regression. The analysis started with a so-called 'maximal model', i.e. a model containing as regression terms all the measured variables that might explain the observed variation in mortality. Non-significant regression terms were removed from the maximal model by backward elimination. The resulting 'minimal adequate model' contained only the significant explanatory variables. For the daily percentage disappearance of naturally-laid eggs, nine explanatory variables were included in the maximal model: densities of four predator groups (Table 2), natural leaffolder egg density, crop leaf area, and three weather variables (daily rainfall, average wind speed, average temperature). Carabid and staphylinid predators were treated as one group because of their low densities. The maximal model for the (corrected) percentage disappearance of exposed laboratory-laid eggs

Table 2. Species included in the explanatory variables for multiple regression analysis of disappearance and parasitism of rice leaffolder eggs.

Variable	Species included	References
Gryllidae	*Anaxipha longipennis* [a,c]	Bandong & Litsinger 1986,
	Metioche vittaticollis [a]	Rubia & Shepard 1987
Tettigoniidae	*Conocephalus longipennis* [a]	Rubia et al. 1990
Coccinellidae	*Micraspis* spp. [a,c]	Bandong & Litsinger 1986,
	(incl. *M. crocea, M. hirashimai*)	Rubia et al. 1990
	Harmonia octomaculata [a]	"
	Coccinella repanda [b]	van den Berg et al. 1992
Carabidae	*Ophionea nigrofasciata* [b,c]	van den Berg et al. 1992
	Ophionea ishii ishii [a]	He 1986
Staphylinidae	*Paederus fuscipes* [a,c]	Pang et al. 1984
	undet. Staphylinidae [b]	Barrion et al. 1991b
Host Eggs	*Cnaphalocrocis medinalis*	Barrion et al. 1991a
T. japonicum	*Marasmia* spp.	"
	Chilo suppressalis	Perez & Cadapan 1986
	Scirpophaga incertulas	"
	Naranga aenescens	van den Berg et al. 1988
	Rivula atimeta	"
	Sepedon sphegea	van Vreden & Ahmadzabidi 1986

[a] accepted rice leaffolder eggs as prey
[b] accepted eggs of other lepidopterous rice pests as prey
[c] most common species in this group

included the average egg density on the exposed plants in addition to the nine variables mentioned above. For the percentage parasitism determined by egg exposure, the maximal model included the three weather variables, crop leaf area, the average egg density on the exposed hills, and the total host egg density. Host eggs included rice leaffolder eggs and eggs of several other species, recorded as host to *Trichogramma* spp. (Table 2). No such analysis was done for the daily rate of parasitism of naturally-laid eggs, because an important explanatory variable, total host egg density, was not determined during most of the natural egg cohort studies.

(3) In addition to multiple linear regression, simple linear correlation coefficients were computed between the percentage egg disappearance and all possible combinations of predator groups, with their pooled densities as a single variable. This was conducted for both laboratory- and naturally-laid egg cohorts to determine which combination of predator groups correlated best with the egg disappearance rates.

All statistical analyses were carried out with the GLIM package (Crawley 1993). Percentage data were analyzed by weighted regression with binomial errors (logit-linked). Overdispersion (large residual errors) was corrected for by using William's procedure. Significance of regression terms in backward elimination was assessed by the F-test for increase in (scaled) deviance ($\alpha=0.05$). Deviance is a measure to assess the goodness of fit of the regression model.

Results

Rice leaffolder egg mortality

Eggs disappeared, remained unhatched or were parasitized by *Trichogramma japonicum* (Hymenoptera: Trichogrammatidae) in almost all of the exposed laboratory-laid or naturally-laid leaffolder egg cohorts, but the percentage disappearance, non-hatching or parasitism per cohort was highly variable (Table 3). After (1) correcting the percentage disappearance of exposed laboratory-laid cohorts for egg loss during transport and handling, (2) basing the percentage parasitism of exposed laboratory-laid eggs on the number of recovered eggs instead of initial egg density, and (3) adjusting the natural cohort mortality levels to a standard egg duration of four days, variation between cohorts remained high (Fig. 1 and 2). Yet, despite the large variation, some general trends in the level of egg disappearance and egg parasitism during a cropping season can be distinguished (Fig. 1). Egg disappearance was low during the first four weeks after transplanting (WT) and then increased to a higher level. Egg parasitism was high at the start of the crop, but decreased to very low levels towards crop maturity, at about 15 WT. Mortality of naturally-laid egg cohorts (Fig. 2) could

Table 3. Fate of rice leaffolder eggs in rice fields, Laguna Province, Philippines. %DIS, %PAR, %UNH = percentage of initial number disappeared, parasitized, or failed to hatch. WT = weeks after transplanting.

a. Laboratory-laid eggs, exposed for 2 days

Location	Year-season	Crop age (WT)	Exposed (no.)			Egg mortality		
			Hills	Eggs	Eggs/hill	% DIS	% PAR	% UNH
Victoria	1991-DS	3	20	70	3.5	12.9	14.3	11.4
		6	36	208	5.8	39.9	3.4	13.0
		9	42	548	13.0	35.4	4.7	5.3
		12	50	1014	20.3	50.4	3.4	4.2
Pila	1991-DS	4	28	133	4.8	6.8	30.8	18.8
		7	36	408	11.3	36.8	11.5	5.1
		10	40	521	13.0	38.2	5.0	8.6
		13	41	444	10.8	39.4	2.0	3.2
		15	41	322	7.9	75.5	0.0	2.5
Pila	1993-DS	4	30	560	18.7	5.0	14.1	14.5
		5	30	688	22.9	18.3	18.8	12.2
		6	31	556	17.9	14.9	25.5	0.9
		7	26	501	19.3	15.8	16.6	1.4
		8	29	515	17.8	19.8	10.1	0.4
		10	23	561	24.4	36.8	2.0	0.4
		13	28	508	18.1	25.2	1.0	0.0
Pila	1993-WS	4	30	448	14.9	11.6	29.7	12.9
		7	40	669	16.7	41.6	9.4	8.8
		9	55	1347	24.5	14.9	8.5	6.0
		12	38	367	9.7	36.0	0.8	8.2
IRRI	1992-WS	3	11	200	18.2	0.5	24.0	0.0
		5	15	358	23.9	17.6	8.7	0.8
		7	20	501	25.1	14.4	10.4	2.2
		9	19	500	26.3	22.0	1.0	1.4
		11	20	484	24.2	7.4	8.3	1.0
		13	17	424	24.9	2.1	1.4	2.6
IRRI	1993-WS	8	35	993	28.4	29.6	15.0	1.1
		9	35	756	21.6	14.6	13.9	6.2

Table 3. *continued*

b. Naturally-laid eggs, marked and monitored for 1 week

Location	Year-season	Crop age (WT)	Eggs marked	T_h [a] (d)	Egg mortality		
					% DIS	% PAR	% UNH
Pila	1991-WS	5	66	3.1	39.4	19.7	0.0
		7	179	2.0	38.5	23.5	0.0
		10	103	2.7	44.7	37.8	0.0
		12	112	1.6	33.9	41.1	0.0
Pila	1992-DS	5	56	3.8	21.5	50.0	0.0
		6	202	3.8	38.6	37.1	1.5
		7	232	2.2	37.9	43.6	0.4
		8	291	2.8	36.1	21.3	0.3
		9	202	2.0	24.3	8.9	1.0
Pila	1993-DS	6	72	2.5	24.6	46.8	0.0
		7	46	2.5	28.3	15.2	0.0
		8	70	2.7	21.4	30.0	4.3
IRRI	1993-WS	7	165	2.6	37.0	15.2	0.6
		8	182	1.9	25.8	9.9	1.1

[a] T_h = average duration of surviving eggs, from marking till hatching.

only be assessed during the main period of leaffolder oviposition. During this period thevariation in the levels of egg disappearance or parasitism was relatively small, and there were no obvious, general temporal trends in these mortality rates.

Most rice leaffolder eggs are laid during the maximum tillering and booting stages of the rice crop, from about 6 to 9 WT (Chapter 1). To compare egg mortality levels between crops, only the laboratory- or naturally-laid egg cohorts exposed during this period were included and mortality data were recalculated for a 4-day egg period (Figure 3). The total percentage egg mortality due to disappearance and parasitism per crop ranged from 42 to 70%, with an average of 55% for exposed laboratory-laid eggs and 63% for naturally-laid eggs. Egg disappearance was the major leaffolder egg mortality factor in all eight crops, but the potential impact of egg parasitism is probably partly masked by disappearance of parasitized eggs. Disappearance averaged 40.4% for exposed laboratory-laid eggs and 45.5% for

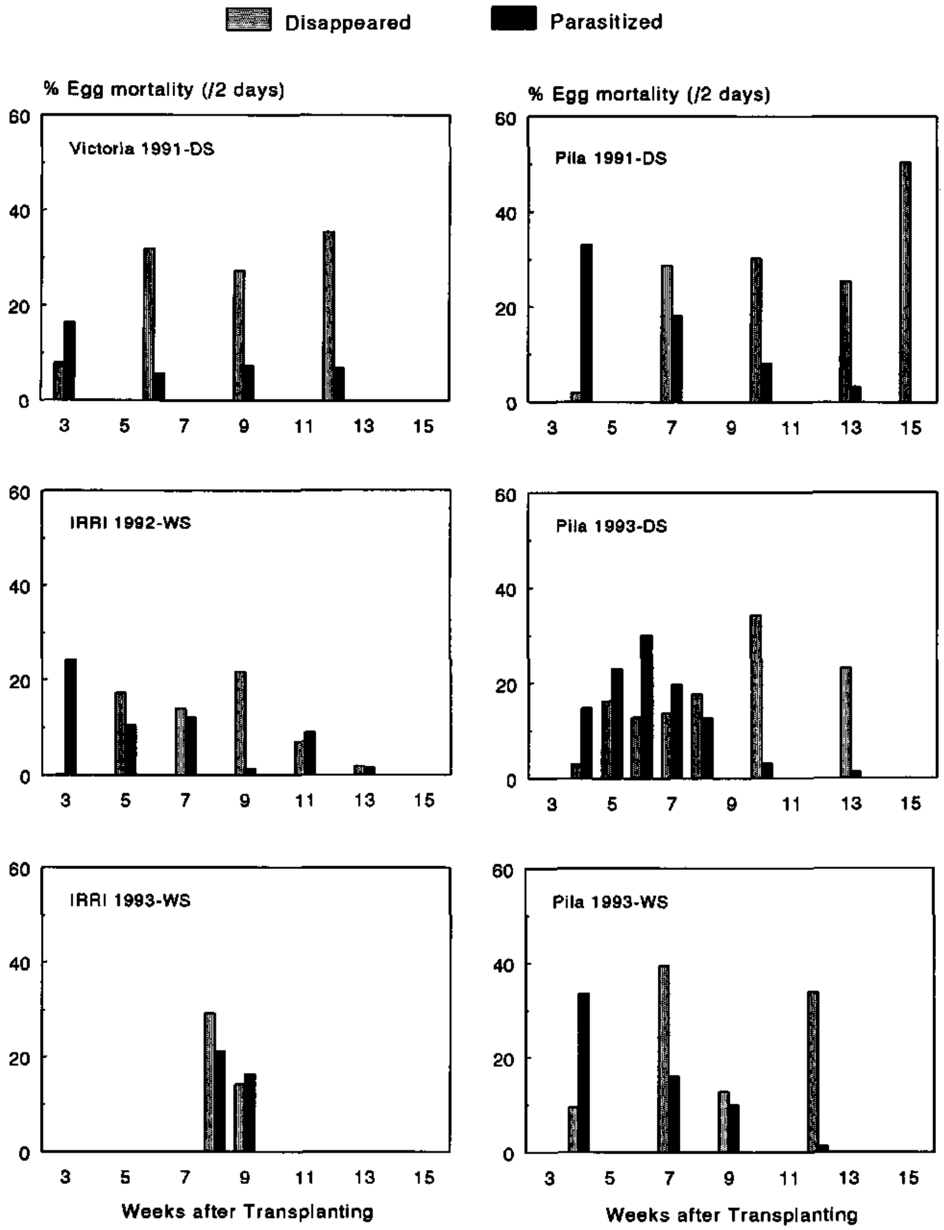


Figure 1. Mortality (%) of laboratory-laid eggs of rice leaffolder due to disappearance and parasitism, during two days field exposure, in six rice crops. Percentage parasitism is based on recovered eggs. DS = dry season, WS = wet season.

naturally-laid egg cohorts, while the average percentage parasitism was 14.6% and 17.7% respectively. The average mortality rates of laboratory- and naturally-laid eggs were not significantly different (t-test, $p > 0.05$).

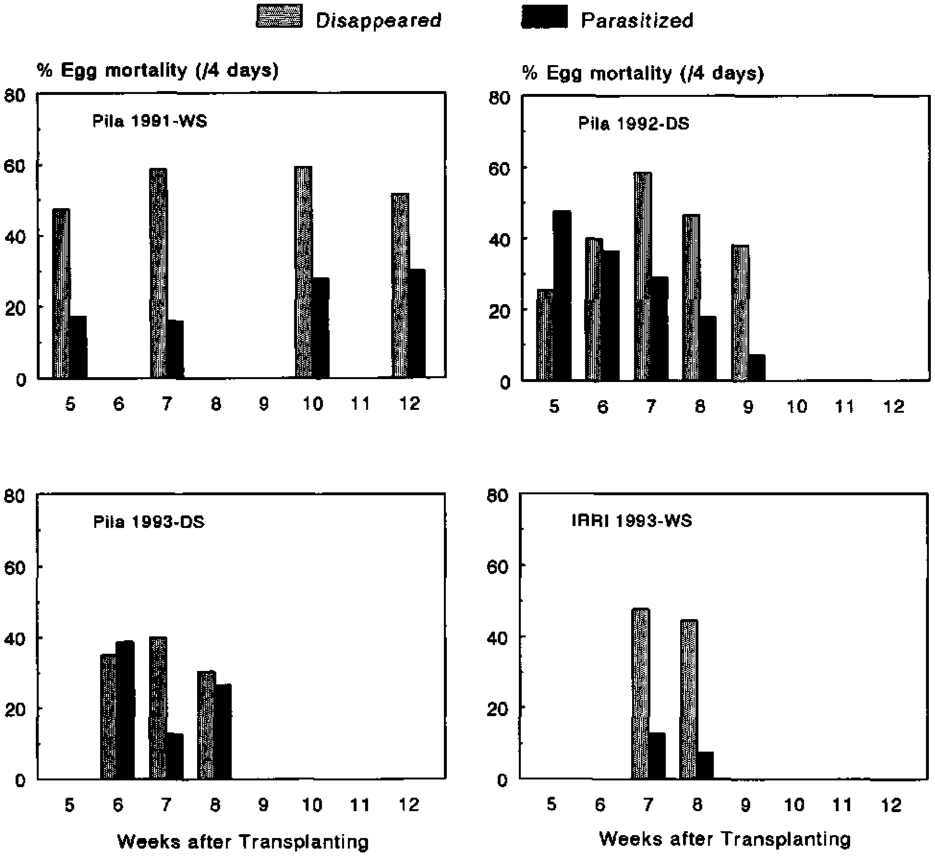


Figure 2. Mortality (%) of naturally-laid eggs of rice leaffolder due to disappearance and parasitism, in four rice crops. Apparent mortality rates were calculated over a 4-day egg period. See text for details. DS = dry season, WS = wet season.

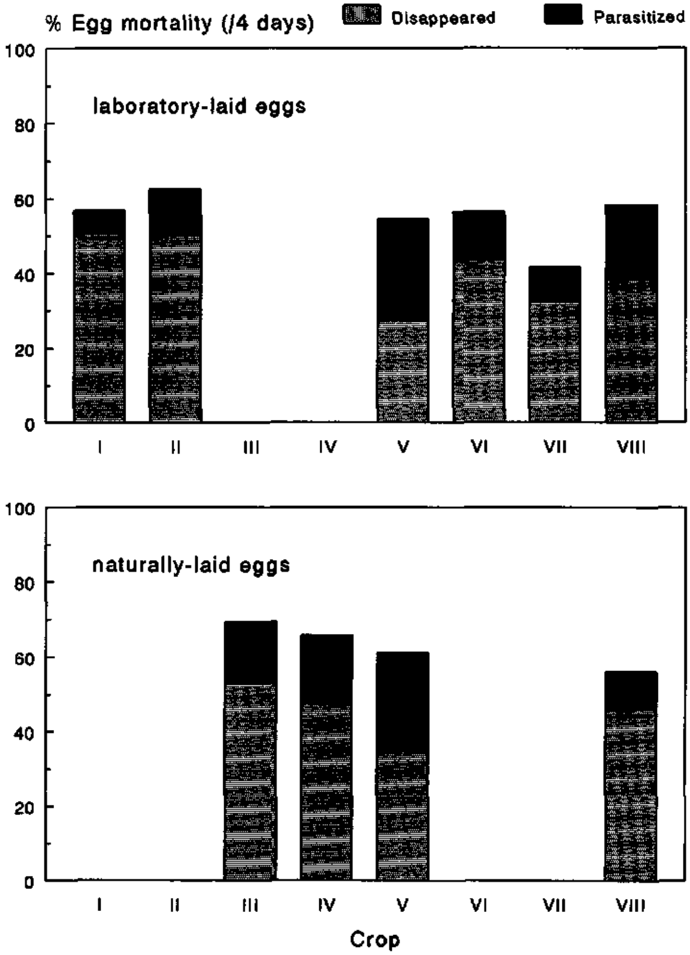


Figure 3. Mortality (%) of laboratory-laid and naturally-laid rice leaffolder eggs over a four-day period, in eight rice crops. To calculate the average values per crop, only mortality rates measured during the main period of leaffolder oviposition (6-9 weeks after transplanting) were included. I = Victoria 1991-DS; II = Pila 1991-DS; III = Pila 1991-WS; IV = Pila 1992-DS; V = Pila 1993-DS; VI = Pila 1993-WS; VII = IRRI 1992-WS; VIII = IRRI 1993-WS.

Factors associated with rice leaffolder egg mortality

Factors were identified, usually by correlation or regression, that could (statistically) explain a part of the observed variation in egg mortality rates.

Non-hatching Non-hatching can be due to an unfavourable micro-climate, infertility or attack by the sucking predator *Cyrtorhinus lividipennis* (Bandong & Litsinger 1986). In the present study there was no correlation between the percentage non-hatching and the density of *C. lividipennis*. The occasionally high levels of non-hatching (Table 3a) were often related to problems with holding the eggs in the laboratory after recovery, such as fungus growth due to high humidity. The percentage of naturally-laid eggs that failed to hatch until seven days after marking was always very low (Table 3b). This is partly explained by the longer 'duration' of non-hatching eggs as compared to healthy eggs, which increases the probability of disappearance over the observation period.

Parasitism of laboratory-laid eggs The number of parasitized eggs per hill was positively correlated with egg density per hill in 13 out of 21 tested cohorts. This association was generally rather weak (r^2=0.14-0.51). The percentage egg parasitism per exposed hill was independent of egg density per hill.

Multiple regression analysis of the percentage parasitism of laboratory-laid egg cohorts resulted in a minimal adequate model with three significant variables (Table 4). This model explained 41% of the total scaled deviation. The percentage parasitism increased with the total density of *Trichogramma* host eggs in the field (positive partial regression coefficient, *prc*), and decreased with the crop leaf area and wind speed (negative *prc*).

Disappearance of laboratory-laid eggs The number of disappeared eggs per hill was positively correlated with egg density in 17 out of 25 tested cohorts. Between cohorts this association varied from rather weak to strong (r^2=0.13-0.92). The percentage egg disappearance per exposed hill was usually independent of the egg density per hill.

None of the ten variables included in the multiple regression analysis explained a significant part of the observed variation in the percentage egg disappearance of exposed laboratory-laid eggs (Table 5a). The analysis was also conducted with predator and prey densities expressed per m^2 leaf area in stead of per hill, implying that the searching universe of the potential predators is the crop's leaf surface, rather then a collection of rice hills. This analysis resulted in a minimal adequate model with two significant variables: 'Gryllidae' and 'exposed egg density' (Table 5b), explaining 40% of the total scaled deviance. The percentage disappearance increased with the density of Gryllidae (positive *prc*), while it decreased with

Table 4. Significance of explanatory variables in the maximal regression model for rice leaffolder egg parasitism (%) of field-exposed laboratory-laid eggs. Significance is based on increase in 'scaled deviance' when the variable is removed from the multiple regression model.

Explanatory variables	Units	Scaled Deviance	Significance [a]
Host eggs [b]	(no. $hill^{-1}$)	11.12	F=8.77 **
Exposed RLF eggs [c]	(no. $hill^{-1}$)	4.76	n.s.
Crop leaf area [c]	(m^2 leaf m^{-2} soil)	7.53	F=5.94 *
Rainfall	(mm day^{-1})	0.41	n.s.
Wind speed	(m s^{-1})	7.68	F=6.06 *
Temperature	(°C)	2.22	n.s.

[a] n.s. = non-significant, $p>0.05$; * = $p<0.05$; ** = $p<0.01$

[b] average density of all naturally-laid *Trichogramma* host eggs

[c] average density of laboratory-laid RLF eggs on the exposed plants

exposed egg density (negative *prc*). The significance of the latter variable is only due to two influential outliers.

Simple linear correlation analysis of the association between egg disappearance and predator density showed that there was not any pooled combination of predator groups that resulted in a better fit than just the density of Gryllidae alone ($r^2=0.21$, df=26, $p<0.05$).

Disappearance of naturally-laid eggs 'Gryllidae' were the only predator group that significantly contributed to the multiple regression model for percentage disappearance of naturally-laid egg cohorts (Table 5a). Other significant variables in the model were 'rainfall' and 'leaffolder egg density'. The minimal adequate model with these three variables explained 79% of total scaled deviance. The fit of this model further improved to 85% of total deviance explained, when predator and prey densities were expressed per m^2 leaf area. Expressing predator and prey density per leaf area did not affect the outcome as much as in the exposure data, because there was less variation in crop leaf area between the natural cohorts.

Again, simple linear correlation analysis of egg disappearance yielded no predator combination resulting in a better fit than 'Gryllidae' alone ($r^2=0.43$, df=12, $p<0.05$).

Table 5. Significance of explanatory variables in the maximal regression model for rice leaffolder egg disappearance (%) of field-exposed laboratory-laid, or naturally-laid eggs. Significance is based on increase in 'scaled deviance' when the variable is removed from the multiple regression model.

a. Predator and egg densities expressed per hill.

		Laboratory-laid eggs		Naturally-laid eggs	
Explanatory variables	Units	Scaled Deviance	Significance [a]	Scaled Deviance	Significance [a]
Gryllidae	(no. hill^{-1})	0.079	n.s.	7.970	F=13.45 **
Tettigoniidae	(")	0.459	n.s.	0.003	n.s.
Coccinellidae	(")	0.023	n.s.	0.238	n.s.
Carab. + Staph.	(")	2.700	n.s.	0.171	n.s.
Leaffolder eggs [b]	(")	0.986	n.s.	5.344	F= 9.02 *
Exposed RLF eggs [c]	(")	4.126	n.s.	–	
Crop leaf area	(m^2 leaf m^{-2} soil)	2.703	n.s.	0.536	n.s.
Rainfall	(mm day^{-1})	0.012	n.s.	5.140	F= 8.68 *
Wind speed	(m s^{-1})	3.265	n.s.	0.613	n.s.
Temperature	(°C)	2.974	n.s.	0.365	n.s.

b. Predator and egg densities expressed per m^2

		Laboratory-laid eggs		Naturally-laid eggs	
Explanatory variables	Units	Scaled Deviance	Significance [a]	Scaled Deviance	Significance [a]
Gryllidae	(no. m^{-2})	4.752	F=4.81 *	12.910	F=16.58 **
Tettigoniidae	(")	0.326	n.s.	0.176	n.s.
Coccinellidae	(")	0.179	n.s.	0.358	n.s.
Carab. + Staph.	(")	0.283	n.s.	0.023	n.s.
Leaffolder eggs [b]	(")	1.190	n.s.	9.416	F=12.81 **
Exposed RLF eggs [c]	(")	7.610	F=7.71 *	–	
Rainfall	(mm day^{-1})	0.191	n.s.	7.310	F= 9.94 *
Wind speed	(m s^{-1})	2.678	n.s.	1.856	n.s.
Temperature	(°C)	0.499	n.s.	0.008	n.s.

[a] n.s. = non-significant, $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$

[b] average density of naturally-laid leaffolder eggs in the field

[c] average density of laboratory-laid leaffolder eggs on the exposed rice plants

Discussion

The two methods applied to assess mortality of rice leaffolder eggs in the field, exposure of laboratory-laid eggs and monitoring naturally-laid eggs, yielded similar results (Fig. 3). Variation in egg mortality rates was large, in particular within a crop season (Fig. 1 and 2). Statistically, this variation could be partly explained by a few variables, but the part explained was rather small, especially for exposed eggs (about 40%). This may be caused by a poor estimation of the variables included in the analysis, or by not having measured and included some important variables. The significant correlations found in this study are no proof of a causal relationship, nor does the absence of a correlation between a mortality factor and the density of a natural enemy mean that this species or group is unimportant. More controlled experiments or direct observations would be required to identify cause-effect relationships (Luck et al. 1988). Below, the various egg mortality factors and correlated variables will be discussed, including the mechanisms that might underlie the observed correlations. Subsequently, the relative importance of the observed egg mortality levels in reducing rice leaffolder injury is considered.

Non-hatching

After recovery from the field, the laboratory-laid eggs were kept in test tubes for about half of their total development period. Thus, the effect of the field micro-climate on non-hatching is probably not reliably assessed with this method, while non-hatching of naturally-laid eggs was underestimated due to disappearance. Hatchability is affected by air humidity and temperature (Zhang et al. 1988). With long-term monthly averages of 25-29°C and 70-80% R.H. (IRRI 1992), wetland field conditions in Laguna Province are close to the optimum for egg hatching (26-28°C, R.H.>75%, Zhang et al. 1988). As under optimal conditions hatchability of both *C. medinalis* and *M. patnalis* eggs is more than 90% (Joshi et al. 1985, Barrion et al. 1991a), non-hatching is probably of minor importance as a field mortality factor.

Egg parasitism

Egg parasitism of *C. medinalis* and *M. patnalis* by *Trichogramma* spp. has been reported from many countries in Asia (Khan et al. 1988). *T. japonicum*, the only species encountered in this study, has been reported on both leaffolder species in the Philippines before (Barrion et al. 1991a), and is the dominant rice leaffolder egg parasitoid in Malaysia and China (van Vreden & Ahmadzabidi 1986, Guo & Zhao 1992). In China *T. japonicum* has been used extensively for inundative biological control of *C. medinalis* in rice (Chiu 1984), while in India it is being studied for that purpose (Bentur et al. 1994). In the present study leaffolder egg parasitism by *Trichogramma* was correlated with three variables: host egg density, crop leaf area and wind speed. Possible mechanisms are discussed below.

Host egg density The short-term parasitization response to differences in leaffolder egg density on a hill scale, as measured by exposure of laboratory-laid eggs, was often proportional and the percentage parasitism per hill was independent of leaffolder egg density. However, the overall percentage egg parasitism of an exposed cohort was positively correlated with the total density of *Trichogramma* host eggs in the field (Table 4). Density dependence of *Trichogramma* parasitism in the field has been studied in other *Trichogramma*-host systems on various spatial and temporal scales, and several mechanisms have been identified. At a small spatial scale, density independence was also found in tomatoes at plant level (Pena & Waddill 1983) and in soybean at stem or pod level (Hirai 1988). Morrison et al. (1980) found that parasitism at leaf level ranged from weakly inversely dependent to weakly positively dependent on host density, due to two opposing trends. The chance of patch discovery increased with host density, and at the same time the proportion parasitized per patch decreased. The latter trend is probably caused by a negative correlation between re-encounter rate with already parasitized hosts and the giving-up time (Morrison & Lewis 1981). At a larger spatial scale (plots and fields), positive density dependence resulting from an intra-generational behavioural response was found by Gross et al. (1984) - retention time probably increased in response to kairomones -, while Hirose (1986) found positive density dependence as a result of an inter-generational reproductive response. Whether the *Trichogramma* population showed such numerical responses in the present study could not be verified with the available sampling data. Trichogrammatidae were caught in the suction samples, but usually not sorted to genus or species level. This means that *Oligosita* spp. were included, a common genus associated with Homoptera. Moreover, determining a temporal trend in *Trichogramma* density by sampling is difficult due to the reduced sampling efficiency of these minute wasps when the crop grows denser.

Leaf area The percentage egg parasitism was negatively correlated with the leaf area index of the crop. Expanding leaf area increases the area the egg parasitoids have to search to find their host. Knipling & McGuire (1968) postulated that *Trichogramma* searching efficiency was inversely proportional to crop leaf area, assuming random search. This inverse relationship between leaf area and percentage parasitism was confirmed by Need & Burbutis (1979) in field and laboratory experiments with *Trichogramma nubilale* and *Ostrinia nubilalis* eggs. Host finding by *Trichogramma* is not a random process, but is partly mediated by semiochemical cues (Noldus 1989). However, the mechanism is by arrestment and not by active directional orientation, so there is still an important random component explaining the strong effect of leaf area.

Wind speed Percentage parasitism was negatively correlated with wind speed. Although the significance of this effect was largely due to one exposure during the aftermath of a typhoon, it has been observed for other *Trichogramma* species that strong winds affect the parasitoid's mobility. Flight initiation is inhibited (Keller et al. 1985), and walking speed reduced (Chen & Chiu 1986).

Egg disappearance

Unlike for egg parasitism, the agents causing egg disappearance are not easily identified. Almost all rice field predators known to accept rice leaffolder eggs are chewing predators (Barrion et al. 1991a), that leave no trace after consuming the egg. Physical factors may also cause dislodgement of the entire egg. In this study the percentage egg disappearance was significantly correlated with gryllid density, leaffolder egg density and total daily rainfall.

Gryllidae The Gryllidae (*M. vittaticollis* and *A. longipennis*) were the only predator group whose density was significantly correlated with egg disappearance. Based on egg consumption trials (Bandong & Litsinger 1986, Rubia et al 1990), *M. vittaticollis, A. longipennis, C. longipennis* (Tettigoniidae) and *Micraspis* spp. (Coccinellidae) have been mentioned as important predators of leaffolder eggs in rice fields (Barrion et al. 1991a, Shepard & Ooi 1992). For the latter two species no significant correlation was found in the present study between their density and rice leaffolder egg disappearance. Their apparent lack of impact under field conditions may be due to their polyphagous nature. *Micraspis* sp. feeds on rice pollen and *C. longipennis* also feeds on rice foliage, florets and young grains (van Vreden & Ahmadzabidi 1986, Barrion & Litsinger 1987, Shepard et al. 1987). In the present study, the density fluctuations of both species seemed associated with the availability of these food sources. Thus, a clear link between the density of these species and leaffolder egg disappearance is likely to be absent, although this does not exclude the possibility that at times these predators do have a major impact on rice leaffolder eggs.

The improved correlation between predator density and egg disappearance when predator densities were expressed per m^2 leaf area, indicates that the implicit assumption of largely undirected search on the rice foliage is probably correct. Considering the generalist nature of the gryllids and the other predator species included in the analysis (Shepard et al. 1987), it is reasonable to expect that these species do not respond directionally to prey-specific cues, such as kairomones (Vet & Dicke 1992).

Further research will be undertaken to confirm the major role of Gryllidae in rice leaffolder egg predation, and to verify the assumptions concerning their searching behaviour, including the role of leaf area (see Chapter 4, 5, 6, 7).

Rainfall Dislodgement of insect eggs laid on leaf surfaces due to physical factors like wind and rain can be considerable (Nuessly et al. 1991). However, the results of the regression analysis were ambiguous concerning the effect of rainfall on leaffolder egg disappearance. Disappearance of naturally-laid eggs was significantly correlated with rainfall, but disappearance of laboratory-laid eggs was not, although higher rainfall extremes were measured during these exposures. This discrepancy might be due to the regression variable, total daily rainfall, being probably a poor measure for the potential impact of rainfall on egg disappearance. The intensity of the rain showers will be more important. However, direct observations of eggs exposed in the field during rain showers indicated that the impact of rain was almost negligible, unless wind speeds were very high, i.e. with a daily average of more than 7 $m\ s^{-1}$ (de Kraker unpublished). The flat, disc-shaped eggs of rice leaffolders are apparently less prone to dislodging than the near-spherical eggs of *Heliothis* spp. (e.g. Nuessly et al. 1991, van den Berg 1993), and the significant effect of daily rainfall on disappearance of naturally-laid leaffolder eggs might be a statistical artefact.

Leaffolder egg density A consistent relationship between the percentage disappearance and leaffolder egg density was not found in the regression and correlation analysis. Within exposures, the percentage egg disappearance was usually independent of the egg density per exposed hill. Between exposures, the average egg density on exposed hills had a significant negative effect on percentage egg disappearance (Table 5b), although this outcome was determined by two influential outliers. Disappearance of naturally-laid eggs was positively correlated with the average leaffolder egg density in the field, while disappearance of laboratory-laid eggs was not (Table 5). These contradictory results are probably related to issues of scale and assessment methodology, but cannot be explained without more substantial information about the identity of the major egg predators and their behaviour. The consistent density dependence of disappearance of naturally-laid eggs suggests that the predators searched more efficiently at high leaffolder egg density, because predator density was already included as a separate variable in the regression model. Given the importance of density dependence in pest control, further research on egg predation should aim to confirm this relationship and identify underlying mechanisms (see Chapter 5, 6, 7).

Relative importance of egg mortality factors and impact on rice leaffolder injury

The major part of rice leaffolder injury is caused by the last two larval instars (Heong 1990). Therefore, the impact of egg mortality on injury will depend on the mortality during the first three larval instars. Young larval mortality in irrigated rice fields at IRRI was estimated at about 55% (Kamal 1981). The estimate was based on exclusion cage experiments and frequent sampling of leaffolder populations. Estimates from South-China, based on exposure experiments, were much higher: the long-term average mortality during the first three larval stages was about 95% (Pang et al. 1984, Pang 1988). Pang et al. may have overestimated larval mortality, due to larval dispersal from the exposed plants. In the rice crops included in this study, larval survival seemed closer to the value reported from IRRI (see Chapter 1). The impact of the two major egg mortality factors, disappearance and parasitism, on survival till 4th instar larva is presented in Table 6, using various parameters to express mortality. The two cited values for young larval mortality (first three stages) are included to demonstrate their effect on the impact of egg mortality. For apparent egg disappearance and parasitism rounded off values (0.45 and 0.15) of the average observed levels were taken. Methods and definitions of mortality parameters are according to Southwood (1978) and Bellows et al. (1992). The marginal attack rate shows per life stage the potential impact of contemporaneous mortality factors, if they acted alone. The apparent mortality rate gives the actual impact per life stage, while the real mortality does the same across all stages included in the life-table. Irreplaceable mortality is that part of the total mortality that would not occur if the factor is removed, and it can be a good measure of the importance of the mortality factor in controlling the pest (Southwood 1978).

The assumption for calculating the marginal attack rate for egg parasitism and the irreplaceable mortality due to egg disappearance, is that parasitized eggs, before the chorion hardens and they turn black, are as vulnerable to predation (or dislodgement) as are healthy eggs. This seems quite plausible considering the generalist feeding habits of the Gryllidae (Shepard et al. 1987). As a result, the marginal attack rate and the irreplaceable mortality rate for egg disappearance and egg parasitism differ less than the observed apparent mortality rate (Table 6). In the latter case, the potential impact of egg parasitism is partly obscured by disappearance of parasitized eggs. Yet, the irreplaceable mortality caused by disappearance is still twice the value caused by parasitism.

Varying mortality of young larvae from 55% to 95% has a dramatic effect on the importance of egg mortality (Table 6). Although the real mortality remains highest during the egg stage, the irreplaceable mortality due to egg mortality factors is strongly reduced from 27 to 3%, when young larval mortality is set at 95%. Enhancing egg mortality, by conservation of natural enemies for example, would under these conditions only result in a slightly higher mortality from egg till 4th instar larva. This does not necessarily mean that this additional mortality would be unimportant, as for pests the resulting population density should be compared with the relatively low economic threshold density, rather than with the high initial population density.

Table 6. Impact of rice leaffolder egg mortality on survival till 4th-instar larvae, with young larval mortality estimates from the Philippines (a) and South-China (b). See text for definition of various mortality parameters; l_x is the number surviving at the beginning of stage x, d_x is the number dying during stage x.

a. Young larval mortality (L1-3) is 55% (Kamal 1981)

Stage	Mortality factor	l_x	d_x	Marginal attack rate	Apparent mortality	Real mortality	Irreplaceable mortality
Eggs		100					
	Disappearance		45	0.45	0.45	0.45	0.15
	Parasitism		15	0.27	0.15	0.15	0.07
	Total		60	0.60	0.60	0.60	0.27
Larvae		40					
(L1-3)	Total		22	0.55	0.55	0.22	0.22
Larvae (L4)		18					

b. Young larval mortality (L1-3) is 95% (Pang et al. 1984)

Stage	Mortality factor	l_x	d_x	Marginal attack rate	Apparent mortality	Real mortality	Irreplaceable mortality
Eggs		100					
	Disappearance		45	0.45	0.45	0.45	0.017
	Parasitism		15	0.27	0.15	0.15	0.008
	Total		60	0.60	0.60	0.60	0.030
Larvae		40					
(L1-3)	Total		38	0.95	0.95	0.38	0.38
Larvae (L4)		2					

Irreplaceable mortalities in Table 6 were based on the assumption that the various mortality factors were not density dependent. The impact of egg mortality will be smaller when young larval survival is inversely density dependent (e.g. van Hamburg & Hassell 1984). However, for rice leaffolder this does not seem to be the case: under laboratory conditions survival of young leaffolder larvae was not related with initial density (de Kraker unpublished), and larval survival in the field was either density independent or positively density dependent (Chapter 1, 2).

Conclusions

In Laguna rice fields disappearance was a more important mortality factor of rice leaffolder eggs than parasitism by *Trichogramma* spp. Non-hatching was of minor importance. The observed egg mortality levels may have a substantial impact on leaffolder injury, depending on the level of young larval mortality.

Mortality rates of egg cohorts were highly variable and can therefore not be extrapolated or used in a predictive way. With correlation and regression analyses, several variables were identified that statistically explained a significant part of the observed variation. In this way the statistical analysis at field level can guide research on the underlying causal mechanisms of leaffolder egg mortality. Hypotheses to be tested in more controlled experiments or direct observations concern the major role of predatory crickets (Gryllidae) in egg disappearance, and the effect of crop leaf area and prey density on their searching efficiency. Identification and quantification of cause-effect relationships will allow a more mechanistic and general explanation of the variation in egg mortality at field level. This can ultimately serve to identify options to conserve natural enemies and enhance natural biological control of rice leaffolder.

Chapter 4

Identification of major egg predators of rice leaffolders in laboratory and field

Abstract Laboratory and field studies on predation of rice leaffolder eggs were conducted to identify the major predator species.

In petri-dish tests the consumption of leaffolder eggs by the predatory crickets *Metioche vittaticollis* and *Anaxipha longipennis* was far greater than that of four other predators. Female cricket adults consumed at least 80 eggs per day, and all individuals accepted leaffolder eggs as food. According to daily egg consumption and acceptance rates, the predators ranked as follows: *M. vittaticollis, A. longipennis* > *Micraspis* sp. > *Ophionea nigrofasciata* > *Paederus fuscipes, Conocephalus longipennis*. Choice tests with common, alternative food types showed that the cricket *M. vittaticollis* preferred leaffolder eggs over nymphs of *Nilaparvata lugens*, and had a slight, but stable preference for eggs of *Rivula atimeta*. The leaffolder egg consumption of *Micraspis* sp. decreased drastically when rice pollen were available, while *C. longipennis* preferred feeding on the rice plant over predation on leaffolder eggs.

Direct observations of predation on field-exposed eggs showed that in two seasons *M. vittaticollis* and *A. longipennis* were the major predators of leaffolder eggs. Together these crickets took the largest part of all eggs consumed during observation (92%) and had the highest ratio of visits with predation to their total observed visits to plants with eggs (0.43). Furthermore, their activity pattern correlated best with the daily pattern of egg disappearance, and their seasonal abundance correlated best with the seasonal trends in egg disappearance. Minor predators observed feeding on field-exposed rice leaffolder eggs, were: *O. nigrofasciata, Micraspis* sp., and *C. longipennis*. The latter species was the most commonly observed egg predator, but had a negligible share in the total predation. Predator ranking according to the ratio of visits with predation to total visits was identical to the one based on the petri-dish tests.

Due to their very large predation capacity the cricket predators will probably play an important role in leaffolder egg predation, even when their densities are low compared to other predator species. Options for conservation of such major predators to sustain natural control of rice leaffolders concern reduced or selective insecticide use and habitat management.

Introduction

Rice leaffolders *Cnaphalocrocis medinalis* and *Marasmia* spp. (Lepidoptera: Pyralidae) are considered major pests in many Asian countries (Reissig et al. 1986, Khan et al. 1988). The larvae cause conspicuous injury by folding leaves and scraping off the green mesophyll tissue

(Fraenkel & Fallil 1981, Fraenkel et al. 1981). Farmers respond usually by applying insecticides, even at very low infestation levels (Heong et al. 1994). However, in many cases it is questionable whether chemical control of rice leaffolder is justified. Modern rice varieties have a high tolerance to defoliation (e.g. Hu et al. 1993, IRRI 1993c), and leaffolders have a large natural enemy complex that may be able keep them below damaging levels most of the time (Khan et al. 1988, Barrion et al. 1991a, Chapter 1). With knowledge of the identity of major natural enemies, i.e. species responsible for a large part of leaffolder mortality, directed conservation strategies can be developed to make optimal use of the naturally-occurring control agents (Shepard & Ooi 1991, Waage 1992).

Field studies in lowland rice in Laguna Province, Philippines, showed that egg predation was a major mortality factor for rice leaffolders, but did not reveal the identity and relative importance of the predators involved (Kamal 1981, Arida & Shepard 1990). In Asia about 20 species of rice field predators are reported to accept rice leaffolder eggs as prey (Table 1). Most of them are chewing predators that do not leave a trace of the eggs after consumption, which complicates identification. Cage predation experiments with a range of predators suggested that *Metioche vittaticollis, Anaxipha longipennis, Conocephalus longipennis*, and *Micraspis* spp. are the major predators of leaffolder eggs (Barrion et al. 1991a, Shepard & Ooi 1992). However, these predator species have not been compared under identical conditions with regards to cage and plant size, and prey and predator density (Bandong & Litsinger 1986, Rubia & Shepard 1987a, Rubia et al. 1990a), while field-based evidence of their relative importance is lacking. Analysis of leaffolder egg mortality in Laguna rice fields showed that a high level of egg predation was correlated with high densities of the predatory crickets *M. vittaticollis* and *A. longipennis* (Orthoptera: Gryllidae) (Chapter 3). No correlation was found for other predator species, suggesting that the crickets were the major egg predators. Correlations however, are no proof of a causal predator-prey relationship.

This chapter reports on experiments conducted to find further evidence regarding the species preying on rice leaffolder eggs and their relative importance. Laboratory studies of egg predation were complemented by direct observations of predation of field-exposed leaffolder eggs. The laboratory tests allowed simultaneous comparison of predators with regards to

Table 1. Predators reported to feed on the eggs of rice leaffolders *C. medinalis* and *Marasmia* spp.. Prey acceptance was either assessed in no-choice laboratory tests, or the method was not specified (ref. 1, 5, 6). In ref. 5 and 6, the predators are reported to feed on eggs of defoliators, species not specified.

Species	Country	References [a]
COLEOPTERA		
Carabidae		
Archicolliurus bimaculata	China	1
Colliurus chaudoiri	China	1
Desera geniculata	China	13
Drypta lineola virgata	China	13
Eucolliurus fuscipennis	China	1
Ophionea indica	China	12
Ophionea ishii ishii	China	13
Coccinellidae		
Coccinella transversalis	China	1
Harmonia octomaculata	China, Philippines	1, 2, 3, 4
Micraspis crocea	Philippines	3, 4
Micraspis discolor	China, Thailand	1, 5
Micraspis vincta	Thailand	5
Staphylinidae		
Paederus fuscipes	China, Malaysia, Thailand	12, 5, 6
Paederus tamulus	China	1
HEMIPTERA		
Miridae		
Cyrtorhinus lividipennis [b]	Philippines	3, 7
HYMENOPTERA		
Formicidae		
Solenopsis geminata	Pakistan, Philippines	2, 8
ORTHOPTERA		
Gryllidae		
Anaxipha spp.	Malaysia, Philippines, Thailand	3, 4, 5, 6, 9
Euscyrtus spp.	Malaysia, Philippines, Thailand	5, 6, 10
Metioche vittaticollis	Malaysia, Philippines, Thailand	3, 4, 5, 6, 11
Tettigoniidae		
Conocephalus longipennis	Malaysia, Philippines, Thailand	4, 5, 6
Conocephalus maculatus	Malaysia, Thailand	5, 6
ACARINA		
Pyemotidae		
Pyemotes ventricosus [b]	Philippines	10

[a] 1 = Pang et al. 1984, 2 = IRRI 1981, 3 = Bandong & Litsinger 1986, 4 = Rubia et al. 1990, 5 = Yasumatsu et al. 1981, 6 = Tai 1981, 7 = IRRI 1988, 8 = Ahmed et al. 1989, 9 = Canapi et al. 1988, 10 = Barrion et al. 1991, 11 = Rubia & Shepard 1987a, 12 = Shen & Pang 1989, 13 = He 1986

[b] sucking predators, all other chewing predators

general attributes under controlled conditions, while the field observations revealed the actual role of the predators under realistic conditions.

In the laboratory two simple parameters, acceptance and maximum daily consumption rate of leaffolder eggs, were measured as indicators of predation potential. In addition, preference for leaffolder eggs relative to other food types was assessed for a few selected predator species. None of the species reported as leaffolder egg predators (Table 1) feeds exclusively on leaffolder eggs. Their diet includes many different insects, while some also feed on plant parts (van Vreden & Ahmadzabidi 1986, Shepard et al. 1987). In the field, the ratio of rice leaffolder eggs to these other food types is highly variable (Chapter 7). Thus, the potential importance of a polyphagous predator in field predation of rice leaffolder eggs is also determined by its preference for leaffolder eggs relative to other prey and the stability of this preference under varying proportions of prey types. The objectives of the field study were to identify predator species that feed on rice leaffolder eggs under field conditions, and to assess the relative importance of each of these species. Although there is a wide array of more sophisticated techniques available for assessing predator-prey interactions in the field (Sunderland 1988), direct observation was preferred as the most simple and unambiguous method.

Materials and Methods

Laboratory and field experiments were conducted between May 1992 and October 1993, at the International Rice Research Institute in Los Baños, Laguna Province, the Philippines (13°14'N, 121°15'E). In the laboratory, temperature ranged from 22 to 30°C, and in the field from 24 to 35°C.

Egg acceptance and consumption capacity

Six predator species were selected for this experiment: *Paederus fuscipes* (Coleoptera: Staphylinidae), *Ophionea nigrofasciata* (Coleoptera: Carabidae), *Micraspis* sp. (Coleoptera:

Coccinellidae), *Anaxipha longipennis* and *Metioche vittaticollis* (Orthoptera: Gryllidae), and *Conocephalus longipennis* (Orthoptera: Tettigoniidae). These are common predators in Laguna rice fields (Chapter 1), and the species or genera are widely distributed in South and Southeast Asia (Chu 1979, Yasumatsu et al. 1981, Krishnasamy et al. 1984, Pang et al. 1984, van Vreden & Ahmadzabidi 1986, Bhardwaj & Pawar 1987, Kamal et al. 1987, Barrion et al. 1991a). Adult predators were collected in nearby rice fields. Only female adults were used in the tests, except for *P. fuscipes* and *O. nigrofasciata*. Nymphs of *M. vittaticollis* were obtained from a laboratory culture maintained on modified cornborer diet (Rubia & Shepard 1987a). The predators were starved individually in test tubes for 24 h prior to the experiment.

Eggs of rice leaffolders *C. medinalis* and *M. patnalis*, and green hairy caterpillar *Rivula atimeta* (Lepidoptera: Noctuidae), were obtained by caging field-collected female moths overnight with potted rice plants. Leaf pieces with prey eggs were placed in petri-dishes (Ø 9 cm) with moist filter paper. One predator was introduced per petri-dish and after 24 h the egg consumption was recorded. Eggs were replenished to the original density and 24 h later egg consumption was recorded again. Egg consumption per predator per 24 h was calculated as the average of the two periods. As a measure of prey acceptability an 'acceptance ratio' was calculated being the proportion of predators that consumed at least one egg of the provided prey species over the entire 2-day period.

Four tests with different combinations of predator and prey species were conducted. Per test the experimental design was completely randomized. When a predator died or moulted during the experiment, the replicate was not included. Significance of differences in mean percentage consumption between prey types was determined with GLIM (binomial errors, logit-link). Overdispersion (large residual error) was accounted for by using Pearson's X^2 (Crawley 1993).

Test 1. For three coleopteran predators *O. nigrofasciata*, *P. fuscipes*, and *Micraspis* sp., the consumption of leaffolder eggs (both species mixed) was determined, and compared with their consumption of *R. atimeta* eggs, a prey type that all three predator species were known to accept (van den Berg et al. 1992). Predators were provided with 20 eggs each.

Test 2. For five predator species the consumption rates were determined of each leaffolder species. The species included were two coleopteran species with the highest egg consumption in test 1, *O. nigrofasciata* and *Micraspis* sp., as well as the orthopterans *C. longipennis*, *A. longipennis*, and *M. vittaticollis*. Predators were provided with 40 eggs each.

Test 3. For different nymphal stages of *M. vittaticollis* the consumption of leaffolder eggs (both species mixed) was determined. Predators were provided with 50 leaffolder eggs each. Due to mortality and moulting during the test, the number of replicates varied from 4 to 12.

Test 4. The maximum amount of leaffolder eggs that the gryllids *M. vittaticollis* and *A. longipennis* could consume, was determined by providing adult female predators with an average of 80 eggs (60 on first day, 100 on second day). There were seven replicates per predator species. In addition, both species were offered 200 eggs of *M. patnalis* and of *C. medinalis* separately. The availability of leaffolder eggs was insufficient to replicate this test.

Food preference

Three predator species were tested for prey preference: *Micraspis* sp., *C. longipennis* and *M. vittaticollis*. The first two are often the most abundant (Chapter 1 and 3), while the latter had the highest egg consumption rate. The predators were collected in the field, and starved individually in test tubes for 24 h prior to the experiment. Only adult females were used in the experiments.

Preference of predators for rice leaffolder (*M. patnalis*) eggs relative to other prey types was tested in three leaffolder-alternative prey combinations. Common rice pests, that co-occur with rice leaffolder and are of similar size, were chosen as alternative prey types: eggs of green hairy caterpillar *R. atimeta*, eggs of rice whorl maggot *Hydrellia philippina* (Diptera: Ephydridae), and 1st-instar nymphs of brown planthopper *Nilaparvata lugens* (Homoptera: Delphacidae). These prey types had been accepted by the tested predators in earlier single-prey studies (Rubia & Shepard 1987a, Win 1989, Rubia et al. 1990a, van den Berg et al. 1992). Field-collected adults of *M. patnalis*, *R. atimeta* and *H. philippina* were caged with rice plants in various species combinations. After oviposition the eggs were counted and marked. Densities were adjusted by removing leaf parts with excess eggs. *N. lugens* nymphs were obtained from a laboratory culture and introduced in the test arena by aspirator. The test arena was a rectangular Mylar cage (22 × 30 × 100 cm) with three rice plants, trimmed to about 15 tillers. Total single-sided leaf area of the plants in a cage was c. 3000 cm^2. Prey was provided once at a standard density of 60 per cage. This density is more than twice the usual peak density in the field.

Two tests were conducted. In the first, all three predator species and the three prey combinations were included. Only the predator-prey combination *C. longipennis* and *H. philippina* eggs was omitted, because there were insufficient adults of this prey for oviposition. The ratio of leaffolder eggs to alternative prey was 1:1. One predator was introduced per cage, and prey consumption was determined after 36 h. The plants were also examined for feeding marks of the predators. Each combination was replicated at least five times. The second test was conducted only with *M. vittaticollis*, and *R. atimeta* or *H. philippina* eggs as alternative prey. The ratios of leaffolder eggs to alternative prey were 3:1 and 1:3. Prey consumption was now determined after 18 h, because the proportion consumed by *M. vittaticollis* in the first test was rather high.

The results were analyzed using Manly's preference index α_i, which represents the proportion consumed of prey *i*, over the sum of the proportions consumed of all prey types (Manly 1974, Chesson 1983). The index varies from 0 to 1, with values greater than $1/m$ indicating preference for species *i* and values less than $1/m$ indicating avoidance (m=total number of prey types). The preference index α was calculated for rice leaffolder eggs, the index for the alternative prey type in each combination is then $1-\alpha$. A t-test was used to determine whether the mean value of α differed significantly from 0.5 ($m=2$), although for a low number of replicates this test is probably not very accurate (Chesson 1983).

With *Micraspis* sp. an additional test was conducted to determine the effect of rice flowering on consumption of rice leaffolder eggs. The test arena consisted of one rice plant with 40 rice leaffolder eggs, covered by a tubular Mylar cage (height 75 cm, ∅ 18 cm). The single-sided leaf area of the plants was c. 1000 cm^2. All rice plants were in the flowering stage, but from one group the panicles and shed pollen were carefully removed. One female adult *Micraspis* predator was introduced per cage and leaffolder egg consumption was determined after 24 h. Both treatments (with or without panicles) were replicated six times.

Direct observation of egg predation in the field

Field observations on predation of rice leaffolder eggs were done in a 0.25 ha plot at the IRRI farm. The plot was located in a corner of the farm, at about 10 m distance from farmers' fields. Two-week old seedlings of rice variety IR72 were transplanted in a 20 × 20 cm spacing. Fertilizer was applied at a standard rate of 90 kg N ha^{-1}. Weeding was done by hand and no insecticides were applied. During the experiment the field was kept permanently flooded. The experiment was carried out during two seasons: 1992 wet season and 1993 dry season. In 1992 the crop was transplanted in the same month as the nearby farmers' fields (23 June). In 1993 the crop was transplanted relatively late (17 March), and observations started when most neighbouring fields were already harvested.

Rice plants with leaffolder eggs were obtained by caging field-collected leaffolder moths overnight with potted plants. The potted plants were of the same age and variety as the plants in the field plot. The location of the newly-laid leaffolder eggs was marked with a felt-tip pen to facilitate field observations. Egg density was about 30 per plant.

Three observers were seated alongside a levee that cut the field in half. The potted plants with eggs were placed between the rice plants in the field, at about 1 m distance from the observer (3 plants per person). The plants were observed for two days during 2-hour periods: at sunrise (5-7 h), morning (9-11 h), afternoon (13-15 h), sunset (17-19 h), and night (20-22 h). For nightly observations flash lights were used, covered with red plastic in order not to disturb the predators. During the first season (1992), no observations were conducted from 13 to 15 h, while on the second day the morning observations (9-11 h) were done around noon, from 10 to 13 h.

For all observed visits by potential egg predators, the species and stage, time and duration of visit, and activities (resting, walking, feeding, other) were recorded. During the second season (1993), the approximate duration of the activities was also recorded. When a predator was observed feeding on the leaffolder eggs, the number of eggs consumed was recorded after the predator had left the plant. In between the observation periods the potted plants with eggs were left in the field. To determine egg disappearance between and during the observation periods, the number of remaining eggs on the exposed plants was recorded at the beginning and the end of each 2-hour observation period. Plants were replaced when the remaining egg density was less than 15.

During the 1992 wet season, the direct observation experiment was repeated at six crop stages: early tillering (3 weeks after transplanting, WT), active tillering (5 WT), maximum tillering (7 WT), booting (9 WT), flowering (11 WT), and ripening (13 WT). During the 1993 dry season, the experiment was repeated at four crop stages: maximum tillering (6 WT), booting (8 WT), flowering (10 WT) and ripening (12 WT). Results were usually pooled over all crop stages, as the number of observations per crop stage was insufficient to compare predators.

Predator abundance in the field plot was estimated by sampling with a Blower-Vac suction sampler (Arida & Heong 1992). The sampler was used in combination with a plastic bucket enclosure, covering four hills. This enclosure was placed abruptly over the hills to include fast-moving insects like orthopterans. During the first season, samples (n=15) were taken at each crop stage that leaffolder egg predation was observed. Sampling was done around 8 h in the morning. During the second season, samples (n=16) were only taken at the last three crop stages (8, 10, 12 WT). This time sampling was done twice a day: around 6 h, early morning, and around 14 h, early afternoon. Differences between the two sampling times in number of insects per sample, were tested for significance with GLIM (Poisson errors, log-link) for six predator species (Crawley 1993).

Results

Egg acceptance and consumption capacity

All six predator species consumed rice leaffolder eggs when offered in a no-choice situation (Table 2). The egg consumption of the predator species was not significantly affected by rice leaffolder species (*C. medinalis* or *M. patnalis*, Table 2b). According to leaffolder egg consumption and acceptance rates, the predators ranked as follows: *M. vittaticollis*, *A. longipennis* > *Micraspis* sp. > *Ophionea nigrofasciata* > *Paederus fuscipes, Conocephalus longipennis*. The egg consumption by the predatory crickets *M. vittaticollis* and *A. longipennis*

Table 2. Egg acceptance and consumption rates of rice field predators in no-choice tests in petri-dishes. The acceptance ratio is the proportion of predators consuming prey over 48 h. Significance of differences in consumption of two prey types are based on the percentage consumed: n.s. = $p > 0.05$, ** = $p < 0.01$. See text for details. S.E. in parentheses.

a. Consumption and acceptance by three coleopteran predators of two prey types: rice leaffolders *C. medinalis* and *M. patnalis* (RLF), and green hairy caterpillar *R. atimeta* (GHC). Each predator was provided with 20 eggs of one prey type (10 replicates).

Predator species	Eggs consumed per day			Acceptance ratio	
	RLF	GHC	Significance of difference	RLF	GHC
Paederus fuscipes	2.5 (0.7)	9.3 (2.1)	**	0.7	1.0
Ophionea nigrofasciata	5.2 (1.6)	18.8 (0.5)	**	0.6	1.0
Micraspis sp.	6.7 (1.5)	14.3 (1.5)	**	1.0	1.0

b. Consumption and acceptance by five predator species of two prey types: rice leaffolders *C. medinalis* (C.m.) and *M. patnalis* (M.p.). Each predator was provided with 40 eggs of one prey type (10 replicates).

Predator species	Eggs consumed per day			Acceptance ratio	
	C.m.	M.p.	Significance of difference	C.m.	M.p.
Ophionea nigrofasciata	2.2 (1.9)	2.6 (1.5)	n.s.	0.3	0.5
Micraspis sp.	10.2 (2.6)	18.7 (4.0)	n.s.	0.7	0.9
Metioche vittaticollis	39.8 (0.2)	39.9 (0.1)	n.s.	1.0	1.0
Anaxipha longipennis	39.8 (0.1)	39.8 (0.2)	n.s.	1.0	1.0
Conocephalus longipennis	0.9 (0.7)	1.0 (0.7)	n.s.	0.2	0.2

was far greater than by other predators. Also the nymphal stages of *M. vittaticollis* were more voracious than the other predators (Table 2c). Cricket predators accepted leaffolder eggs as prey in each replicate. *C. longipennis* consumed the lowest number of leaffolder eggs per day, and only in two out of ten replicates predators consumed one or more eggs (Table

Table 2. *continued*

c. Consumption and acceptance of *M. vittaticollis* nymphs of rice leaffolder eggs (*C. medinalis* and *M. patnalis* mixed). Each predator was provided with 50 eggs; N = number of replicates.

M. vittaticollis nymphal stage	(sex)	N	Eggs consumed per day	Acceptance ratio
1st-2nd instar	(undet.)	4	24.9 (6.8)	1.0
3rd instar	(undet.)	12	44.4 (2.8)	1.0
4th instar	(female)	9	42.4 (4.9)	1.0

2b). In fact, these predators only consumed leaffolder eggs by feeding on the leaf pieces on which the eggs were laid. The three coleopteran predators consumed significantly more *R. atimeta* (GHC) eggs than leaffolder eggs, and also a larger proportion of the tested individuals accepted this prey (Table 2a). Consumption rates of *R. atimeta* and differences therein between predators were similar to those found by Van den Berg et al. (1992).

The maximum consumption of leaffolder eggs by female adults of *M. vittaticollis* and *A. longipennis* was more than 40 eggs per day: when on average 80 leaffolder eggs were offered, nearly all eggs were consumed (93.3 and 91.5% respectively). Even when 200 eggs of *C. medinalis* or *M. patnalis* were offered, both *M. vittaticollis* and *A. longipennis* consumed more than 90% of the eggs in one day.

Food preference

Significant prey preferences were found in three out of eight predator-prey combinations when rice leaffolder (*M. patnalis*) eggs and an alternative prey type were offered in a 1:1 ratio (Table 3a). *M. vittaticollis* preferred *R. atimeta* (GHC) eggs over rice leaffolder eggs, while the latter were preferred over *N. lugens* (BPH) nymphs. *C. longipennis* also preferred *R. atimeta* (GHC) eggs over rice leaffolder eggs. In case of *C. longipennis* the number of replicates included in the mean value of Manly's preference index was less than five, because several times the predator did not consume any prey. Feeding marks on the rice plants were found in three replicates of the *C. longipennis* - rice leaffolder - *N. lugens* (BPH)

Table 3. Preference tests: prey consumption and preference indices in predator-leaffolder (RLF) - alternative prey (Alt) combinations. RLF = rice leaffolder *M. patnalis* eggs, GHC = green hairy caterpillar *R. atimeta* eggs, RWM = rice whorl maggot *H. philippina* eggs, BPH = brown planthopper *N. lugens* 1st-instar nymphs. Number of replicates (N) indicated. S.E. in parentheses.

a. Relative prey densities equal, consumption determined after 36 h.

Predator	Prey combination	Density RLF:Alt	N	Eggs consumed		Preference index α	Significance [a]
				RLF	Alt		
M. vittaticollis	RLF / GHC	30 : 30	10	16.1 (2.4)	21.7 (2.8)	0.35	**
	RLF / RWM	30 : 30	10	15.6 (1.7)	14.7 (1.9)	0.52	n.s.
	RLF / BPH	30 : 30	10	10.4 (1.1)	0.5 (0.3)	0.97	**
Micraspis sp.	RLF / GHC	30 : 30	6	5.3 (2.3)	11.0 (3.1)	0.40	n.s.
	RLF / RWM	30 : 30	5	2.8 (1.0)	1.0 (0.4)	0.60	n.s.
	RLF / BPH	30 : 30	5	2.6 (1.0)	1.2 (0.6)	0.63	n.s.
C. longipennis	RLF / GHC	30 : 30	5	0.6 (0.7)	8.8 (3.6)	0.04 [b]	**
	RLF / BPH	30 : 30	5	0.8 (0.5)	0.0 –	1.00 [c]	–

b. Relative prey densities variable, consumption determined after 18 h.

Predator	Prey combination	Density RLF:Alt	N	Eggs consumed		Preference index α	Significance [a]
				RLF	Alt		
M. vittaticollis	RLF / GHC	45 : 15	14	14.1 (1.9)	8.6 (1.0)	0.30	**
	RLF / GHC	15 : 45	13	4.6 (1.0)	20.9 (2.5)	0.30	**
	RLF / RWM	45 : 15	8	7.7 (1.9)	2.6 (0.9)	0.56	n.s.
	RLF / RWM	15 : 45	6	2.8 (0.8)	8.7 (1.6)	0.45	n.s.

[a] α different from 0.5 (=no preference): n.s. = $p>0.05$, ** = $p<0.01$

[b] mean value of 4 replications

[c] mean value of 3 replications

combination, but not in any of the other combinations. Prey consumption rates in the preference experiment (Table 3a) reflected the differences between predators found in the petri-dish test (Table 2b), although the arenas were quite different (area petri-dish 65 cm^2 vs. cage with 3000 cm^2 single-sided leaf area).

The preference of *M. vittaticollis* for *R. atimeta* (GHC) eggs relative to rice leaffolder eggs did not change when the relative abundance of the two prey types was varied (Table 3b). In the leaffolder/*H. philippina* (RWM) combination, egg consumption was proportional to the relative abundance of the prey types, which is consistent with absence of preference.

The preference indices presented in Table 3 were estimated with Manly's formula for a situation with prey depletion. According to Manly (1974) these estimates may be biased when prey consumption is relatively high (*M. vittaticollis*) or low (*Micraspis* sp. and *C. longipennis*). However, the values differed little from those calculated with the assumption of constant prey density.

Leaffolder egg consumption by *Micraspis* sp. was much lower on plants with a flowering panicle, than on plants where the panicle and pollen were removed: 1.7 and 13.3% respectively ($F= 26.56$, $df=1,11$; $p<0.001$).

Direct observation of egg predation in the field

In two seasons of observation, five insect species were observed to feed at least one time on the exposed leaffolder eggs in the field: *Ophionea nigrofasciata* (adult), *Micraspis* sp. (larva and adult), *Metioche vittaticollis* (adult), *Anaxipha longipennis* (nymph and adult), and *Conocephalus longipennis* (adult). The observations on actual field predation by these species confirm the results of the laboratory tests on prey acceptance (Table 2). The staphylinid beetle *P. fuscipes*, which consumed low numbers of leaffolder eggs in the petri-dish test, was not observed feeding on the exposed eggs in the field. This might be due to their relatively low densities in the field during both seasons (Table 4).

Predator densities in the experimental field were higher during the 1993 dry season than during the 1992 wet season (Table 4). The average values overestimate this difference, because the 1992 value includes three more early sampling occasions with relatively low densities. However, the peak densities per predator show the same trend. The high predator

Table 4. Predator density (no./4 hills) - average and peak - during field observations on rice leaffolder egg predation. Sampling with Blower-Vac. In 1993 samples were taken twice a day (6 and 14 h). Sample size: n=15 (1992) or n=16 (1993).

Predator species	1992 [a]		1993 [b]		
	Average	Peak	6 h	14 h	Peak
Paederus fuscipes	0.00	0.00	0.15	0.08	0.31
Ophionea spp.	0.20	0.40	1.73	1.73	2.75
Micraspis sp.	0.01	0.07	0.56	0.90	1.44
Anaxipha longipennis + *Metioche vittaticollis*	0.30	0.60	1.53	1.33	1.75
Conocephalus longipennis	0.71	1.13	2.27	2.06	3.31

[a] average of 6 sampling dates (3, 5, 7, 9, 11, 13 WT), [b] average of 3 sampling dates (8, 10, 12 WT)

Table 5. Visits to exposed plants with rice leaffolder eggs and egg predation by six predator species (seasonal totals): total observed visits and visits with predation, the ratio of visits with predation to total visits observed (P:T), the number of eggs consumed per species, and the fraction of all consumed eggs per species.

Predator species	Observed visits Total (+Predation)		Ratio P:T		Eggs consumed		Fraction of total consumed	
	1992	1993	1992	1993	1992	1993	1992	1993
P. fuscipes	2 (0)	0 (0)	–	–	0	0	–	–
Ophionea spp.	77 (2)	59 (0)	0.03	0.00	3	0	0.10	–
Micraspis sp.	10 (2)	37 (1)	0.20	0.03	4	2	0.13	0.02
A. longipennis	2 (1)	65 (24)	0.50	0.37	2	45	0.06	0.41
M. vittaticollis	22 (5)	69 (38)	0.23	0.55	20	62	0.65	0.57
C. longipennis	120 (1)	203 (0)	0.01	0.00	2	0	0.06	–
TOTAL	233 (11)	433 (63)			31	109	1.00	1.00

densities in the 1993 dry season crop were probably a result of planting late relative to other crops. The experimental field then acted as a sink for predators from the maturing neighbouring crops. No significant differences were found in predator densities between suction samples taken at 6.00 h and at 14.00 h, at any of the three crop stages during the 1993 season.

The observed number of predator visits to the exposed plants was much higher in 1993 (Table 5). In 1992, 233 predator visits were recorded, with 11 resulting in predation on the exposed rice leaffolder eggs, while in 1993 out of 433 predator visits 63 predation events were recorded. The number of visits recorded per predator reflected their estimated abundance rather well, but will be biased by the activity pattern and the mobility of the species. During both seasons *C. longipennis* scored highest in the number of recorded visits. However, only once out of 323 visits *C. longipennis* was observed feeding on rice leaffolder eggs (Table 5). The predatory crickets *M. vittaticollis* and *A. longipennis* had the highest ratio of visits with predation to total visits observed, 68:158 (=0.43).

During the 1992 wet season, 31 rice leaffolder eggs were observed to be consumed, and during the 1993 dry season consumption of 109 eggs was observed. In both seasons the gryllids took the largest part of these eggs: the fractions consumed by both gryllid species together were 0.71 and 0.98 in 1992 and 1993 respectively (average: 0.93).

As indicated by several behavioural characteristics (Table 6), the observed predators were very mobile and actively searching. Most predators spent less than five minutes on a plant with leaffolder eggs. Except for *C. longipennis*, they spent most of the time walking. All species were observed to feed on rice pollen during the flowering stage (10 WT). When the predators found and consumed leaffolder eggs during a visit, they took only a small proportion of the eggs on the plant. The gryllids *A. longipennis* and *M. vittaticollis* made relatively longer visits to the plants. Consumption of a single leaffolder egg took the gryllids 15-30 s.

In both seasons observed predation accounted for c. 20% of all eggs that disappeared during two days of field exposure. The remaining 80% disappeared in between observation periods, or their predation escaped the attention of the observers. Correlations between total egg disappearance (observed and not observed) and predator visits were used to confirm the

Table 6. Observations of predator behaviour on field exposed plants with rice leaffolder eggs: length of visits, activities, and eggs consumed during visit.

Predator species	Median length visit		Fraction of visit time [a]				Eggs consumed/visit [b]	
	1992	1993	Walking	Sitting	Feeding	Other [c]	1992	1993
Ophionea spp.	3-4	1-2	0.94	0.04	0.00	0.03	1.5	–
Micraspis sp.	1-2	1-2	0.88	0.10	0.02	0.00	2.0	2.0
A. longipennis	–	7-8	0.73	0.23	0.04	0.00	2.0	1.9
M. vittaticollis	5-6	5-6	0.76	0.16	0.07	0.01	4.0	1.6
C. longipennis-Adult	4-5	4-5	0.27	0.71	0.00	0.02	2.0	–
C. longipennis-Nymph	3-4	1-2	0.38	0.62	0.00	0.00	–	–

[a] recorded only in 1993, average values of all visits
[b] includes only visits with egg consumption
[c] mostly feeding on pollen, sometimes oviposition

direct observations. The percentage egg disappearance during the 2-day exposures was quite variable between seasons and crop stages: in 1992 it ranged from 5 to 18% and in 1993 from 6 to 77%. This percentage disappearance (arcsine transformed) per crop stage was positively correlated with the number of visits of cricket predators ($r=0.95$, $df=9$, $p<0.001$). For the other predators correlations were not significant. A daily pattern of egg disappearance on the exposed plants was derived from the hourly rates of egg disappearance during and between the observation periods (Fig. 1a). During both seasons egg disappearance was lowest around noon and high in the early morning. For the three most abundant predator groups a daily pattern of visits to exposed plants was determined by computing the relative frequency of visits per observation period (Fig. 1b). Relative frequencies were taken to facilitate comparison of the predators, which differed substantially in their absolute visit frequencies (Table 5). As the field densities of the predators did not change between 6.00 h and 14.00 h, the daily patterns of predator visits must reflect the activity patterns of resident populations, and are not the result of a diurnal movement between the rice field and

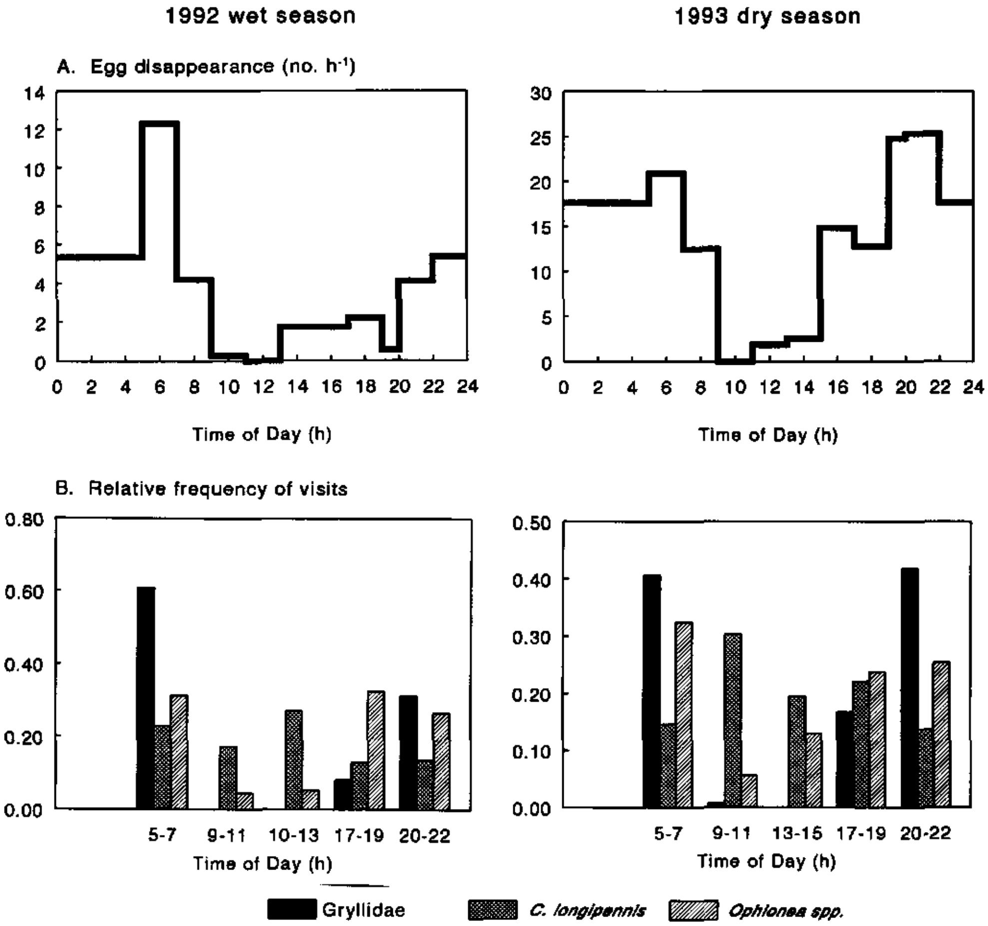


Figure 1. Daily patterns in egg disappearance and predator activity on rice plants with leaffolder eggs, exposed in the field in two seasons: 1992 wet season and 1993 dry season. **A.** Rice leaffolder egg disappearance (no. h^{-1}) during and between observation periods. **B.** Visits to exposed plants per observation period for each of three predator groups, expressed as a relative frequency (sum of frequencies over all observation periods is unity).

surrounding habitats (e.g. field borders). The activity pattern of the Gryllidae, with nearly all observed visits between 17.00 and 7.00 h, correlated best with the observed daily pattern of egg disappearance during both seasons (Fig. 1). *Ophionea* spp. followed a similar, though less pronounced activity pattern. *C. longipennis* was active throughout the day, with the peak of visits in the morning hours. The most notable difference between the two seasons is the lower predator activity and egg disappearance in the late afternoon and at night during the wet season. This is probably caused by the frequent rainfall at that time of day during the wet season. Strong wind and rain seemed to have an indirect effect on egg disappearance: a severe tropical rain storm during the 2-day observation period at 9 WT, 1992, caused a marked dip in both the number of predator visits recorded and the percentage egg disappearance. A direct impact of these abiotic factors on egg disappearance was not observed.

Discussion

Laboratory studies

The laboratory studies showed that the rôle of the two gryllid species *M. vittaticollis* and *A. longipennis* as predators of leaffolder eggs is potentially large. Their maximal leaffolder egg consumption rates were very high, and *M. vittaticollis* clearly preferred eggs over the usually very abundant *N. lugens* nymphs. *M. vittaticollis* had a significant and stable preference for *R. atimeta* over leaffolder eggs, but this preference was not very strong. The predation of leaffolder eggs by *M. vittaticollis* was not negatively affected by its prey preferences (Table 3a). Preference for *R. atimeta* will reduce daily predation of leaffolder eggs only when the total daily predation rate of *M. vittaticollis* is limited by satiation or handling time. In the field this condition is unlikely to occur, as with the prevailing prey densities the total daily predation rate of the cricket predators is limited by their search rates to levels far below their potential daily consumption capacity (Chapter 8).

The potential impact on leaffolder eggs of the other predators seems very limited. *Micraspis* sp. consumed only a moderate amount of leaffolder eggs per day, and did not show a distinct prey preference. The coccinellid predators are usually very abundant during the flowering stage of the crop, but the availability of pollen as alternative food will probably reduce their impact on leaffolder eggs. *C. longipennis* consumed very few leaffolder eggs in a single-prey situation, and preferred either rice plant tissues or eggs of other species in a choice situation. *P. fuscipes* and *O. nigrofasciata* consumed few leaffolder eggs in the petri-dish test, and seemed to prefer the eggs of green hairy caterpillar *R. atimeta* (Table 2a).

Field observations

Although direct observation of predation on leaffolder eggs in the field is a very labour-intensive method, it has provided unique information on the identity and relative importance of species preying on leaffolder eggs. The ratio of visits with predation to total visits observed (Table 5) revealed large differences between the various species. This ratio is an indicator of the species' potential contribution to leaffolder egg disappearance, independent of time and location-specific variations in predator abundance. The ranking of the predators according to this ratio, was consistent with the ranking according to the laboratory measured egg consumption and acceptance rates.

The predatory crickets *M. vittaticollis* and *A. longipennis* were the major predators responsible for rice leaffolder egg disappearance in the experimental field in two crop seasons. These crickets had the highest ratio of visits with egg predation to total visits, and took the largest part of all eggs consumed during observations (Table 5). Furthermore their activity pattern correlated best with the daily pattern of egg disappearance (Fig. 1), and their seasonal abundance correlated best with the seasonal trends in egg disappearance. The other predators played only a minor role at best. *C. longipennis*, in spite of being the most abundant, had a negligible share in the total predation. This demonstrates the importance of complementing a correlation analysis with direct observations, as predator species often follow similar seasonal trends in abundance.

Predator behaviour and density dependent predation

In earlier experiments disappearance of leaffolder eggs was apparently independent of their density on the plant level, but was positively correlated with the average leaffolder density per field (Chapter 3). Behavioural mechanisms explaining density dependence are for example 'area-restricted search' in patches with high prey density, and 'switching' of the predators. The short time predators spent on a single plant in the field, and the relatively low exploitation of the total prey per plant (Table 6), indicate that the size of 'prey patches' to which these predators possibly respond is at least larger than a single plant. This is in agreement with the finding that leaffolder egg disappearance was not dependent on the egg density per hill. 'Switching' means that the preference of the predators for rice leaffolder eggs would increase as the relative density of that prey type increases (Murdoch 1969). This explanation seems unlikely considering that leaffolder eggs generally make up only a modest proportion of all potential prey (Chapter 7). The outcome of the prey preference test also contradicts the possibility of switching behaviour: the prey preference of the major predator *M. vittaticollis* did not change when the ratio of leaffolder eggs to an alternative prey type was varied. The tested alternatives, *R. atimeta* and *H. philippina* eggs, were the most common insect eggs that co-occurred with leaffolder eggs in the study area (Chapter 7). Thus, the present studies of leaffolder egg predators did not provide evidence of behavioural mechanisms that might explain the density dependence earlier observed.

Can the findings be generalized ?

The observations revealing the major role of the predatory crickets (*M. vittaticollis* and *A. longipennis*) in leaffolder egg predation were limited to one field. Therefore, the question rises whether the findings can be generalized. Data from other fields and seasons in Laguna Province, and the large difference in predation potential between the crickets and the other species involved, do suggest that these crickets are the major predators of leaffolder eggs over a larger area. In a study of leaffolder egg mortality covering various seasons and locations in Laguna Province, the crickets were the only predator group significantly correlated with egg disappearance (Chapter 3). *Metioche* and *Anaxipha* species are distributed throughout the Indo-Australian region (Chopard 1969), and also the egg predators included in the present study seem to be a good representation of the species or genera reported from irrigated rice all over Asia (cf. Table 1). Considering the very large differences in predatory capacity between the crickets and the other predators, as determined both in laboratory and field, the crickets will probably play a relatively important role, even when their densities are low compared to other predator species (cf. Chapter 7).

Implications for rice IPM

The predatory crickets are also important predators of exposed eggs of rice pests other than leaffolders. Using direct observation and precipitin tests, Rothschild (1970, 1971) found that *Anaxipha* spp. were major predators of egg masses of rice stemborers (*Scirpophaga incertulas* and *Chilo* spp.) and rice bugs (*Leptocorisa* spp.). Egg disappearance of the foliar pests *R. atimeta*, *Naranga aenescens* (Lepidoptera: Noctuidae) and *H. philippina* was correlated with the abundance of a complex of chewing predators, including *M. vittaticollis* and *A. longipennis* (van den Berg et al. 1988). Comparison of the predator species in laboratory and field cages, showed that the crickets were the most effective predators of these prey types (van den Berg et al. 1992). Thus, conservation of *M. vittaticollis* and *A. longipennis* will probably not only result in lower populations of rice leaffolder, but of several other pests as well. Conservation in the rice crop may also benefit pest control in other crops grown nearby or in rotation, as *Metioche* and *Anaxipha* spp. are reported as common predators in other cereals and legume crops in Southeast Asia, where they were observed to feed on insect eggs and aphids (Suharto 1989, van den Berg 1992, 1993, A.T. Barrion, pers. comm.).

Options for conservation of the cricket predators concern pesticide use and habitat management. Both *M. vittaticollis* and *A. longipennis* are very susceptible to broad-spectrum insecticides like methyl parathion, monocrotophos, and pyrethroids (Bandong & Litsinger 1986, Rubia & Shepard 1987b). Unfortunately these chemicals are still widely used for leaffolder control (Heong et al. 1994). When chemical control is inevitable, selective application or selective insecticides should be used, such as buprofezin or azinphos-ethyl (Bandong & Litsinger 1986, Rubia & Shepard 1987b). Another option for conserving or even enhancing predator populations is habitat manipulation (Altieri & Letourneau 1982, Waage 1992). Surveys of the arthropod fauna in the vegetation surrounding rice fields showed that the predatory crickets can be very abundant in these habitats (R.C. Joshi, J. de Kraker, unpublished). This vegetation may act as source and refuge for the rice field populations, and careful management of these non-rice habitats could be an effective component of a conservation strategy.

In conclusion, the predatory crickets *M. vittaticollis* and *A. longipennis* were found to be major predators of leaffolder eggs. This knowledge can serve as a basis for directed conservation measures, such as reduced or no insecticide usage and habitat manipulation. These measures will probably also result in enhanced natural and sustainable control of other rice pests.

Chapter 5

Predation of rice leaffolder eggs by crickets:

1. Effect of prey and predator density

Abstract Cage experiments were conducted to quantify the predation rate of the crickets *Metioche vittaticollis* and *Anaxipha longipennis* on the eggs of rice leaffolder *Marasmia patnalis*. Egg predation was measured in response to changes in egg density, predator density and leaf area per cage. The predator types included were nymphs, females and males of *M. vittaticollis*, and females of *A. longipennis*.

The number of eggs consumed per cricket predator increased significantly with egg density, without reaching a plateau level. The predation rate decreased with increasing leaf area per cage. The functional response of all predator types could be adequately described by a linear model, with the effect of leaf area included. This indicates that the response to leaffolder egg density was not limited by prey handling time or satiation, but by the search rate. The search rate can be interpreted as the (single-sided) leaf area effectively searched for leaffolder eggs by a single predator in one day. Estimated search rates ranged from 0.05 m^2 day^{-1} for *M. vittaticollis* nymphs to 0.13 m^2 day^{-1} for *M. vittaticollis* females. Search rates of *M. vittaticollis* females, males, and *A. longipennis* females were not significantly different. The search rate of *M. vittaticollis* females increased significantly with prey density, but the density dependent model explained only an additional 3% of the total variation in search rate. Increasing predator density per cage led to a decrease in the per capita egg predation rate when predator density was more than 2 m^{-2} leaf area. Interference may thus reduce the effectiveness of enhancing leaffolder egg predation through conservation of cricket predator populations.

Introduction

Rice leaffolders *Cnaphalocrocis medinalis* and *Marasmia* spp. (Lepidoptera: Pyralidae) are considered major pests in many Asian countries (Reissig et al. 1986, Khan et al. 1988). A large part of early-season insecticide applications in Southeast-Asian rice is targeted against leaf-feeding insects, of which rice leaffolders are the major species (Heong et al. 1994). However, most sprays might not be justified as modern rice varieties can tolerate a substantial amount of defoliation without suffering yield loss (e.g. Hu et al. 1993, IRRI 1993c). Moreover, leaffolders have a large natural enemy complex which may keep them below economic damage levels most of the time (Khan et al. 1988, Barrion et al. 1991a). In unsprayed Philippine rice fields predators and parasitoids of eggs and larvae cause considerable mortality (Kamal 1981, Arida & Shepard 1990, Guo 1990, Chapter 1 and 3). Predation by chewing predators is the major egg mortality factor for leaffolders (Chapter 3). Two species of predatory crickets, *Metioche vittaticollis* and *Anaxipha longipennis* (Orthoptera: Gryllidae), were identified as the most important egg predators. During direct observations in the field they were responsible for over 90% of the observed egg predation (Chapter 4).

Metioche and *Anaxipha* spp. are distributed throughout the Indo-Australian region (Chopard 1969). The diet of both species includes a wide variety of small, slow-moving or immobile insect prey (Rothschild 1970, 1971, Rubia & Shepard 1987a, Canapi et al. 1988). The crickets are reported as predators of rice pests in Thailand, Malaysia and the Philippines, both in lowland and upland environments (Tan 1981, Yasumatsu et al. 1981, van Vreden & Ahmadzabidi 1986, Litsinger et al. 1987a, Barrion et al. 1991a). *Metioche* and *Anaxipha* spp. are also common predators of insect eggs and aphids in other cereals and in legume crops (Suharto 1989, van den Berg 1992, 1993). Conservation of such major natural enemy species is an essential part of rice IPM in Asia (Kenmore 1991, Shepard & Ooi 1991).

For a better insight in the impact of conservation or enhancement of cricket populations in rice fields on leaffolder egg mortality, the relationship between cricket predator density and the level of predation of rice leaffolder eggs should be quantified. In the field, most factors involved in this relationship are quite variable. Densities of both cricket predator and rice leaffolder eggs per plant vary considerably during a crop season and between fields (Chapter 1 and 2). In the period that leaffolder eggs are present in the field, the plant's leaf area increases five- to tenfold. For predators that randomly search the foliage for prey, the plant leaf area constitutes the searching universe and will thus also determine the predation rate (O'Neill 1990). The composition of the cricket population in terms of species (*M. vittaticollis* and *A. longipennis*), developmental stage and sex is quite variable, while a large array of other prey types co-occur with rice leaffolder eggs (Chapter 7).

The objective of the present study was to determine the effects of leaffolder prey and predator density on the egg predation rate in cage experiments with varying plant leaf area. The predators included in the experiments were nymphs, adult males and females of *M.*

vittaticollis and females of *A. longipennis*. Most experiments were conducted with *M. vittaticollis* females, as these were responsible for the major part (c. 60%) of leaffolder egg predation in field observations (Chapter 4). Their prey preference was studied in a previous experiment (Chapter 4). Temperature was not explicitly included as a treatment factor, because the average daily temperatures in Philippine lowland areas show only moderate variation, ranging from 25 to 30 °C (IRRI 1992). Simple mathematical models were applied to describe the relationships between predation rate, and prey and predator density quantitatively. These quantitative descriptions can increase our insight in the impact of cricket populations and may serve as a basis for a model of predation of leaffolder eggs in the field. In contrast to a linear regression model (Chapter 3), such a model is based on functional relationships and will be more widely applicable.

Materials and Methods

Materials

Predators Wingless adults of *Metioche vittaticollis* and *Anaxipha longipennis* were collected from rice fields. Nymphs of *M. vittaticollis* were obtained from a laboratory culture, reared on modified cornborer diet (Rubia & Shepard 1987a). The predators were starved individually in test tubes 24 h prior to the experiment. All predators were used only once.

Prey Rice leaffolder moths (*Marasmia patnalis*) were collected in the field. Potted rice plants were placed overnight in oviposition cages with different densities of female moths, to obtain plants with a range of egg densities. After oviposition, the location of the eggs on the leaves was marked with a felt-tip pen. Egg densities were adjusted by removing leaves or leaf pieces with excess eggs. At the start of the predation experiments the eggs were one to two days old.

Plant material Rice varieties used were IR36 and IR72, which are both susceptible to rice leaffolder (Khan & Joshi 1990). Per trial all plants were of the same age and had a standardized number of tillers. Only plants in the pre-flowering stage were used in the trials.

After each experiment the single-sided leaf area per plant was measured from a sub-sample with an electronic leaf area meter (LI-COR LC3100).

Cages Three types of cages were used in the egg predation experiments:

- tubular cages (0.85 × 0.14 Ø) made from clear plastic, covering one potted rice plant,
- nylon mesh cages (0.75 × 0.75 × 1.5 m) with four rice plants in a 20 × 20 cm spacing,
- nylon mesh cages (1 × 1 × 1.5 m) with 16 or 25 rice plants in a 20 × 20 cm spacing.

Experiments with the single-plant cages were carried out in the laboratory with natural light and a temperature of 27±4°C. The mesh cages were placed outside in screen-covered plots. The plots were flooded during the experiment. Temperature, R.H., rainfall, and sunshine-hours were recorded at a weather station at 500 m distance.

Predation experiments

Ten cage experiments were conducted with the predatory crickets *M. vittaticollis* and *A. longipennis* to determine the effect of prey and predator density on predation of rice leaffolder eggs (Table 1). The experiments were conducted at the International Rice Research Institute (IRRI), Los Baños, Philippines. Egg consumption was recorded per cage as the difference between the offered and the recovered eggs. In Experiment 5 to 8, the spatial distribution on the rice leaves of the offered and consumed eggs was determined by classifying the location of each egg as tip, middle or base. Tip represented the upper 3 cm of a leaf, base the lower 3 cm, and middle the part in between. Predator density was always one per cage, unless stated otherwise. In each experiment the time between predator introduction and recovery was 24 h. All experiments were set up in a completely randomized design. Replicates with dead or missing predators were excluded from the results.

The functional response of 2nd and 3rd instar nymphs of *M. vittaticollis* to different leaffolder egg densities was determined in single-plant cages (**Experiment 1 and 2**). The functional response of adult female of *M. vittaticollis* was measured in three different arenas: single-plant, 4-plant and 25-plant cages (**Experiment 3, 4 and 5**). The experiments with 4- and 25-plant cages were repeated at various plant ages to determine the effect of leaf area separate from cage size. In the 25-plant cages two predators were introduced per cage, and the leaffolder eggs were equally divided over 5-10 plants. Predator and prey densities in

Table 1. Experiments (1-10) on predation of rice leaffolder eggs by the crickets *M. vittaticollis* and *A. longipennis*. Given are: treatments per experiment; number of replicates (N); predator and arena type; age (in weeks after transplanting, WT), single-sided leaf area (LA), and variety of test plants. Age of plants is only given when the same experiment is repeated at different plant ages.

Experiment No. Treatments	N	Predators	Arena	Test plants		
				Age (WT)	LA (cm^2)	Variety
1. Functional response: 1,5,10,30 eggs/cage	4-6	*M. vittaticollis* nymphs, 2nd	1 plant, tube cage		830	IR72
2. Functional response: 5,10,30 eggs/cage	4-6	*M. vittaticollis* nymphs, 3rd	1 plant, tube cage		810	IR72
3. Functional response: 1,5,10,35 eggs/cage	5	*M. vittaticollis* adult females	1 plant, tube cage		380	IR36
4. Functional response: 4,8,20,40,80 eggs/cage	9-10	*M. vittaticollis* adult females	4 plants, mesh cage	4 6 8	1,820 3,440 4,980	IR72
5. Functional response: 5,20,80,160 eggs/cage	5	*M. vittaticollis* adult females	25 plants, mesh cage	4 6	18,650 27,850	IR36
6. Functional response: 4,8,20,40,80 eggs/cage	9	*A. longipennis* adult females	4 plants, mesh cage		4,900	IR72
7. Effect of leaf area: a. 1840 vs. 3280 cm^2/cage b. 2250 vs. 5300 cm^2/cage	10	*M. vittaticollis* adult females	4 plants, mesh cage		–	IR72
8. Effect of egg density: 8 vs. 80 eggs/cage	10	*M. vittaticollis* adult females	4 plants, mesh cage		3,720	IR72
9. Effect of predator density: 1,2,4,8 predators/cage	5	*M. vittaticollis* adult females	16 plants, mesh cage	4 8	23,310 39,970	IR36
10. Effect of predator type and density: 1,2 predators/cage	4	*M. vittaticollis* male + female *A. longipennis* female	4 plants, mesh cage		4,780	IR72

these cages reflected the field situation best. Comparison of search rates estimated with the different cage types can indicate the presence of a cage effect. The functional response of *A. longipennis* females was determined in 4-plant cages only (**Experiment 6**).

Two experiments were conducted to test the predictions of a functional response model for *M. vittaticollis* females, that was based on the results of Experiment 4 and 5. This model predicted that an increase in leaf area would reduce egg predation, and that high prey densities would increase the percentage egg predation. In **Experiment 7** leaf area was varied, while the number of eggs per cage was constant (40). **In Experiment 8** prey density per cage was varied, with a constant leaf area per cage.

The effect of predator density on per capita egg predation by *M. vittaticollis* females was determined in large 16-plant cages (**Experiment 9**). Prey density was constant at 75 eggs per cage, divided over five plants. The experiment was repeated at two plant ages to determine the influence of leaf area.

Predation of leaffolder eggs by *M. vittaticollis* females, *M. vittaticollis* males and *A. longipennis* females was compared in a single experiment with a standard prey density of 40 eggs per cage (**Experiment 10**). To determine whether combining the predators would affect the per capita egg predation rates, two treatments with two different predators per cage (*M. vittaticollis* male + female, females of *M. vittaticollis* + *A. longipennis*) were included in the same experiment.

Statistical analysis

For all experiments, the effect of the treatment variables on number and/or percentage of consumed eggs was tested using the GLIM package (Crawley 1993). Count data (number of eggs consumed) were analyzed with Poisson errors, log-linked. Percentage data were analyzed with binomial errors, logit-linked. Overdispersion (large residual error) was corrected for by using Pearson's X^2 (Poisson), or William's procedure (binomial). The effect of variables not included as treatment variable in the same trial, but varying between otherwise similar trials, like predator stage, predator species and leaf area, was determined by comparing the slopes of the regression lines of egg consumption versus egg density. Difference in slope was assessed with an F-test. To determine whether the distribution per leaf part was the same for the consumed eggs and the offered eggs, their frequencies per leaf part were subjected to a test of independence, with offered and consumed as explanatory categories.

Descriptive models of predation

The relationship between egg predation rate and egg density was described with a mathematical model for the functional response of a randomly searching predator, allowing for prey depletion (Rogers 1972). This 'Random Predator Equation' (RPE) was simplified by assuming that in the predation experiments prey handling time was negligible. The assumption was based on the absence of a plateau in the observed functional responses. When handling time is zero, the RPE takes the form of the Nicholson-Bailey model (Rogers 1972), representing a linear, Holling type I functional response:

$$N_a = N_0 [\, 1 - \exp(- a' \, T \, P/A)\,] \qquad (1)$$

where N_a is the number of eggs consumed per cage, N_0 is the initial number of eggs per cage, P is the number of predators per cage, A is the total single-sided leaf area per cage (m^2), and a' is the search or attack rate (m^2 day^{-1}) of a single predator. As the total time T available for searching was always one day and the search rate is expressed in m^2 per day, $T=1$ for all experiments. The search rate a' is then equal to Nicholson's 'area of discovery', and can be interpreted as the area effectively searched for a given type of prey by one predator during 24 h (Nicholson & Bailey 1935). Effectively means here that all prey in this area were found and consumed. For each functional response trial, the search rate was calculated by fitting Eq. 1 with linear regression. Adequacy of the linear model was checked with a lack-of-fit test (Draper & Smith 1981, Trexler et al. 1988). Significance of differences in search rates between trials was assessed by t-test.

Several trials indicated that the egg predation rate of *M. vittaticollis* females increased with egg density. A model describing a density dependent search rate, adapted from Hassell (1978), was fitted to the values of a' calculated from Exp. 4 and 5:

$$a' = (\, a_{min} + c_1 \, a_{max} \, N_0/A \,) \,/\, (\, 1 + c_1 \, N_0/A \,) \qquad (2)$$

where a_{min} is the minimum search rate when prey density approaches zero, while a_{max} is the upper asymptote of the search rate at high prey densities. Constant c_1 determines the increase in search rate with prey abundance. Combining Eq. 1 and 2 results in a Holling type III functional response (Hassell 1978).

The effect of predator density on the individual predation rate is often interpreted as a result of mutual interference (Hassell 1978). Time-consuming encounters between searching predators would reduce the time available for prey searching. The model of Beddington (1975), based on this assumption, was used to describe the effect of predator density on the search rate:

$$a' = a_0 \,/\, (\, 1 + c_2\,(P-1)/A\,) \qquad (3)$$

where a_0 is the search rate when there is no interference, and c_2 is the product of the predator encounter rate and the time 'wasted' per encounter. The model was fitted to the data of Exp. 9, with a'/a_0 as the dependent variable, thus eliminating the effect of differences in a_0, the search rate at one predator per cage, between the two trials.

Equations 2 and 3 were fitted with non-linear regression (Levenberg-Marquardt method). Adequacy of the model was assessed with a lack-of-fit test, followed by an F-test for significance of the regression model.

Results

Effect of egg density

In all functional response experiments the number of eggs consumed per cricket predator increased significantly with egg density, apparently without reaching a plateau level (Fig. 1, Table 2). The percentage egg consumption was independent of egg density, except in Exp. 4/4 WT, where the percentage consumed increased with egg density. The linear functional response model (Eq. 1) gave an adequate description without significant lack-of-fit in all but one trial. Lack-of-fit in Exp. 3 was due to low predation rates at an intermediate density (10 eggs per cage). The fitted linear functional response models explained about 40-95% of the observed variation in egg predation rates (Table 2, r^2-values).

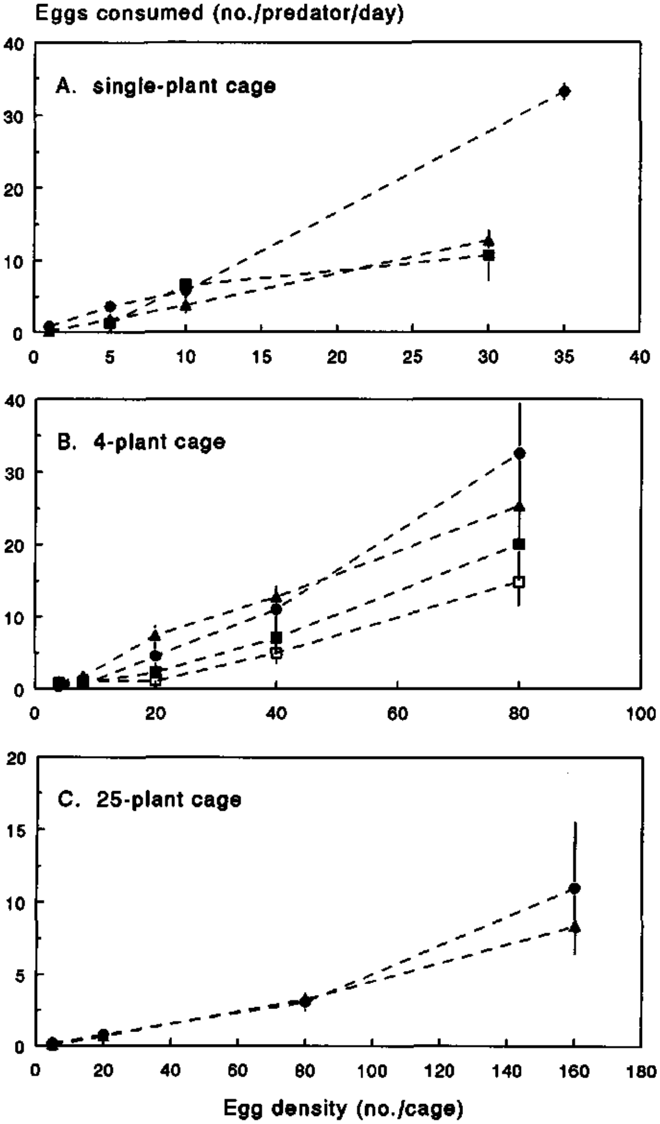


Figure 1. Functional response to rice leaffolder egg density of predatory crickets. Means ± S.E.; see Table 2 for significance of effects. **A.** Single-plant cage (Exp. 1-3): *M. vittaticollis* 2nd (▲) and 3rd (■) instar nymphs, and females (●). **B.** 4-plant cage (Exp. 4, 6): *M. vittaticollis* females, at three plant ages: 4 WT (●), 6 WT (▲), 8 WT (■), and *A. longipennis* females (□). **C.** 25-plant cage (Exp. 5): *M. vittaticollis* females, at two plant ages, 4 WT (●), 6 WT (▲). WT = weeks after transplanting.

Table 2. Functional response of *M. vittaticollis* and *A. longipennis* to rice leaffolder egg density (Exp.1-6, Table 1): significance of effect of egg density on egg consumption; average consumption (%) per experiment; fit statistics of linear model (Eq. 1); and search rates (+S.E.). Search rates are calculated from the fitted models. See text for details on statistical analysis and model fitting.

Experiment	Arena	Plant age (WT)	Effect of egg density on egg consumption [a]		Average percentage consumed [b]	Lack-of-fit to linear model [a]	Coeff. of Determ. (r^2) linear model [a]	Search rate a' (m^2 day^{-1})
			No.	%				
M. vittaticollis								
1. nymphs, 2nd	1-plant		**	n.s.	33.4	n.s.	0.43 **	0.049 (0.013)
2. nymphs, 3rd	1-plant		*	n.s.	42.2	n.s.	0.39 **	0.039 (0.009)
3. adult females	1-plant		**	n.s.	76.2	*	0.96 **	0.095 (0.015)
4. adult females	4-plant	4	**	**	26.2	n.s.	0.56 **	0.106 (0.013)
		6	**	n.s.	29.6	n.s.	0.66 **	0.132 (0.012)
		8	**	n.s.	16.1	n.s.	0.42 **	0.129 (0.017)
4. adult females	25-plant	4	**	n.s.	4.7	n.s.	0.39 **	0.124 (0.026)
		6	**	n.s.	3.8	n.s.	0.77 **	0.147 (0.013)
A. longipennis								
6. adult females	4-plant		**	n.s.	14.6	n.s.	0.48 **	0.090 (0.011)

[a] n.s. = non-significant, * = $p<0.05$, ** = $p<0.01$

[b] averaged over all egg densities

Cage type, plant age and leaf area The functional response of *M. vittaticollis* females differed per cage type (Fig. 1). In the single-plant cages a predator consumed on average 33.2 eggs per day at the maximum density of 35 eggs. In contrast, a predator in the 25-plant cages (at 6 WT) consumed only 8.4 eggs per day at the maximum density of 160 eggs per cage. Egg predation rates in the 4-plant cage were intermediate. Thus, the larger the cage and the number of plants, the smaller was the percentage of the available eggs consumed by *M. vittaticollis* females (Table 2). These differences might be attributed to cage size, and number and size (or age) of the plants included. Increasing plant size by using the same number of plants, but of different ages in identical cages (Exp. 4 and 5), also reduced the predation rate. The effect was best visible at the highest prey density (Fig. 1b,c). In the 4-plant cage, the slopes of the regression lines for egg predation at 4 WT and 6 WT were both significantly higher than at 8 WT. In the 25-plant cage differences in slope at 4 WT and 6 WT were not significant.

The search rates of *M. vittaticollis* females, calculated with Eq. 1 which includes the total leaf area per cage, ranged from 0.095 m^2 day^{-1} in the single-plant cage to 0.147 m^2 day^{-1} in the 25-plant cage (Table 2). Search rates were not significantly different between trials that were conducted with the same cage type but with different plant ages (Exp. 4 and 5, t-test). When differences in total leaf area are accounted for, plant age has apparently no effect on the search rate. The search rates estimated with the 4- and 25-plant cages did not differ significantly, indicating that cage size separate from total leaf area also had no effect. In the single-plant cage experiment the estimated search rate was somewhat lower than in the 4- and 25-plant cage experiments. There were several replicates with 100% predation, meaning that the total search area in the single-plant cages was too small for a proper estimation of the search rate by fitting Eq. 1. When all eggs are consumed before the end of the experiment, the search rate will be underestimated.

Predation by *M. vittaticollis* nymphs and *A. longipennis* females In the single-plant cages, 2nd and 3rd instar nymphs of *M. vittaticollis* did not differ significantly in their response to egg density. Both instars consumed less eggs than *M. vittaticollis* females (Fig. 1a), but for a fair comparison of the functional responses their search rates should be considered, as the leaf area per cage was much lower for the *M. vittaticollis* females (Table 1). The search rates of the nymphs were about 50% of the values estimated for adult females (Table 2). The response of *A. longipennis* females to egg density was not different from that of *M. vittaticollis* at a similar leaf area per cage (Fig. 1b). The search rate (0.090 m^2 day^{-1}) was lower than for *M. vittaticollis* females, but not significantly (Table 2).

Density dependent search rate A linear functional response implies a constant percentage predation over all egg densities. However, for *M. vittaticollis* females a significant positive effect of prey density on percentage egg consumption was found in one trial (Table 2, Experiment 4/4WT). Non-significant trends were found in three other trials (Exp. 4/8WT, 5/4 WT and 5/6 WT). Fitting Eq. 2 for a prey density dependent search rate to the combined data of Exp. 4 and 5, gave a curvilinear relationship with a minimum search rate of 0.072 m^2 day^{-1} in the absence of prey, and an asymptotic maximum search rate of 0.160 m^2 day^{-1} at high prey densities (Fig. 2). Lack-of-fit was not significant, indicating that the non-linear model was adequate. However, the model explained only a small part of the observed

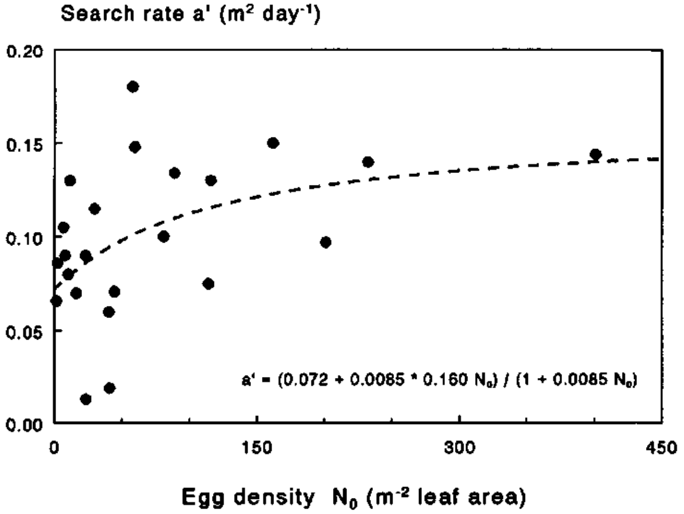


Figure 2. Search rate (a') of *M. vittaticollis* females as a function of initial leaffolder egg density (N_0). Data points are treatment means of Experiment 4 and 5; dotted line represents fitted model (Eq. 2: F=3.14, Df=2,177, $p<0.05$).

variation in search rates ($r^2=0.03$). More than 65% of the residual sum of squares was due to variation within treatments ('pure error'), thus variability in response between individual predators (replicates) was an important cause of the poor fit (Draper & Smith 1981).

Test of functional response model The combined model (Eq. 1 and 2) of the functional response of *M. vittaticollis* females, calibrated with the data of Exp. 4 and 5, was tested in terms of trends as well as magnitude of the predictions (Table 3). In Exp. 7 the predation rates (no. day^{-1}) decreased when the total leaf area per cage was approximately doubled. In Exp. 8 the percentage egg predation increased with egg density. These treatment effects were conform the predicted trend, but were not significant due to the large variability in predator response. The predicted values matched the observations reasonably well: most differences between observed and predicted were not more than one time the standard error of the observed values.

Table 3. Observed and predicted levels of rice leaffolder egg predation by *M. vittaticollis* females in 4-plant cages (Exp.7-8, Table 1). Predictions from combined functional response model (Eq. 1+2, $a'_{min}=0.072$, $a'_{max}=0.160$, $c'_1=0.0085$). Treatment effects on egg consumption were non-significant ($p>0.05$). S.E. in parentheses.

Experiment	Treatment	Egg consumption		Search rate *a'*	
		Observed	Predicted	Observed	Predicted
7. Initial density	Leaf area/cage	Number			
a. 40	1,840 cm^2	18.4 (1.8)	20.2	0.119 (0.015)	0.13
	3,280 cm^2	14.1 (3.0)	12.0	0.165 (0.041)	0.12
b. 40	2,250 cm^2	14.3 (2.4)	17.1	0.109 (0.022)	0.12
	5,300 cm^2	9.1 (1.8)	7.3	0.146 (0.034)	0.11
8. Leaf area/cage	Initial density	Percentage			
3,720 cm^2	8	18.1 (4.2)	20.6	0.079 (0.019)	0.09
	80	33.3 (6.9)	29.3	0.170 (0.041)	0.13

Effect of predator density

Increasing the density of female *M. vittaticollis* predators per cage did not result in a consistent, significant increase in the percentage consumed eggs per cage. At high predator densities (4 and 8 per cage) the egg consumption per predator was significantly reduced in the trial with small plants (4 WT), but not in the trial with large plants (8 WT) (Fig. 3). The absence of an effect of predator density on the egg predation per cage was not caused by cannibalism, as all introduced predators were still alive at the end of the experiment. The interference model (Eq. 3) did not fit the data of Exp. 9. The model overestimated the effect of interference at low predator densities: below a density of two predators per m^2 leaf area ($P-1 = 1$), the individual search rate was not affected (Fig. 4).

Egg consumption and search rates of single predators did not significantly differ between *M. vittaticollis* females, males, and *A. longipennis* females (Exp. 10, Table 4). The estimated search rates for females of *M. vittaticollis* and *A. longipennis* were close to the estimates from Exp. 4, 5 and 6. Egg predation *per cage* was not significantly different between treatments with one predator and treatments with two predators per cage. Combining *M. vittaticollis* male and female in one cage reduced the egg consumption *per predator* significantly compared with single females, but not compared with single males. Combining females of *M. vittaticollis* and *A. longipennis* in one cage did not reduce egg consumption per predator significantly compared with single predators. For both combinations the search rates decreased relative to the average search rate of the single caged predators, but the decrease was not significant. The reduction in search rate for the combination of *M. vittaticollis* male and female was similar to reductions for combinations of females only (Fig.4).

Effect of egg location

The distribution of the consumed eggs per leaf part did not differ from the distribution of the offered eggs in any of six trials (Fig. 5). For eggs, the probability of predation by *M. vittaticollis* or *A. longipennis* is thus independent of their location on the leaf.

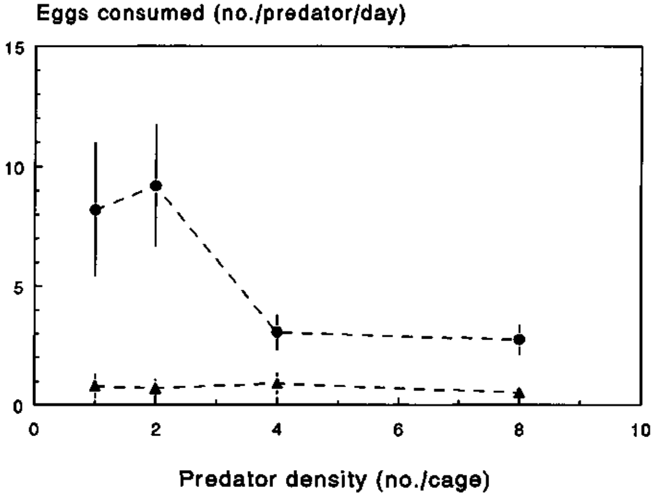


Figure 3. Rice leaffolder egg consumption per *M. vittaticollis* female at four predator densities (Exp. 9), at two plant ages: 4 WT (●) and 8 WT (▲). Means ± S.E.

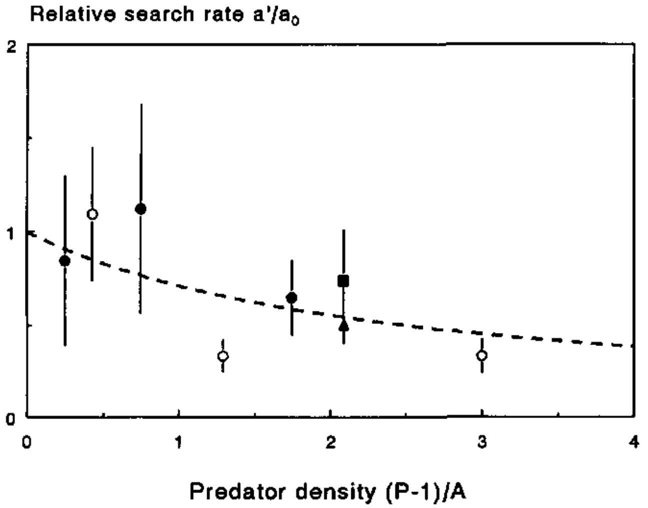


Figure 4. Relative search rate (a'/a_0) of predators, in relation to predator density (P) per leaf area (A) (Exp. 9, 10): *M. vittaticollis* females only, 4 WT (●), 8 WT (○); *M. vittaticollis* male plus female (▲), and *M. vittaticollis* female plus *A. longipennis* female (■). Means ± S.E.; dotted line represents model (Eq. 3) fitted to data from treatments with *M. vittaticollis* females only. Model fit was not significant.

Table 4. Egg predation and search rates of *M. vittaticollis* female, male and *A. longipennis* female: single and combined in 4-plant cages (Exp.10, Table 1). S.E. in parentheses.

Treatment	Egg consumption per predator [1]	Search rate a'
M. vittaticollis: adult female	8.5 (1.5) [a]	0.116 (0.022)
M. vittaticollis: adult male	5.3 (1.2) [ab]	0.069 (0.016)
A. longipennis: adult female	6.3 (1.7) [ab]	0.083 (0.024)
M. vittaticollis: adult male + female	3.5 (0.7) [b]	0.047 (0.010)
A. longipennis: adult female + *M. vittaticollis*: adult female	5.0 (1.8) [ab]	0.074 (0.027)

---

[1] in a column, means followed by a common letter are not significantly different at 5% level (LSD-test)

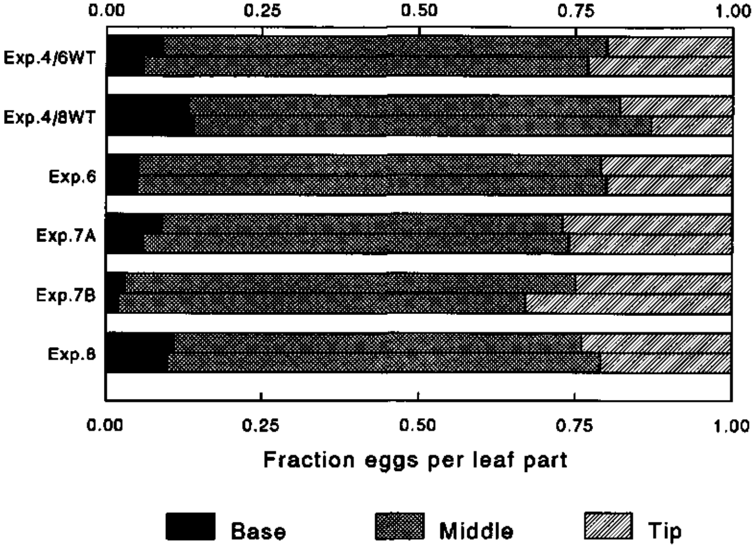


Figure 5. Distribution per leaf part of the offered eggs (upper bar) and the consumed eggs (lower bar) in six egg predation trials with *M. vittaticollis* and *A. longipennis* females.

Effect of weather conditions

The predation experiments with larger (4- and 25-plant) cages had to be conducted outside the laboratory, adding weather as a source of variation. Possible effects of four weather variables, viz. average daily temperature, R.H., rainfall and sunshine-hours, on the average search rates calculated from eight trials with *M. vittaticollis* females (Exp. 4,5,7 and 8, Tables 2 and 3) were assessed with a correlation analysis. The search rates were significantly negatively correlated with rainfall ($r^2=0.58$, df=6, $p<0.05$), but not with the other weather variables. A test with an artificial rain generator confirmed that rainfall can significantly affect egg predation by *M. vittaticollis*. Predation in mesh cages under constant 24 h rainfall was only 20% of predation under similar, but dry conditions (de Kraker unpublished). A reduction in search rates due to rainfall will have partly masked the effect of leaf area in Exp. 4 and 5, as rainfall was considerably higher during the trials with low leaf area.

Discussion

Experimental set-up

Arena size Previous studies on rice leaffolder egg predation by *M. vittaticollis* and *A. longipennis* were always conducted in single-plant arenas in the laboratory (Bandong & Litsinger 1986, Rubia & Shepard 1987a, Canapi et al. 1988, Rubia et al. 1990a). This type of arena may be suitable for a first comparison of predator or prey species (e.g. van den Berg et al. 1992), but in case of predators with high search rates and short handling times like the adult crickets, the percentage egg predation measured over 24 h is normally very high (>80%). Such predation levels are too high for a proper estimation of the functional response parameters. This problem does not occur in arenas with a very large leaf area like the 25-plant cages. These cages have the additional advantage of allowing more realistic prey and predator densities, but also require more resources and labour. The 4-plant cage was a reasonable compromise between the single- and 25-plant cages, as there was no significant difference with the 25-plant cages in the estimated cricket search rates (Table 2).

Cage effect A problem with fixed-time predation experiments in closed cages, is that predation at low densities may be overestimated due to the predator's inability to disperse (van Lenteren & Bakker 1976). The predator is forced to stay and search in low density areas, which it may leave sooner in the field. The relevance of this problem depends on whether *M. vittaticollis* and *A. longipennis* do allocate their search time in a density dependent way under field conditions. This is not likely to occur in response to leaffolder density alone, as this prey type constitutes only a moderate part of the total available prey and does not have a highly aggregated distribution pattern.

Variability in search rate The search rate of females of *M. vittaticollis* and *A. longipennis* was determined in a number of trials. These trial averages showed limited variation, partly attributed to rainfall, but did not differ significantly (Table 2 and 4). With the search rate parameters estimated in two experiments (4 and 5) the average predation rates in independent trials were reasonably well predicted (Table 3). However, at the individual level (within treatments) the variation in search rate was high, with CV values around 100%. Likely causes of this variability are purely stochastic effects due to the relatively low prey densities, and the limited pre-trial standardization of the predators. The search rate of an individual predator is related to its motivational state, which in turn is a function of its relative satiation level (Sabelis 1992, Mols 1993). A one-day starvation period was probably insufficient to standardize large differences in relative satiation level, caused by variation in body size, feeding history and reproductive stage among the field-collected predators. Predators of equal age, reared in the laboratory on a standard diet, will probably vary less in searching efficiency. However, the advantage of the use of field-collected predators is a better insight in the average potential and variability of field populations with respect to leaffolder egg predation.

Alternative approach The problems mentioned above can be partly avoided by taking a more fundamental approach to quantification of predation rates. The search rate (a') of a randomly searching predator can be determined as a product of several behavioural components: the locomotory activity, the searching speed, the reaction distance and the success ratio (Holling 1966). These components of behaviour are dependent on a variety of external and internal factors, of which temperature and satiation level are the most important

(Bell 1991, Mols 1993). In acarine predator-prey systems predation rates under variable conditions could be successfully simulated after quantifying the underlying relationships between the behavioural components and the most important driving factors (e.g. Fransz 1974, Rabbinge 1976, Sabelis 1981). The considerable advantage of this approach lies in the explanatory nature of the model, which allows application under a broad range of conditions once the model is validated.

However, in carabids, which are of comparable size as the cricket predators, assessment of the relative satiation level proved to be quite complicated, while at the lower level of physiological parameters still large differences between individuals were found (Mols 1988, 1993). For the cricket predators, measurements of the behavioural components of the search rate is very difficult due to their high mobility and large size relative to the leaffolder eggs (see Chapter 6). Because in the studied predator-prey system temperature fluctuations are only moderate and satiation effects were apparently absent over the prey range commonly found in the field, a descriptive approach based on cage predation experiments seemed most appropriate. A more explanatory approach, based on the quantification of the motivational state and its relation to behavioural components would require relatively too much effort.

Functional response and searching behaviour

The Nicholson-Bailey model, used to describe the functional response of individual cricket predators, rests on the assumptions that the effect of handling time or satiation is negligible and that the predator searches at random (Hassell 1978). The first assumption was supported by the data, as there was no decrease in the percentage predation over the tested range of egg densities. The assumption of random search cannot be confirmed by the experimental results. Although the effect of leaf area on the predation rates suggests that the predator does not find its prey through directed search (e.g. in response to kairomones), the possibility of undirected systematic search (no researching) cannot be ruled out with the current data. However, the highly mobile searching behaviour observed in the field, characterized by short visits and low exploitation of available prey on single plants (Chapter 4), makes systematic search unlikely. The similarity in distribution per leaf part between offered and consumed eggs (Fig. 5), shows that the predators do not have a search pattern biased to particular parts of the leaves.

Although the linear functional response was an adequate model for all cricket predators (Table 2), the search rate of *M. vittaticollis* females appeared to depend on prey density (Fig. 2). In this case, random search would only hold within a patch of equal prey density. A density dependent search rate could be caused by area-restricted search or by an increased searching effort motivated by frequent prey encounters (Bell 1991). There are no observational data for *M. vittaticollis* available to confirm the presence of such behavioural mechanisms. The model with a density dependent search rate was significantly better than the grand mean, but the added value was very low. It explained only about 3% of the variation in search rate. Hence, there is only little advantage in using this model over using the average search rate.

Interference

Increasing predator density did not consistently result in higher egg predation rates per cage, similar to findings by Van den Berg et al. (1992). The reason is that beyond a given predator density the per capita egg predation and search rate declined, sometimes significantly (Fig. 3 and 4). These results stress the importance of investigating the effect of predator density in addition to functional response experiments conducted with single, isolated predators. In the field, encounters between cricket predators are likely to occur, while also encounters with other species, perhaps their own natural enemies, may further reduce their searching efficiency (Bell 1991).

The model of Beddington (1975), assuming that the search rate will decline as a direct result of time-consuming encounters between predators (Eq. 3), did not fit to the data. An immediate reduction of the search rate with increasing predator density, as predicted by the model, was not observed (Fig. 4). The mechanisms underlying the observed reduction in search rate at higher predator densities are probably different or more complex than a reduction of search time due to random encounters between the predators alone. Free et al. (1977) showed that the search rate will decline as a function of predator density when their individual searching efficiency is positively dependent on prey density. This phenomenon is called 'pseudo-interference' as no direct interference is involved. In fixed-time experiments, more predators will deplete the prey faster and hence their density dependent search rate will decrease faster as well, resulting in a lower average search rate. In our experimental set-up, however, pseudo-interference cannot explain the strong reductions in search rate at the higher predator densities. The required positive relationship between predator search rate and prey density is rather weak (Fig. 2), while the search rates at the highest predator densities were much lower than expected from the egg densities at the end of the experiment. In fact, prey depletion was not even significantly affected by predator density.

Interference between individuals of the same species has been studied extensively in field crickets (subfamily Gryllinae) (Alexander 1961). These are ground-inhabiting species, which display territoriality and where aggressive behaviour is found in both males and females (Fuentes & Shaw 1986). *M. vittaticollis* and *A. longipennis* belong to another subfamily (Trigonidiinae), most of which are highly mobile foliage-inhabiting species. A comparative study of three cricket species showed that the Trigonidiinae species was not territorial and less aggressive than the Gryllinae species (Evans 1988). In crowded rearing cages antennal contacts between *M. vittaticollis* predators were frequent, but aggression was not observed (de Kraker, pers. obs.). Field observations on interference in *M. vittaticollis* and *A. longipennis* are lacking. It might be possible that the strong effect of *M. vittaticollis* density on the per capita egg predation rate is only a cage artefact.

Field predation of leaffolder eggs

Over the range of egg densities covered by this study, *M. vittaticollis* and *A. longipennis* usually showed a type I and sometimes a type III functional response, but without a plateau level (Fig. 1). Even at a density of 20 eggs per plant, i.e. 200-400 eggs per m^2 leaf area, the searching efficiency (N_a/N_0) was not reduced. Average field densities of rice leaffolder eggs are usually much lower than 20 eggs per hill (Chapter 1). A saturation of the predator's functional response is therefore not expected. The predation rates of leaffolder eggs in the field are thus limited by the capacity of the predators to find the eggs and not by their capacity to consume them, unless the density of other prey types is very high. The searching efficiency proved to be dependent on the leaf area to be searched, as postulated in the functional response model (Eq. 1). Thus, for a proper understanding of the dynamics of the leaffolder-predator interactions during the crop season, it is very important to account for the often large changes in crop leaf area.

The estimated search rates indicate that an adult cricket predator can search a leaf area of about 1,000 to 1,500 $cm^2\ day^{-1}$ effectively for leaffolder eggs, an area roughly comparable to one rice hill. The search rates of cricket nymphs were only 50% of the search rates of adults, hence it will be necessary to distinguish between the various stages when relating predator densities to egg predation levels.

The search rate of *M. vittaticollis* females may increase with prey density. The increase is steepest up to 100 eggs per m^2 leaf area (Fig. 2), which is also the range of prey densities in the field (Chapter 7). Field data seem to confirm this phenomenon as disappearance of naturally-laid leaffolder eggs was positively correlated with average egg density per field (Chapter 3). However, considering the importance of other, unknown sources of variation and the relatively weak effect of egg density on the search rate, it is questionable whether this relationship, established in cage experiments, would be detectable at field level and sufficiently explain the observed density dependence.

According to the results of the predator density trials, an increase in adult cricket density beyond 2 m^{-2} leaf area would not increase predation of leaffolder eggs significantly, due to reduced search rates. Average rice field densities of adult predatory crickets exceeding this level are not uncommon in Laguna province, Philippines. Due to their aggregated distribution local densities may often be even higher (de Kraker unpublished). When interference does occur in the field as well, it would reduce the perspectives of enhancing leaffolder egg mortality through conservation of cricket predators.

The search rates estimated in the cage predation experiments may be used to quantify the predation rate of leaffolder eggs by a field population of *M. vittaticollis* and *A. longipennis*, but this should first be validated with field measured predation rates. The relevance of density dependence and interference under field conditions can then be judged by the extent to which these factors improve the predictions of the predation rate.

Chapter 6

Predation of rice leaffolder eggs by crickets:

2. Searching behaviour and time budgets

Abstract The searching behaviour of the crickets *Metioche vittaticollis* and *Anaxipha longipennis*, important egg predators of rice leaffolder, was studied in the laboratory. Predators were observed during 1.5 or 2.5 h periods on isolated rice plants or in 30-plant cages, with rice leaffolder *Marasmia patnalis* eggs as prey.

Movement of predators over plants and between plants was close to random and the predators appeared to detect the eggs only by direct physical contact. Consumption of a single leaffolder egg took 5-30 s. After egg consumption the walking activity and speed of the predator *M. vittaticollis* did not change markedly, but locations where eggs had been consumed were revisited more often than locations where the eggs had not been detected and consumed.

The predators spent 25-50% of their time walking, and were more active and successful in the early morning and the evening than during daytime. The median residence time per plant in the 30-plant cage was 2-3 min. On isolated plants the predators covered 12-20 cm^2 leaf area per minute walking time, but failed to find and consume the leaffolder eggs in this area in about nine out of ten times. The walking activity of *A. longipennis* and *M. vittaticollis* was similar, but *A. longipennis* covered less area and visited fewer plants per unit walking time.

Estimates of the daily search rate, based on observed walking activity, encounter rate and probability of consumption, ranged from 0.01 m^2 day^{-1} for *A. longipennis* to a maximum of 0.12 m^2 day^{-1} for *M. vittaticollis*. These values are lower than calculated from cage experiments and may be underestimated because observations were done during daytime, when cricket predation activity is relatively low.

The functional response of the crickets to leaffolder egg density in previous cage experiments could be adequately described with a Nicholson-Bailey model (Chapter 5). The present analysis of cricket behaviour supports the model assumption of negligible handling time, but the assumptions of random search and constant search rate are contradicted by the apparently area-restricted searching behaviour after egg consumption.

Introduction

Rice leaffolders, *Cnaphalocrocis medinalis* and *Marasmia* spp. (Lepidoptera: Pyralidae), are considered major pests in many Asian countries (Reissig et al. 1986, Khan et al. 1988). In the Philippines a large complex of leaffolder natural enemies has been identified, that might be able to keep leaffolder populations below economic damage levels (Barrion et al. 1991a).

Field studies in irrigated rice showed that egg predation was an important mortality factor to leaffolders (Arida & Shepard 1990, Chapter 3). Two species of predatory crickets, *Metioche vittaticollis* and *Anaxipha longipennis* (Orthoptera: Gryllidae) were identified as the major predators (Chapter 4).

Metioche and *Anaxipha* spp. are distributed throughout the Indo-Australian region (Chopard 1969). The diet of both species includes a wide variety of small, slow-moving or immobile insect prey (Rothschild 1970, 1971, Rubia & Shepard 1987a, Canapi et al. 1988). The crickets are reported as predators of rice pests in Thailand, Malaysia and the Philippines, both in lowland and upland environments (Tan 1981, Yasumatsu et al. 1981, van Vreden & Ahmadzabidi 1986, Litsinger et al. 1987a, Barrion et al. 1991a). They are also common predators of insect eggs and aphids in other cereals and legume crops (Suharto 1989, van den Berg 1992, 1993).

To evaluate the impact of *M. vittaticollis* and *A. longipennis* on rice leaffolder populations, their predation rates of leaffolder eggs were determined in cage experiments. The functional response to prey density of both predator species could be adequately described by the linear Nicholson-Bailey model (Chapter 5). This model is based on the assumptions that (1) the predator searches at random, (2) prey handling time is negligible, and (3) the predator's search rate is constant and does not change with prey density (Nicholson & Bailey 1935). The search rate in the cricket predation model can be interpreted as the leaf surface area (m^2, single-sided) effectively searched by a single predator in one day (Chapter 5). The variation in search rate between individual crickets was large. For *M. vittaticollis* a small, but significant part of this variation could be explained by positive density dependence, meaning that the search rate increased with egg density (Chapter 5).

Knowledge of the behavioural mechanisms underlying egg predation by crickets would be helpful to evaluate the findings from the cage experiments and will enhance our insight in the predatory potential of these cricket species. Except for some field observations (Chapter 4) no information is available on searching behaviour of *M. vittaticollis* and *A. longipennis*. This chapter reports on direct observation experiments on the searching behaviour and time budgets of both cricket species. The aim of the present study was to derive a qualitative and quantitative description of this behaviour from predator observations under various conditions on isolated rice plants and in 30-plant cages. The outcome can be used to check the assumptions and results of the predation model based on cage experiments, and may be helpful in further modelling of field predation of leaffolder eggs by crickets.

Materials and Methods

Materials

One or two days before each experiment, potted rice plants (variety IR72) were caged overnight with female rice leaffolder *Marasmia patnalis* moths for egg deposition. The following morning the locations of the eggs were marked with a felt-tip pen by drawing 0.5 cm wide lines on the leaves, at 0.5-1.0 cm distance from the eggs. The numbers of eggs per plant were adjusted by removing leaves or leaf pieces with excess eggs. Test plants were replaced after one or two observation periods of 1.5 or 2.5 h. After each experiment the leaf area of the plants was determined with an electronic leaf area meter (LI-COR LC3100).
Predators were collected in the field and fed for one day on modified cornborer diet (Rubia & Shepard 1987a). Prior to the observations, they were starved individually for 24 h in test tubes lined with moist filter paper. For each observation period another predator was used. Predators were always wingless female adults of *M. vittaticollis*, unless mentioned otherwise.
Five experiments were carried out with single-plant observation cages. These were tubular cages (height: 100 cm, ∅: 35 cm), made from clear Mylar plastic, with a sleeve window and a nylon mesh top. Because in the first experiment predators spent considerable time feeding at the cut end of removed tillers, access to these cut ends was prevented in subsequent experiments by raising the water level in the pots. In two experiments predator behaviour was studied in a large 30-plant cage (250 × 80 × 130 cm), with walls from clear Mylar plastic. Three rows of 10 potted rice plants were spaced at 20 × 20 cm, with the leaves touching each other.
The observation cages were placed in a laboratory, where daylight could enter from two sides. Temperature ranged from 22 to 30°C. The reduction in light intensity compared to

outside was about 95%. As predators appeared to be more active at low light intensities, the daytime observations for Experiment 3-7 were done in a semi-dark room. Light intensity was reduced to about 15 lux.

Observations

Predators were observed for 1.5 h, unless stated otherwise. The frequency of events ('egg encounter', egg consumption, and oviposition) and the duration of activities (walking, sitting still, plant feeding, prey feeding, and ovipositing) were recorded. In the analysis the time spent feeding on leaffolder eggs was included in the walking bouts, as it represented only a tiny proportion of time, relative to the other activities.

As the eggs themselves are quite small (0.3 × 0.7 mm) compared to the predators (1.6 × 8 mm) and the predators fast-moving, it could not be observed whether predators contacted eggs with their palps when they did not stop to consume the egg. A success ratio (consumptions per contacts) could therefore not be determined. Instead, as a measure of searching efficiency, a 'consumption ratio' was calculated being the number of eggs consumed per number of encounters. An 'egg encounter' was defined as the event of crossing the location mark near an egg. In two experiments with single plants (Exp. 4 and 5) the egg locations were numbered, so encounters could be recorded separate per location and re-encounters could be determined. In the 30-plant cage the 'plant location' of the predator was recorded as well.

Treatments

Experiment 1: effect of starvation period. Predators were starved for 6 or 24 h prior to observation. Observations were done in daylight between 9.00 h and 16.30 h.

Experiment 2: effect of time of day. Predators were observed during four periods of 2.5 h: 4.00 - 6.30 h, 8.30 - 11.00 h, 13.30 - 16.00 h, and 18.00 - 20.30 h. During the first and the last period, flash-lights covered by red plastic were used to observe the predators' behaviour.

Experiment 3: effect of prey presence. Predator behaviour was observed on plants with 15 to 20 rice leaffolder eggs, and on plants without eggs. On the latter 15 to 20 marks were placed randomly on the leaves, to enable comparison of the walking speed.

Experiment 4: effect of prey density (no. cm^{-2} leaf area). Predator behaviour was observed on plants with 7 tillers and c. 750 cm^2 leaf area, and on plants with 14 tillers and c. 1250 cm^2 leaf area. The number of eggs per plant was the same (17.5) in both treatments, so the density in the 'high' density treatment was 0.023 and in the 'low' density 0.014 eggs per cm^2 leaf area

Experiment 5: comparison of predator species *M. vittaticollis* and *A. longipennis*. The predators were compared with regards to walking activity, encounter rate and consumption ratio on isolated plants.

Experiment 6: behaviour of *M. vittaticollis* in a 30-plant observation cage. Three of the 30 plants, all located in the same cage half, contained leaffolder eggs. Each observation period two predators were released on the border of the cage halves, on opposite sides.

Experiment 7: comparison of predator species *M. vittaticollis* and *A. longipennis* in a 30-plant cage. Four of the 30 plants contained leaffolder eggs. All four plants were located in the same cage half. The cage half with these plants was alternated between replications, to control for the effects of a light intensity gradient. Each observation period two predators (one *M. vittaticollis* and one *A. longipennis*) were released on the border of the cage halves, on opposite sides.

Analysis

Searching behaviour was characterized by three components (1) *walking activity* (fraction of time spent walking), (2) *encounter rate* (the number of egg locations encountered per minute walking time), and (3) *consumption ratio* (the number of consumed eggs per total encounters with egg locations). For predators observed in the 30-plant cage, a *plant visit rate* was calculated (plants visited per minute walking time) as a measure of between-plant mobility. Treatment effects were tested using the GLIM package (Crawley 1993), with binomial errors for fraction walking time and consumption ratio, and normal errors for encounter rate and plant visit rate. In all tests the standard level for significance was 5%. To check whether the encounter rate of predators in the same experiment was constant, linear regression was conducted on the number of encounters per walking time per predator. Observations were pooled per experiment when treatment effect on encounter rate was not significant. For the encounter rate and the consumption ratio weighted averages were calculated per experiment, with the denominators as weights. This weighted average will be less biased by stochastic effects, which can be large for relatively rare events such as egg encounters during short walking times, or egg feeding when there are few encounters.

The assumption of random search was tested by comparing observations on predator movement with predictions based on systematic or random search (cf. Morrison 1986). If a randomly searching predator makes in total k encounters with egg locations, these encounters should be randomly distributed among the total number of egg locations (N_t) on the test plant. The expected number of egg locations encountered at least one time (N_e) can then be calculated with the 'classical occupancy formula' (Johnson & Kotz 1977). In case of a systematically searching predator, the expected number of egg locations encountered at least one time will simply be equal to k, with a maximum of N_t. The randomness of predator movement between plants in the 30-plant cage was tested in a similar way. In this case, k is the total number of plant visits, N_e is the number of plants visited at least one time, and N_t is the total number of plants per cage.

To determine whether the presence of eggs affected predator searching behaviour in the 30-plant cage, total residence time and time budgets, and the number of visits were compared for plants with and without eggs. The same variables on a larger scale were compared for cage halves with and without eggs.

Calculation of a search rate

For the predators in the single-plant cages search rates were calculated, defined as the leaf area effectively searched for leaffolder eggs per time unit. The search rate is thus the product of the searching speed, the searching activity and the efficiency of searching. The searching speed, i.e. the area covered by the predators per minute walking time, was calculated by dividing the encounter rate by the number of egg locations per leaf area per plant. This implies the assumption that the predator's walking pattern over the plant was unbiased. The searching activity and the efficiency of searching per area covered were represented by the fraction of observation time spent walking and the consumption ratio respectively. For the encounter rate and the consumption ratio the weighted average was used per treatment, or per experiment when treatments were not significantly different. After conversion to the units m^2 day^{-1} the search rate estimates from the behavioural observations can be compared with the estimated values from 24 h cage predation experiments (Chapter 5).

Results

Predator behaviour

All predators spent a part of their time walking on the plant surface and sitting still on a leaf or stem. Several predators also laid eggs during the observations. Oviposition behaviour included insertion of eggs with the ovipositor into stem, leaf sheath or midrib, often followed by covering the insertion site with a dome-shaped 'plug', probably of a secreted substance. A single insertion lasted about two minutes, while covering took usually one minute. In between two ovipositions the predator moved around rather slowly.

Non-ovipositing predators walked at an apparently constant speed, continuously tapping on the plant surface with their palps. When walking, the predators did not show a distinct preference for certain parts of the plant. When predators stopped at a leaffolder egg, they invariably consumed it. Consumption of a single rice leaffolder egg took on average 22 seconds (range: 5-30 s). After consumption the predator moved on at the same speed. In the 30-plant cage the predators moved from plant to plant, either by walking when leaves touched, or by hopping. The predators spent on average 5-10 min per plant, the median being 2-3.

Some predators spent considerable time at the cut ends of removed tillers or leaves, particularly in Exp. 1. This behaviour was recorded as 'plant feeding'. These predators moved their mouth-parts, but were not consuming a noticeable amount of plant tissue. Probably they were feeding on plant sap flowing out of the cut ends. Predators were never observed to feed on undamaged plants.

Table 1. Time budgets of *M. vittaticollis* on rice plants with rice leaffolder eggs, SINGLE-PLANT CAGE. Average fractions (+S.E.) of total observation time (1.5 h; Exp. 2: 2.5 h) per activity. N = number of replicates.

Experiment			Fraction of time [a]			
No.	Treatments	N	Walking	Sitting still	Ovipositing	Plant feeding
1. **Starvation period**	6 h	12	0.26 (0.05)	0.65 (0.09)	0.00 (0.00)	0.09 (0.05)
	24 h	11	0.21 (0.04)	0.78 (0.04)	0.00 (0.00)	0.01 (0.01)
	Overall average		0.23 (0.03)	0.72 (0.05)	0.00 (0.00)	0.05 (0.03)
2. **Time of day**	4.00 - 6.30 h	4	0.48 (0.11)	0.41 (0.08)	0.11 (0.05)	0.00 (0.00)
	8.30 - 11.00 h	6	0.25 (0.09)	0.75 (0.09)	0.00 (0.00)	0.00 (0.00)
	13.30 - 16.00 h	6	0.17 (0.07)	0.79 (0.09)	0.04 (0.04)	0.00 (0.00)
	18.00 - 20.30 h	4	0.31 (0.13)	0.48 (0.06)	0.21 (0.09)	0.00 (0.00)
				*	*	
	Overall average		0.29 (0.05)	0.63 (0.05)	0.08 (0.03)	0.00 (0.00)
3. **Prey presence**	(+) eggs	12	0.42 (0.05)	0.44 (0.07)	0.09 (0.03)	0.05 (0.03)
	(−) eggs	12	0.42 (0.03)	0.42 (0.04)	0.11 (0.05)	0.05 (0.04)
	Overall average		0.42 (0.04)	0.43 (0.05)	0.10 (0.04)	0.05 (0.03)
4. **Prey density**	high	4	0.28 (0.12)	0.72 (0.12)	0.00 (0.00)	0.00 (0.00)
	low	6	0.42 (0.13)	0.58 (0.13)	0.00 (0.00)	0.00 (0.00)
	Overall average		0.36 (0.09)	0.64 (0.09)	0.00 (0.00)	0.00 (0.00)
5. **Species comparison**	*M. vittaticollis*	13	0.33 (0.06)	0.65 (0.07)	0.02 (0.01)	0.01 (0.01)
	A. longipennis	14	0.22 (0.06)	0.76 (0.06)	0.02 (0.02)	0.00 (0.00)
	Overall average		0.27 (0.04)	0.71 (0.05)	0.02 (0.01)	0.00 (0.00)

[a] non-significant treatment effects are not indicated; * = significant treatment effect, $p<0.05$

Treatment effects on searching behaviour

The average fraction of observation time spent walking ranged from 0.23 to 0.42 in the single-plant cage (Table 1), and from 0.41 to 0.49 in the 30-plant cage (Table 2). Starvation period, presence of eggs, and egg density did not affect the time spent walking. Predators

Table 2. Time budgets and plant visit rate of cricket predators, 30-PLANT CAGE. Time budgets in average fractions (+S.E.) of total observation time (1.5 h). Plant visit rate is the number of plants visited by a predator per minute walking time. N = number of replicates.

Experiment			Fraction of time [a]				Plant visit rate [a]
No.	Predator	N	Walking	Sitting still	Ovipositing	Plant feeding	
6.	*M. vittaticollis*	6	0.49 (0.08)	0.50 (0.08)	0.01 (0.01)	0.00 (0.00)	0.50 (0.09)
7.	*M. vittaticollis*	4	0.34 (0.08)	0.66 (0.08)	0.00 (0.00)	0.00 (0.00)	0.44 (0.06)
	A. longipennis	4	0.47 (0.05)	0.50 (0.05)	0.03 (0.02)	0.00 (0.00)	0.20 (0.06)
							*
	Overall average		0.41 (0.05)	0.57 (0.05)	0.02 (0.01)	0.00 (0.00)	0.30 (0.08)

[a] non-significant treatment effects are not indicated; * = significant treatment effect, $p<0.05$

seemed to be more active in the early morning and evening, with a higher walking activity and relatively more predators feeding on eggs (Table 1 and 3: Exp. 2). Although the fraction walking time did not change significantly with the time of the day, the fraction of time the predators were sitting still was significantly lower in the early morning and evening than in the morning and afternoon (Table 1: Exp. 2). Differences in walking activity between *M. vittaticollis* and *A. longipennis* were not significant in the single-plant cage, nor in the 30-plant cage.

On single plants the number of egg locations encountered per minute walking time ranged from 0.27 to 0.35 between experiments, while the consumption ratio varied from 0.04 to 0.09 (Table 3, weighted average). Starvation period, time of day, and presence of rice leaffolder eggs did not affect the encounter rate, nor (the first two factors) the consumption ratio. The encounter rate increased with egg density, but the difference was not significant. The consumption ratio of *A. longipennis* was significantly lower than of *M. vittaticollis*.

A linear relationship between the number of encounters and walking time per predator on single plants was found in Exp. 1, 2 and 5, but not in Exp. 3 and 4. The slopes of the regression lines for *M. vittaticollis* (0.41) and *A. longipennis* (0.24) were significantly different ($p<0.05$, t-test), meaning that *M. vittaticollis* encountered more egg locations per

Table 3. Percentage of predators consuming at least one rice leaffolder egg, encounter rates with egg locations (no. min^{-1} walking time) and consumption ratios of *M. vittaticollis* (average+S.E.), SINGLE-PLANT CAGE. N = number of replicates.

Experiment No.	Treatments	N	Predators feeding (%)	Encounter rate [a]	Consumption ratio [a]
1. **Starvation period**	6 h	12	13	0.40 (0.11)	0.03 (0.03)
	24 h	11	25	0.26 (0.05)	0.25 (0.25)
	Weighted average		17	0.35	0.06
2. **Time of day**	4.00 - 6.30 h	4	75	0.29 (0.10)	0.12 (0.05)
	8.30 - 11.00 h	6	17	0.38 (0.11)	0.02 (0.02)
	13.30 - 16.00 h	6	17	0.23 (0.07)	0.05 (0.05)
	18.00 - 20.30 h	4	75	0.30 (0.16)	0.07 (0.03)
	Weighted average		40	0.33	0.07
3. **Prey presence**	(+) eggs	12	25	0.27 (0.04)	0.03 (0.02)
	(−) eggs	12	–	0.32 (0.05)	–
	Weighted average		–	0.29	0.05
4. **Prey density**	high	4	25	0.52 (0.22)	0.08 (0.09)
	low	6	17	0.29 (0.11)	0.04 (0.04)
	Weighted average		20	0.27	0.04
5. **Species comparison**	*M. vittaticollis*	13	46	0.39 (0.05)	0.09 (0.03)
	A. longipennis	14	7	0.26 (0.06)	0.01 (0.01) *
	Weighted average		26	0.33	0.09

[a] non-significant treatment effects are not indicated; * = significant treatment effect, $p < 0.05$

unit walking time. In the 30-plant cage, the number of plants visited per minute walking time by *M. vittaticollis* was about 0.5 (Table 2). Compared with *M. vittaticollis*, *A. longipennis* visited significantly fewer plants at a rate of 0.2 plants per minute.

Effect of egg consumption on behaviour

The percentage of predators that consumed one or more leaffolder eggs during the observation period ranged from 17 to 40% between experiments with single plants (Table 3). In the 30-plant cage egg predation occurred only in one replicate. To test whether egg consumption affects behaviour, predators that fed on eggs ('successful') and predators that did not feed ('unsuccessful') should be compared within one treatment. Only in Exp. 5 more than five predators (*M. vittaticollis*) of both classes were available to compare the behaviour of successful predators ($n=6$) *after* the first feeding, with that of unsuccessful predators ($n=7$). The average encounter rate of successful predators after the first egg consumption was higher than of unsuccessful predators (0.58 vs. 0.33), but the difference was not significant. There was no difference between the two groups in walking activity (0.35 vs. 0.30), or in the average number and distribution of re-encounters per egg location (1.7 vs. 1.0). However, the successful predators re-encountered locations where an egg was consumed more frequently than locations where the eggs were not consumed (2.1 vs. 0.6, $p<0.01$, paired t-test).

Searching pattern

In Figure 1a the relationship between the total number of encounters (k), and the expected number of egg locations encountered at least once (N_e), is given both for a systematically and for a randomly searching predator. Most observed values for N_e fall below the 'random encounter line', meaning that on an isolated plant egg locations were more frequently re-encountered than predicted by the random search model. The pattern of encounters appears to be similar for *M. vittaticollis* and *A. longipennis*.

Figure 1b shows the relationship between the total number of plant visits (k), and the expected number of plants visited at least once (N_e) in the 30-plant cage. Again most observed values for N_e fall below the 'random visit line', meaning that some plants were more frequently visited than predicted by the random search model. *A. longipennis* seems to follow the same pattern of visits as *M. vittaticollis*. In the 30-plant cage the predators spent more time walking and plants were more frequently visited in the cage half that was near the main source of daylight. However, both variables (walking time and plant visits) were not

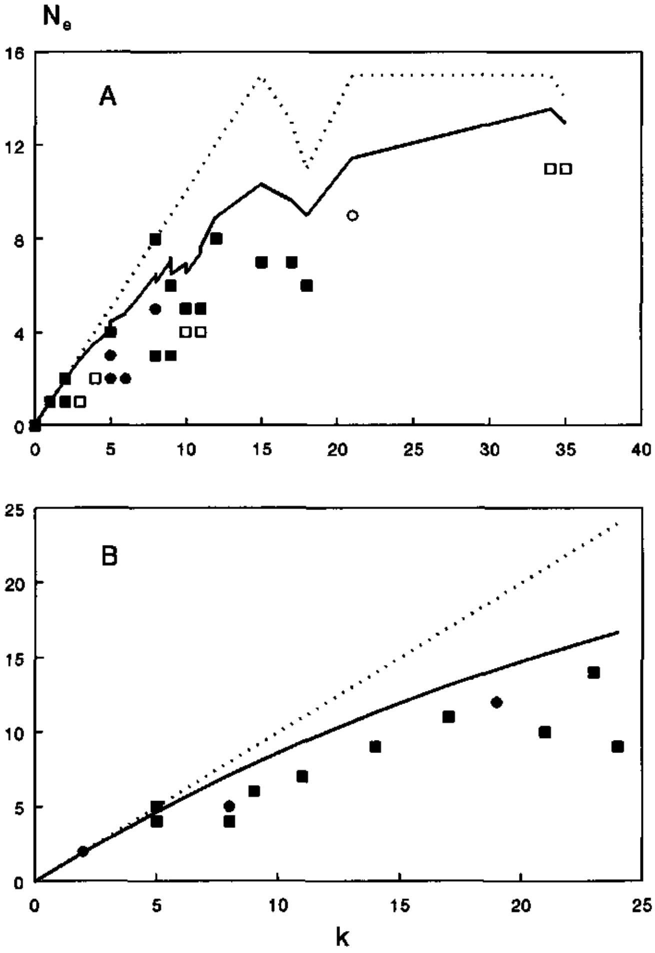


Figure 1. Cricket 'encounters' with egg locations or plants. Symbols represent observations for *M. vittaticollis* (■), and *A. longipennis* (●). Open symbols represent replicates with egg consumption. Broken line gives expected values for a systematically searching predator, where $N_e = k, k \leq N_t$, and drawn line for a randomly searching predator, where $N_e = N_t (1 - [1 - (1/N_t)]^k)$.

A. Number of **egg locations** encountered at least once (N_e), as a function of the total number of encounters per predator (k). The lines are not fluent because the total number of egg locations (N_t) differed slightly per replication. Data are from Exp. 4 and 5, SINGLE-PLANT CAGES.

B. Number of **plants** visited at least once (N_e), as a function of the total number of plant visits per predator (k). Data are from Exp. 6 and 7, 30-PLANT CAGE.

different between the cage halves with and without eggs. Plants with eggs were not more often revisited than plants without eggs. Predators spent more time sitting still on plants with eggs than on plants without eggs, but the time spent walking per plant was independent of the presence of eggs.

Search rates derived from direct observation

For the Experiments 1-5 search rates were derived from the observed walking activity, encounter rate and consumption ratio (Table 4). The search rate, defined as the total (single-sided) leaf area effectively searched for leaffolder eggs per time unit, ranged from 0.02 to 0.12 m^2 day^{-1} for *M. vittaticollis*, and was estimated at 0.01 m^2 day^{-1} for *A. longipennis*. The large difference between these predator species in Exp. 5 is mainly caused by the difference in consumption ratio. The searching speed of *M. vittaticollis* (cm^2 leaf area covered per minute walking time) ranged from 12 to 21 cm^2 min^{-1}, and the searching speed of *A. longipennis* was about 12 cm^2 min^{-1}.

Table 4. Search rates (total area effectively searched per day by a single predator) and searching speed (area covered per minute walking time), calculated from parameters measured in direct observation experiments: walking activity, encounter rate and consumption ratio, SINGLE-PLANT CAGES.

Experiment No. Predator	Leaf area (cm^2)	Egg locations (no.)	Walking activity	Encounter rate (min^{-1})	Consum. ratio	Searching speed (cm^2 min^{-1})	Search rate (m^2 day^{-1})
1. *M. vittaticollis*	750	15-20	0.23	0.35	0.06	15	0.03
2. *M. vittaticollis*	750	15-20	0.29	0.33	0.07	14	0.04
3. *M. vittaticollis*	1250	15-20	0.42	0.29	0.05	21	0.06
4. *M. vittaticollis*	750	15-20	0.36	0.27	0.04	12	0.02
	1250	15-20	0.36	0.27	0.04	19	0.04
5. *M. vittaticollis*	650	10-15	0.33	0.39	0.12	20	0.12
A. longipennis	650	10-15	0.22	0.24	0.03	12	0.01

Discussion

How do these predatory crickets find their prey ?

The direct observation experiments with rice leaffolder eggs as prey, provide elements for a qualitative description of how *M. vittaticollis* and *A. longipennis* find their prey in the rice habitat.

Prey detection The presence of eggs in single-plant experiments did not affect the searching effort, as indicated by walking activity and encounter rate (Tables 1 and 3: Exp. 3). Leaffolder eggs on a few plants in the 30-plant cage did apparently not attract or arrest the predators. The low consumption ratio shows that even when the predator almost literally runs over the eggs, it often fails to detect them. Thus, the 'reactive distance' of the predator must be very short. It seems that the predator can only detect the presence of the prey by physical contact with its palps, and that it does not make use of olfactory cues. Prey detection only by palp contact excludes the possibility of directed search, and is consistent with the observed near-random movement pattern on plants and between plants (Fig. 1). Absence of infochemical use in prey searching by *M. vittaticollis* and *A. longipennis* is understandable, as both have a broad diet and attack prey in a variety of crops. Such generalist predators are unlikely to respond to specific olfactory prey cues, while the presence of a chemical cue common to all prey species is improbable due to the wide variety in prey species and host-plants (Vet & Dicke 1992).

Effect of prey consumption Upon finding and accepting prey, a predator may shift from random search in a larger area to more intensive so-called area-restricted search (Bell 1991), or be motivated to increase its searching effort more generally by spending more time searching or walking faster (Hassell 1978). After consumption of a leaffolder egg, 'successful' *M. vittaticollis* predators did not differ in their searching effort from 'unsuccessful' predators, as the walking activity and the encounter rate were not significantly affected. However, there were indications of a change to area-restricted search after egg consumption: the number of re-encounters per egg location tended to be higher for successful than for unsuccessful predators, while the successful predators revisited the locations where they had consumed an egg more often than locations where the egg was not consumed. This behaviour on isolated plants could not be confirmed with observations from the 30-plant cage, because here feeding occurred only in one replicate. In the single-plant set-up predators searched for about 30 min on one plant, while in the 30-plant cage the walking time per plant was only 2-5 min, corresponding with field observations (Chapter 4). To conclude about the significance of area-restricted search for field predation, further study of predator behaviour after egg consumption is needed under more realistic conditions, where predators can move freely between plants.

Area-restricted search at within-plant level will be advantageous over random search when the distribution of prey is aggregated at the same level. However, data on the prey distribution of cricket predators at this small spatial scale are lacking. The distribution of prey (leaffolder eggs and other) between plants irrigated rice fields varied from random to moderately aggregated (average k value about 1.5, de Kraker unpublished). Area-restricted search at this level is therefore not expected, and appeared to be absent on field-exposed plants with a relatively high density of rice leaffolder eggs. Here, successful visits by cricket predators lasted only a few minutes, during which on average two eggs were consumed, representing less than 10% of all eggs on these plants (Chapter 4).

Differences between *M. vittaticollis* and *A. longipennis*

A. longipennis was less mobile than *M. vittaticollis*. The time spent walking was the same for both species, but *A. longipennis* searched plants at a lower speed (lower encounter rate) and visited fewer plants within a certain time period (lower visit rate). *A. longipennis* was also less efficient in detecting and accepting leaffolder eggs in the area covered (lower consumption ratio). As a result the search rate calculated for *A. longipennis* was only one-tenth of *M. vittaticollis*' search rate (Table 4: Exp. 5). It appears that *A. longipennis* is a less efficient predator of rice leaffolder eggs compared to *M. vittaticollis*. In 24 h predation experiments in 4-plant cages (Chapter 5), the search rate of *A. longipennis* was also lower than of *M. vittaticollis*, although this difference was not significant.

Search rates: comparison with cage predation experiments

The search rates estimated from the observation experiments (Table 4) are, with the exception of *M. vittaticollis* in Exp. 5, only 25-50% of the values estimated with the Nicholson-Bailey model from cage experiments with the same prey and predator combinations (Chapter 5). In these 24 h predation experiments the average search rate of female predators ranged from 0.09 (*A. longipennis*) to 0.13 m^2 day^{-1} (*M. vittaticollis*). This difference suggests that in the direct observations the values of search rate components have been underestimated. This may be caused by conducting (most of) the observations between 9.00 and 16.00 h. When observed at different times of the day, the predators were more active during early morning and evening (Table 1: Exp. 2). They also appeared to search more efficiently during those periods, as indicated by the percentage of predators feeding and the higher consumption ratios (Table 3). Field observations on leaffolder egg predation by *M. vittaticollis* and *A. longipennis* also showed that these crickets were most active around sunrise and sunset (Chapter 4). Such circadian rhythms in searching and feeding involve usually a mixture of endogenous and exogenous effects (Saunders 1982). It appears that in *M. vittaticollis* the daily pattern is partly determined exogenously by light intensity, because the daily pattern in the laboratory was not as pronounced as in the field, while reduction of light intensity in the observation room also seemed to stimulate predator activity. Sensitivity to light intensity is common in crepuscular (twilight-active) species (Saunders 1982), and considering its activity pattern, *M. vittaticollis* may be such a species. However, when the circadian rhythm is co-determined by endogenous factors, twilight and night time observations will be imperative for a proper estimation of the daily search rate.

In addition to the complications caused by a daily activity pattern, the egg density proved too low or the observation period of 1.5 or 2.5 h too short for a reliable estimation of the consumption ratio. On average feeding occurred in one or two out of twenty encounters with egg locations. As the number of encounters per predator was usually less than twenty per observation period, stochastic effects will produce large variation, and, with insufficient replication, strongly biased values for the consumption ratio.

Do the observations support the assumptions of the predation model ?

Random search The cricket predators did not search rice plants in a systematic way, while the random search model fitted better to the observations (Fig. 1a). Most of the observations fall below the 'random search line', indicating that the predators re-encountered eggs more frequently than predicted by the random search model. Similar results were found for predator movement between plants (Fig. 1b). These less-than-random movement patterns may have been caused by the experimental set-up, e.g. by restricting movement to one isolated plant or by the light intensity gradient in the 30-plant cage. Area-restricted search induced by egg consumption was not an important factor underlying the pattern in encounters, as egg consumptions were relatively rare and replicates with and without egg consumption show the same trend (Fig. 1a).

When success-motivated area-restricted search by cricket predators would occur in the field, a predation model based on constant random search is in principle incorrect, although it may give an adequate description over a range of prey densities (Chapter 5). The error in predictions by such a model will depend on the intensity and duration of area-restricted searching behaviour and on prey density and distribution. Then, a better approach would be to base the functional response model on directly measured behavioural components, including a variable for the deviation from randomness in walking behaviour (e.g. Mols 1993).

Negligible handling time Consumption of a single leaffolder egg took about 20 s, a value comparable to earlier field observations (15-30 s, Chapter 4). The short consumption time alone will not be a limiting factor in predation, unless prey densities are extremely high. This does not necessarily mean that handling time, as it appears in the Random Predator Equation (RPE, Rogers 1972), is negligible, because it also includes periods of non-searching activity induced by feeding, e.g. a digestive pause and cleaning (Hassell 1978). The absence of a plateau level in the functional response of *M. vittaticollis* and *A. longipennis* (Chapter 5) demonstrated that this component of handling time was not limiting predation over the tested density range. Moreover, in the present behavioural study no clear pattern of sitting still or grooming after egg consumption was observed.

Search rate: constant or density dependent Search rate components may be affected by numerous factors (see for review Bell 1991), but for the Nicholson-Bailey functional response model the effect of prey density is most relevant. For *M. vittaticollis* the three components of the search rate, walking activity, searching speed and particularly consumption ratio were highly variable within and between the observation experiments. However, they were not significantly affected by predator starvation period and presence or density of leaffolder eggs, suggesting that the search rate was independent of prey density.

The starvation period, or time since last meal, will be indicative of the prey density in the predator's habitat. The lower the prey density, the more hungry the predator will be. As a predator's searching behaviour changes almost invariably with hunger level (Bell 1991, Sabelis 1992), its search rate will be, usually negatively, density dependent. In *M. vittaticollis* however, an extension of the starvation period from 6 to 24 h after feeding *ad libitum* on artificial diet did not lead to observable changes in behaviour, suggesting that hunger (or satiation) affects behaviour more strongly when gut fullness is approached. This is consistent with the cage predation experiments, where the functional response of predators starved for 24 h did not reflect satiation effects up to leaffolder egg consumption levels of about 25% of the daily maximum (Chapter 5).

A problem with the egg presence and density treatments is that the predators may not have perceived the difference. As contacts without consumption could not be observed, we can only be sure that the predator perceived the presence of an egg in case of egg consumption, which was a fairly rare event in both experiments (in <25% of replicates). In Exp. 5 egg consumption was more common and appeared to induce area-restricted search by *M. vittaticollis*, but did not affect general searching effort. Area-restricted search may result in a positively density dependent predation rate when prey aggregation increases with density. However, it cannot explain the density dependence observed in cage predation experiments (Chapter 5), as in these cages the distribution between and within plants did not change with density.

Conclusions

The direct observations experiments provided insight into the searching behaviour of these predatory crickets and how they find their prey in a rice field habitat. The observations were useful in evaluating predation model assumptions. Predators moved nearly random on and between plants, and seemed to detect leaffolder eggs only by direct physical contact with their palps. The time needed to consume a single egg was short (20 s), supporting the assumption that prey handling time can be neglected. On isolated plants the predator's searching behaviour after egg consumption was apparently area-restricted. When such behaviour is significant in the field, it would make a model based on random search inadequate. No evidence was found for an effect of prey density on the search rate, but considering the large variation in search parameters determined in 1.5-2.5 h observation periods, relatively small changes in searching behaviour will not be detected with the present approach.

Although estimates of daily search rates could be derived, the observation set-up appeared not suitable for this purpose. Direct measurement of behavioural components was complicated by the small size of the eggs relative to the predator and its high walking speed, and due to a circadian activity pattern. These direct observation experiments did therefore not provide an alternative to cage predation experiments and the descriptive models based on these experiments.

Chapter 7

A model of predation of rice leaffolder eggs in the field

Abstract A preliminary, deterministic model of predation of rice leaffolder eggs in the field is described and evaluated with independent data from eight different rice crops in Laguna Province, the Philippines. The model is based on cage predation experiments and includes the functional response of five predator types: three types of predatory crickets (*Metioche vittaticollis* adults, *Anaxipha longipennis* adults, and nymphs of both species), a coccinellid (*Micraspis* sp.), and carabids (*Ophionea* spp.). In the model, the search rate of adult crickets depends positively on prey density and decreases when cricket density exceeds a given threshold density.

Evaluation of the preliminary model with field data showed that it could be simplified to a large extent. Predictions of the field predation rates improved after removing predation by *Micraspis* sp. and *Ophionea* spp., the effect of prey density on the search rate of *M. vittaticollis*, and the distinction between *M. vittaticollis* and *A. longipennis* adults. The resulting simplified model included only the functional response of cricket adults and nymphs, and a 50% reduction of adult cricket search rates when their density was more than 1.5 m^{-2} leaf area. The evaluations confirmed field observations on the major role of predatory crickets in leaffolder egg predation and suggest that predator interference is an important mechanism limiting their predation rates. The effect of alternative prey on the predation rate seemed negligible. The simplified model described the observed trend in egg predation rates reasonably well and can be applied to explore the effects of changes in predator abundance.

Introduction

Rice leaffolders *Cnaphalocrocis medinalis* and *Marasmia* spp. (Lepidoptera: Pyralidae) are considered a major pest in many Asian countries (Reissig et al. 1986, Khan et al. 1988). The larvae injure the rice plants by folding the leaves and scraping off the green mesophyll tissue inside the leaffolds (Fraenkel & Fallil 1981, Fraenkel et al. 1981). Leaffolder injury is highly visible and rice farmers usually respond to it by applying insecticides, even at very low infestation levels (IRRI 1993c, Heong et al. 1994). However, most sprays are probably not economical, because under good growing conditions a rice crop can tolerate a substantial amount of defoliation without suffering yield loss (e.g. Hu et al. 1993, IRRI 1993c). Mortality inflicted by the numerous naturally-occurring predators and parasitoids may therefore be sufficient to keep the leaffolder population below economic damage levels most of the time (Khan et al. 1988, Barrion et al. 1991a). With knowledge of the identity and the impact of the major natural enemies, strategies can be developed to make optimal use of natural biological control (Shepard & Ooi 1991, Waage 1992).

In irrigated rice in the Philippines, egg predation by chewing predators is an important mortality factor to rice leaffolders (IRRI 1981, Arida & Shepard 1986, Chapter 3). The level of egg disappearance was positively correlated with the density of the predatory crickets *Metioche vittaticollis* and *Anaxipha longipennis* (Orthoptera: Gryllidae), but not with the density of other predators (Chapter 3). The importance of *M. vittaticollis* and *A. longipennis* was confirmed by direct observation of egg predation in the field (Chapter 4). The two species took about 90% of all consumed eggs, the remaining 10% being consumed by *Micraspis* sp. (Coleoptera: Coccinellidae), *Ophionea nigrofasciata* (Coleoptera: Carabidae), and *Conocephalus longipennis* (Orthoptera: Tettigoniidae). *M. vittaticollis* and *A. longipennis* also ranked highest in petri-dish tests on acceptance and daily consumption of rice leaffolder eggs (Chapter 4).

In a series of cage experiments, prey preference, functional response and interference were quantified for several predators of rice leaffolder eggs (Chapter 4 and 5). These relationships, determined at a small scale with only one or two predator and prey types, are combined in a model with the aim to predict the predation levels of leaffolder eggs under the multiple predator - multiple prey conditions in the field. In contrast to regression models (Chapter 3), this model describes egg predation in terms of functional relationships with predator density. It should therefore be more generally applicable. The model may serve to evaluate the potential impact of rice field predators on leaffolder egg mortality, and, with a combined pest-crop model, to study their impact on rice leaffolder damage. This chapter describes the predation model and its evaluation with independent field data. The applicability of the model is illustrated with an exploration of the effects of enhanced peak densities or earlier immigration of the major egg predators on the egg predation rate.

Materials and Methods

Description of the model

The model calculates a daily field predation rate of leaffolder eggs based on the actual abundance of the major predators. The decision which predator species should be included was based on direct field observations of predation events and on laboratory feeding tests (Chapter 4). Five predator types are included in the model: *M. vittaticollis* adults, *A. longipennis* adults, nymphs of *M. vittaticollis* and *A. longipennis*, adults and larvae of *Micraspis* sp., and adults of *Ophionea* spp. *C. longipennis*, in spite of being the most abundant chewing predator, was not included as it had a negligible share in field observed predation of leaffolder eggs ($<2\%$). Moreover, its consumption rate on leaffolder eggs in petri-dishes was relatively low, and it preferred to feed on the rice plants rather than on leaffolder eggs (Chapter 4).

Model structure Daily predation rates of leaffolder eggs are a function of the density of the various predators per m^2 leaf area and predator-specific search rates. The predation rate is calculated as a *relative* rate (proportion of eggs consumed):

$$N_a/N = 1 - \exp[-\Sigma\, a'_i\, T\, P_i\, /\, A\,] \qquad \text{(Eq. 1)}$$

where N_a is the number of eggs consumed in one day (m^{-2} ground day^{-1}), N is the initial egg density (m^{-2} ground), P_i is the density of predator i (m^{-2} ground) ($i=1,..,n$), a'_i is the search rate for leaffolder eggs of predator i (m^2 leaf day^{-1}), A is the crop leaf area index (m^2 leaf m^{-2} ground), and T ($=1$) is the total time available for predation (day). The search rates represent the crop leaf area that can be effectively searched in one day by a single predator. Effectively searched means that within the area searched all prey are found and consumed (Chapter 5). The predators are assumed to search the crop foliage randomly for prey. Laboratory observations on the searching behaviour of *M. vittaticollis* and *A. longipennis* females indicated that their searching pattern may deviate from random (Chapter 6), but a model assuming random search gave an adequate description of the functional response in cage experiments over a large range of leaffolder egg densities (Chapter 5).

In cage experiments, the search rate of *M. vittaticollis* increased significantly with initial leaffolder egg density (Chapter 5). Therefore, the search rate of *M. vittaticollis* adults in the model is made dependent on total prey density, on the assumption that for this generalist predator the positive effect of prey density is independent of prey type. The search rate is at a minimum when no prey is present and approaches an upper limit as prey density increases:

$$a' = (a'_{min} + c_1\, a'_{max}\, N / A) \,/\, (1 + c_1\, N / A) \qquad \text{(Eq. 2)}$$

where a' is the density dependent search rate, a'_{max} the maximum search rate (or: maximum leaf area effectively searched per predator in one day), a'_{min} the minimum search rate, and c_1 a constant, representing the rate of increase in search rate with prey density.

The search rates of adult *M. vittaticollis* and *A. longipennis* are also made dependent on their own density. A model commonly used to describe the effect of interference between predators on the search rate (Beddington 1975, Hassell 1978) did not fit the experimental results (Chapter 5). Therefore, the effect of predator density is described with a simple switch function: the search rates of both predators are reduced when their combined density exceeds a threshold value.

Equation 1 is in fact a multiple-predator functional response model of the Nicholson-Bailey type, without any effects of satiation or handling time on the predation rate. Experiments on the functional response to rice leaffolder egg density of *M. vittaticollis* females and nymphs, *A. longipennis* females and *Micraspis* sp., showed that an effect of satiation or handling time was absent over a wide range of leaffolder egg densities (Chapter 5 and unpublished data). However, in the field none of the predators feeds only on leaffolder eggs. Their diet includes a wide variety of small insect stages, such as eggs, young lepidopterous larvae and hopper nymphs (van Vreden & Ahmadzabidi 1986; Shepard et al. 1987). Predation on prey types other than rice leaffolder eggs may affect the predation rate of leaffolder eggs by reducing the available time for searching through increased handling time, or by satiation effects on searching behaviour (Hassell 1978). The more these other prey types are preferred over rice leaffolder eggs, the lower the predation of leaffolder eggs will be when the daily predation rate is limited by handling time or satiation. The possibility that the presence of alternative

Table 1. Parameter values for the egg predation model: average search rates (a'_{avg}) and parameters of the density dependent search rate (a'_{max}, a'_{min}, c_1). Data are from chapter 5 and unpublished experiments.

Predator	a'_{avg}	a'_{min}	a'_{max}	c_1
M. vittaticollis - adults	0.13	0.07	0.016	0.0085
M. vittaticollis - nymphs	0.05	–	–	–
A. longipennis - adults	0.09	–	–	–
Micraspis sp. - adults+larvae	0.012	–	–	–
Ophionea spp. - adults	0.005	–	–	–

prey will affect the predation rate of leaffolder eggs was therefore investigated with the available field data.

Model parameters The search rates for leaffolder eggs of the various predator types (Table 1) were determined in single- or multiple-plant cages, with known egg density and leaf area (Chapter 5 and unpublished data). No significant difference in search rate between *M. vittaticollis* females and males was found, so for both sexes the same, average value is taken. The search rate of *A. longipennis* females was lower than that of *M. vittaticollis* females. Although this difference was not significant, behavioural observations in the laboratory also indicated that *A. longipennis* was a less efficient predator of leaffolder eggs than *M. vittaticollis* (Chapter 6). Therefore, separate values for their search rates are included. It is assumed that *A. longipennis* males have the same search rate as females. The search rates of *M. vittaticollis* nymphs (instar 1-3) were significantly lower than those of adults. There was no difference in search rates between instar 1-2 and instar 2-3, while the search rate of 4th instars was not determined. In the model, all *M. vittaticollis* nymphal stages are lumped, with a single average search rate value and it is assumed that nymphs of *A. longipennis* have a similar search rate. The search rates for adults of *Micraspis* sp. and *O. nigrofasciata* were determined with a single-plant set-up. In addition to the adults of *Micraspis* sp. and *O. nigrofasciata*, relatively low numbers of *Micraspis* sp. larvae and *Ophionea ishii-ishii* adults were found in field samples. It is assumed that *Micraspis* larvae have the same search rate as adults, and that adults of *O. ishii ishii* have the same search rate as *O. nigrofasciata*.

The parameters for the relationship between prey density and the search rate of *M. vittaticollis* adults (Eq. 2) were estimated with non-linear regression from cage predation experiments with rice leaffolder eggs (Chapter 5). These experiments were only conducted with females, but it is assumed that males of *M. vittaticollis* respond in the same way to prey density.

Predator density had a significant effect on the search rate of *M. vittaticollis* adults and *A. longipennis* females in cage predation experiments (Chapter 5). *A. longipennis* males were not included in the experiments, nor was the effect of all possible cricket predator combinations studied. It is assumed that the effect of predator density is the same, irrespective of the sex ratio and species composition of the predatory cricket population. The search rates are reduced by 50% when the density of adult cricket predators exceeds a 'threshold value' of 1.5 m^{-2} leaf area (Fig. 1).

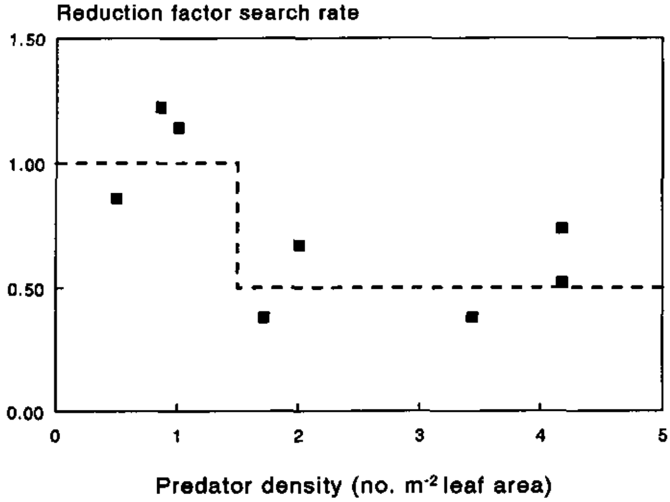


Figure 1. Effect of adult cricket density on the individual search rate for rice leaffolder eggs. Symbols: data recalculated from cage experiments with *M. vittaticollis* and *A. longipennis* (Chapter 5); broken line: input relationship for the egg predation model.

Model evaluation

The presented predation model is a synthesis of relationships determined in controlled cage experiments. This model, from now on called the 'preliminary' model, may contain variables or relationships (components) which are not valid or not important under field conditions. The first step in the evaluation of the predation model was to check whether the preliminary model could be simplified by identifying and removing these components. The second step in the evaluation was to test the resulting 'simplified' model by comparing predictions with predation rates measured in the field.

Collection of field data An independent set of field data was used to evaluate the predation model. The data were collected in eight unsprayed rice crops in Laguna Province, Philippines, and cover three locations and five seasons (Table 2). Rice leaffolder egg predation rates were measured by field exposure of laboratory-laid eggs for two days, or by daily monitoring the fate of naturally-laid eggs (see Chapter 3 for details). In the same week, the abundance of predators and prey, and the leaf area of the crop were determined. Sedentary insect prey were sampled by collection and examination of whole rice plants, while mobile prey and predators were sampled with a suction sampler in combination with an enclosure covering four rice hills. Crop leaf area was measured from an additional plant sample with an electronic leaf area meter (LI-COR LC3100).

Data collection in 1993 was more detailed than in previous years. Distinction was made between adults and nymphs of predatory crickets (*M. vittaticollis*, *A. longipennis*). Sedentary insect stages other than lepidopterous eggs were also recorded. When no information was available on their acceptability, frequently encountered species of potential prey were offered to *M. vittaticollis* females in petri-dishes. The more detailed data from the three 1993 crops will be referred to as the 'core' data set, while the data from the other five crops will be called the 'additional' data set (Table 2).

Effect of alternative prey The assumption that the presence of alternative prey does not reduce the predation on leaffolder eggs was tested by comparing the highest predicted field predation rates (per capita) of adult *M. vittaticollis* and *Micraspis* sp. on their major prey

Table 2. Field experiments on rice leaffolder egg predation, Laguna Province, Philippines. Methods used to measure predation rates: (a) exposure of laboratory-laid eggs, (b) monitoring naturally-laid eggs. Prey and predator densities were estimated by whole plant sampling and suction sampling respectively; sample sizes are indicated; sampling units: plant samples = 1 hill, suction samples = enclosure covering 4 hills.

Location	Area (ha)	Variety	Year	Season	Transplanting date	Time of measurement (week after transplanting)	Methods used	Sample size	
								Plant	Suction
'CORE' data set:									
Pila	0.34	IR72	1993	dry	4 February	4, 5, 6, 7, 8, 10, 13	a, b	65	25
Pila	0.34	IR72	1993	wet	16 August	4, 7, 9, 12	a	50	30
IRRI	0.25	IR72	1993	wet	17 July	7, 8, 9	a, b	50	30
'ADDITIONAL' data set:									
Victoria	0.49	R-10	1991	dry	12 January	3, 6, 9, 12	a	50	25
Pila	0.62	C-4	1991	dry	4 January	4, 7, 10, 13, 15	a	50	25
Pila	0.08	IR70	1991	wet	31 August	5, 7, 10, 12	b	15	6
Pila	0.34	C-4	1992	dry	27 January	5, 6, 7, 8, 9	b	100	24
IRRI	0.25	IR72	1992	wet	23 June	3, 5, 7, 9, 11, 13	a	30	15

types, with their maximum daily consumption rates. For *M. vittaticollis* the available estimates of the maximum daily consumption rates of prey other than rice leaffolder eggs are probably conservative values, as they are derived from experiments where either the supply or the search rate was limiting prey consumption.

Field predation rates were calculated with the field densities of the prey and predator, and the predators' search rates for the respective prey types. Search rates for prey types other than rice leaffolder eggs were calculated from a preference index, determined in choice tests with rice leaffolder eggs (Chapter 4), and the search rate for leaffolder eggs (Table 2). The preference index α_i (Manly 1974) can be interpreted as the search rate for prey type *i*, relative to the sum of the search rates for all the prey types present (Chesson 1983).

Model simplification Simplification of the 'preliminary' model was conducted in two steps: (1) assessment of the potential impact of model components based on field input values; (2) assessment of the contribution of model components to model performance based on comparison with field measurements.

(1) The effect of the various components of the preliminary predation model on the calculated predation rates was tested with the field data set. Depending on their potential contribution under field conditions the components were either excluded or retained in the model, resulting in an 'intermediate' model. The potential contribution of the various predator types was determined by calculating their (relative) predation rates of leaffolder eggs over the observed density range. The potential effect of total prey density on the search rate of *M. vittaticollis* females was assessed with the observed range in prey density as input values. The potential importance of the interference function was judged by the frequency that the density of adult predatory crickets exceeded the 'interference-threshold' of 1.5 m^{-2} leaf area.

(2) Predictions by the resulting 'intermediate' model were compared with the observed field predation rates, using the 'core' data set. All variables or relationships that did not contribute positively to model performance were removed from the intermediate model. To quantify model performance two criteria were used: the deviance of model predictions from the observed values, measured by the 'mean absolute error' (MAE), and the overall goodness of fit of model predictions to the observations, measured by the 'modelling efficiency' (EF).

MAE and EF are defined as:

$$\mathrm{MAE} = (\Sigma\ |o_i - p_i|)\ /\ n$$

$$\mathrm{EF} = 1 - \Sigma(o_i - p_i)^2\ /\ \Sigma(o_i - \bar{o})^2$$

where o_i represent observed values of the predation rate, $\bar{o}$ the mean of the observations, p_i predicted values, and n the number of pairs (Mayer & Butler 1993). For the modelling efficiency EF an upper value of 1 indicates that the predictions perfectly match the observations, while if EF is less than 0 the model predicts worse than the mean of the observations. The procedure followed to arrive at the simplified model was stepwise elimination from the intermediate model. During each step all remaining components were removed from the model one at the time. The component resulting in the largest improvement in model performance when removed, was eliminated. Only those components were retained in the model that resulted in an increase in deviance and decrease of overall fit when removed from the model.

Model testing The simplified model was tested with both the 'core' and the 'additional' field data set. As the distinction between cricket nymphs and adults turned out to be important, the percentage nymphs at each sampling date in the 'additional' data set had to be estimated. This was done by determining a linear relationship between the percentage crickets in nymphal stages and crop stage using the 'core' data set ($r=0.67$, $p<0.01$).

To test the model, plots of observed vs. predicted predation rates were made and the regression lines calculated. A simultaneous F-test was conducted for intercept=0 and slope=1, to determine whether the regression line was significantly different from the 1:1 line (Dent & Blackie 1979). A significant F-value indicates model bias. The error in model predictions and overall goodness of fit were assessed with the MAE and EF statistics as above.

So far, the variance of model predictions has been ignored. In fact model output is probabilistic due to the sample variance of the input variables, viz. predator densities and crop leaf area. The predicted predation rates are therefore not exact values, but may even have large standard errors (e.g. Stewart & Dixon 1988). Approximate values for the error variance of model output were calculated as a function of the error variances of the input variables (ten Berge 1990, Rossing 1991). The error variance of the (mean) observed predation rate per plant was calculated from the predation rates measured on exposed plants with laboratory-laid eggs. Knowledge of the error variance of both model output and observed values permits statistical evaluation of the difference between the predicted and observed predation rates on each observation date with a t-test (cf. ten Berge 1990).

Results

Field data

The five predator types were present in all eight crops, with no large differences in their average densities (Table 3). Also their seasonal trends in abundance followed roughly the same pattern: densities started to increase about one month after transplanting, and peaked during the ripening stage. Apart from the eggs of rice leaffolders *C. medinalis* and *Marasmia* spp., green hairy caterpillar *Rivula atimeta* and rice whorl maggot *Hydrellia philippina*, two other potential prey types were commonly found on the rice plants. These were the egg-masses of marsh flies (*Sepedon* spp.), and the pupae of the rice whitefly *Aleurocybotus* sp. Both prey types were readily accepted by female *M. vittaticollis* predators when offered in petri-dishes. Eggs of rice ear bugs *Leptocorisa* spp. are also common during the ripening phase of the crop, but these hard-shelled eggs are not accepted by *M. vittaticollis* (Rubia & Shepard 1987a). Egg densities of other species, mostly egg masses of stemborers, were relatively low. The seasonal trend in abundance was similar for most prey types: densities increased from three weeks after transplanting and peaked at the booting stage. An exception are *H. philippina* eggs, which are abundant at the start of the crop and then sharply decline in numbers, because *H. philippina* prefers a young open crop for oviposition (Reissig et al. 1986).

Table 3. Values of input variables (average and range) in field data sets (Table 2), used for evaluation of the egg predation model. Predator and prey density in no. m^{-2}. Plant density in the fields was 25 hills m^{-2}. Crop leaf area in m^2 leaf area m^{-2} soil.

Variable		Average	Range	Data set
Predator density				
M. vittaticollis	adults	1.2	(0 - 3.8)	'core'
A. longipennis	adults	2.3	(0 - 7.9)	'core'
Gryllidae [a]	nymphs	3.0	(0 - 11.6)	'core'
Gryllidae [a]	nymphs + adults	4.8	(0 - 19.1)	'core'+'additional'
Micraspis spp.	larvae + adults	2.3	(0 - 19.8)	'core'+'additional'
Ophionea spp.	adults	1.4	(0 - 6.1)	'core'+'additional'
Prey density				
rice leaffolders [b]	eggs	6.0	(0 - 25.5)	'core'
R. atimeta	eggs	5.5	(0 - 16.5)	'core'
H. philippina	eggs	20.8	(0 - 122.3)	'core'
Sepedon spp.	eggs	6.3	(0 - 28.0)	'core'
other	eggs	1.0	(0 - 2.3)	'core'
Aleurocybotus sp.	pupae	9.0	(0 - 37.0)	'core'
Homoptera	nymphs + adults	75.8	(0 - 399.8)	'core'+'additional'
Crop leaf area		3.8	(0.7 - 6.3)	'core'+'additional'

[a] includes *M. vittaticollis* and *A. longipennis* [b] includes *C. medinalis* and *Marasmia* spp.

Effect of alternative prey

Even the highest predicted predation rates of several prey species per predator were far below the maximum daily consumption rates of both *M. vittaticollis* and *Micraspis* sp. (Table 4). Also the highest predicted predation rates on all prey types together (*M. vittaticollis*: 7, *Micraspis* sp.: 2) were low compared to the highest daily consumption rates known from laboratory tests.

Model simplification

The potential contribution of *Ophionea* spp. to rice leaffolder egg predation was negligible compared with the other four predator types, even at their highest densities (Fig. 2). On average its predation rate on rice leaffolder eggs was less than 20% of the predation rate of *Micraspis* sp. and less than 10% of the predation rates of the predatory crickets. Therefore,

Table 4. Search rate (*a'*), highest predicted field predation rate (Field), and maximum consumption rate (Maximum) of various prey types for the predators *M. vittaticollis* and *Micraspis* sp. RLF = rice leaffolder eggs; GHC=green hairy caterpillar eggs; RWM=rice whorl maggot eggs; Other=other sedentary prey; Hopper=nymphs of plant- and leafhoppers.

Predator		Prey					
		RLF	GHC	RWM	Other	Hopper	ALL
M. vittaticollis	*a'*	0.13	0.30	0.13	0.30	0.005	
	Field	< 1	2	3	2	< 1	7
	Maximum	200	28	38 [c]	10	5-10 [a]	
Micraspis sp.	*a'*	0.012	0.018	0.008	0.018	0.008	
	Field	< 1	< 1	< 1	< 1	1	2
	Maximum	19	14	-	-	3-6 [b]	

[a] Rubia & Shepard 1987, [b] Win 1989, [c] van den Berg et al. 1992

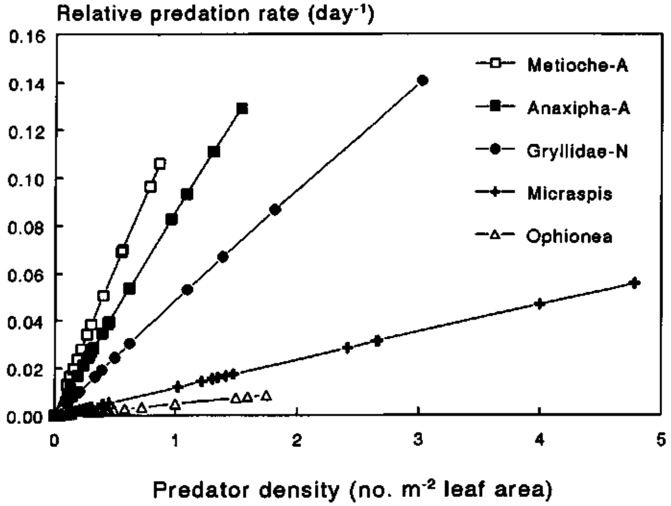


Figure 2. Relative predation rates of rice leaffolder eggs (fraction day^{-1}) by each of the five predator types included in the predation model, based on their observed densities (field data sets, Table 3).

this predator was excluded from the model. Despite its low search rate, *Micraspis* sp. could have a considerable impact due to its relatively high abundance. The predatory crickets clearly had the highest potential contribution to leaffolder egg predation.

The observed range in prey density of *M. vittaticollis* was wide enough to have a considerable effect on the search rate, when this was made density dependent (Fig. 3). The maximum increase in the search rate was over 60%. The observed density of adult *M. vittaticollis* and *A. longipennis* exceeded the 'interference threshold' (1.5 m^{-2} leaf area) about 25% of the time. Both mechanisms, density dependent search rate and interference among predators, were therefore retained in the intermediate model.

This model could further be simplified by removing the components that did not contribute positively to model performance when tested against the 'core' data set (Table 5). Replacing the density dependent search rate of *M. vittaticollis* by its average value considerably

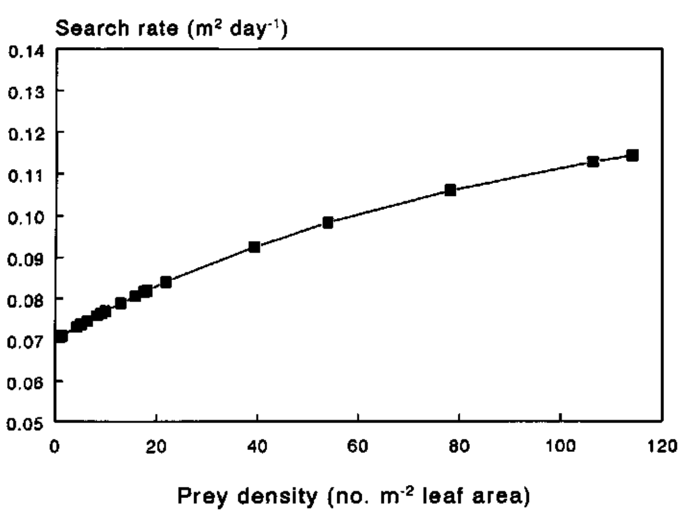


Figure 3. Effect of the observed prey density (field data sets, Table 3) on the search rate of *M. vittaticollis* adults.

Table 5. Stepwise simplification of the egg predation model. MAE = mean absolute error, EF = modelling efficiency. See text for details.

Step	Change in model	Model performance		Conclusion
		MAE	EF	
0.	'intermediate' model	0.049	−0.156	
1.	remove density dependence	0.046	−0.018	remove from model
2.	single value for search rate of cricket adults	0.046	+0.047	adopt single value
3.	exclude *Micraspis*	0.043	+0.108	exclude *Micraspis*
4a.	exclude cricket nymphs	0.052	−0.190	retain cricket nymphs
4b.	exclude cricket adults	0.085	−2.107	retain cricket adults
4c.	remove interference	0.070	−1.221	retain interference effect

improved model fit (EF value). Subsequently, adoption of one single value for the predation rate of *M. vittaticollis* and *A. longipennis* adults (a'=0.13) further increased modelling efficiency. Excluding *Micraspis* sp. in the third simplification step improved model performance even more. In the fourth step removal of each of the remaining components had negative effects on model performance. The resulting simplified model included two predator types, cricket adults and nymphs, and a 50% reduction of adult cricket search rates when their density was more than 1.5 m^{-2} leaf area.

Model testing

The modelling efficiency (EF) of the simplified model was +0.108, indicating that the observed values were closer to predicted values than to the grand mean. Mean absolute error was 0.046 (Table 5), which represents a relative error of about 40% of the observed mean predation rate. The simplified model tended to underestimate egg predation rates: most predicted predation rates were lower than the observed values, in both the 'core' and the

Table 6. Performance of the simplified egg predation model: bias, assessed by F-test for difference between the regression line of 'predicted' vs. 'observed' predation rates and the 1:1 line; mean absolute error of predictions (MAE); and modelling efficiency (EF). N = number of data pairs (observed and predicted). S.E. in parentheses.

Data set	N	Linear regression [a]			F-value [a] (bias)	MAE	EF
		Slope	Intercept	R^2			
CORE'	14	0.62 (0.24)	0.03 (0.03)	0.37 *	1.68 n.s.	0.043	+0.11
'CORE' minus Rain	10	0.90 (0.27)	0.00 (0.03)	0.58 *	0.21 n.s.	0.034	+0.38
'ADDITIONAL'	24	0.62 (0.17)	0.01 (0.02)	0.38 **	6.71 **	0.096	−0.62
'ADDITIONAL' minus Rain	15	0.79 (0.25)	0.00 (0.06)	0.43 **	1.82 n.s.	0.049	−0.07

[a] n.s.: non-significant; * = $p < 0.05$; ** = $p < 0.01$

'additional' data set (Fig. 4). The simultaneous F-test for intercept and slope indicated no significant difference between the regression line and the 1:1 line for the 'core' data set, but did indicate significant model bias for the 'additional' data set (Table 6). As both slope and intercept of the 'core' and 'additional' regression lines were similar, this difference must be due to the larger number of data pairs in the 'additional' set. Removal of observations with high rainfall (>20 mm per day) improved the predictions for both the 'core' and the 'additional' data sets: bias and error were reduced and modelling efficiency increased (Table 6).

The approximate standard error of model predictions was fairly large, about 30% of the predicted mean predation rate. The standard errors of the observed predation rates per plant were about 10% of the mean. For the 'core' data set predictions were not significantly different from observations in 80% of cases, while none of the predictions were significantly from the observations when observations with high rainfall were excluded (two-tailed t-test). However, the relatively large standard error of model predictions considerably enhances the probability that predicted and observed values are not significantly different. Therefore the test is not very powerful to assess the accuracy of the model predictions. To increase model precision, i.e. to lower the standard error of model predictions, a much larger sampling effort would be required to estimate the input variables more precisely. In particular this is required for the density estimates of adult crickets, which are in the present data set responsible for 85% of the total error variance of model predictions.

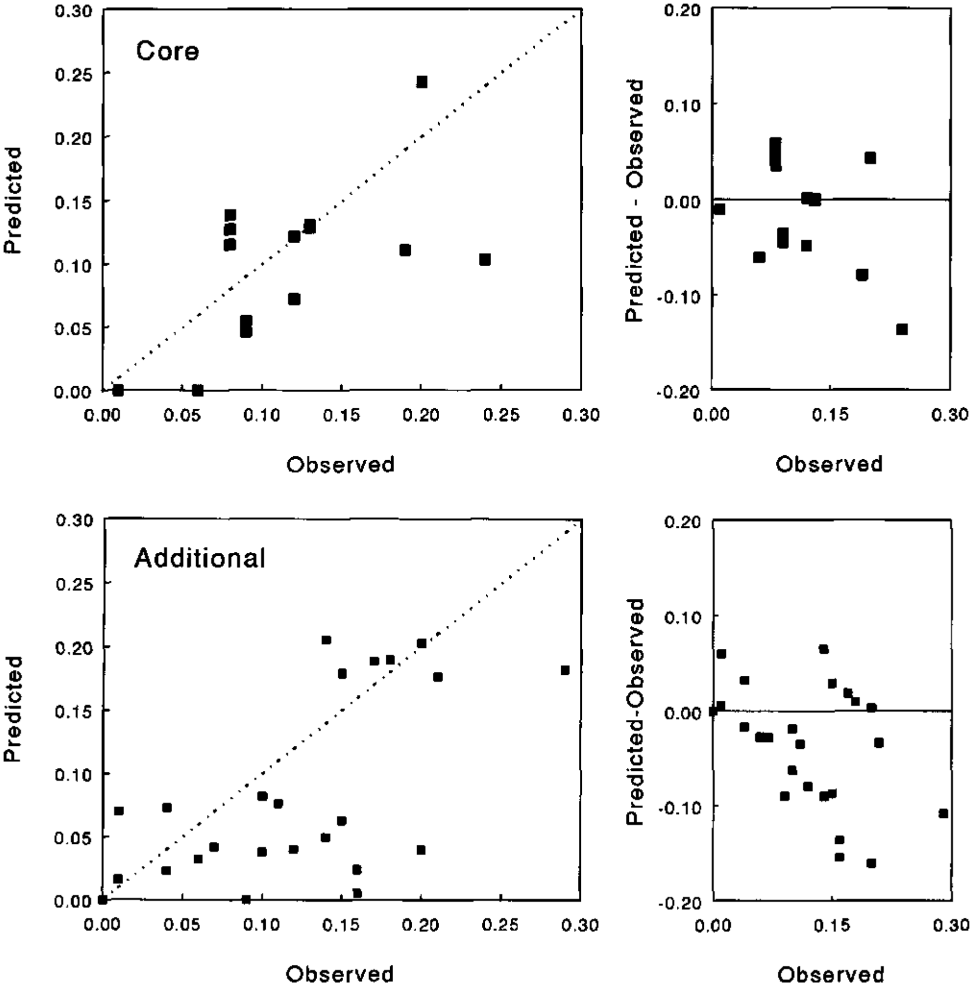


Figure 4. Predicted vs. observed relative predation rates of rice leaffolder eggs (fraction day^{-1}) with 1:1 line indicated, and prediction errors (predicted − observed), both for the 'core' and 'additional' data set.

Discussion

Modelling and measuring field predation rates

In this paper a model based on cage predation experiments was evaluated with measurements of predation rates in the field and it proved to describe the observations fairly well. In the literature very few comparable reports on field evaluation of predation models are found. Numerous predation models have been developed as part of larger population models. However, in most cases separate testing of this component is omitted and the accuracy of the predation sub-model is only crudely assessed by comparing simulated and observed population dynamics (e.g. Rabbinge 1976, Carter et al. 1982, Gutierrez et al. 1984, 1988, Wilhoit et al. 1991). When field measurements of predation rates are reported (see Luck et al. 1988, Sunderland 1988), attempts to explain these rates quantitatively on the basis of well-studied functional relationships are rare. This gap between modelling and empirical studies of field predation is probably due to the large number of polyphagous predators that are often involved, the complex behaviour of many predators, and practical problems, such as accurate assessment of field predation rates and absolute predator densities. In the present study on predation of leaffolder eggs these problems were largely solved. Modelling was facilitated by the limited number of predator species responsible for the major part of egg predation, while the functional response of these predators could be described adequately with a simple linear model without effects of satiation. Field testing of the model was possible, as both input variables and predicted predation rates could be measured in the field. An absolute sampling method could be used to estimate the densities of the major predators, while reliable measurement of egg predation was feasible due to the sedentary nature of the prey. In future studies, the precision of model predictions can be improved by concentrating the sampling efforts on the two predator types that were retained in the simplified model.

Model simplification

The effect of the availability of alternative prey on the predation rate of rice leaffolder eggs was not considered in the model. This seems justified under the observed conditions, because the highest predicted predation rates per predator were far below their maximum daily consumption (Table 4). In that case, it is unlikely that predation on leaffolder eggs will be constrained by handling time or satiation. The predicted daily predation rates of *M. vittaticollis* are remarkably low compared to its maximum intake, although this has been found for other predators as well (cf. O'Neil 1989, Wiedenmann & O'Neil 1991). It would be interesting to determine whether the predicted predation rates are sufficient for the development and reproduction of these crickets. If not, other food sources were probably overlooked.

Two predator types were excluded from the model in the process of simplification. In case of *Ophionea* spp., their field densities did not compensate for their low search rate. *Micraspis* sp. could have contributed substantially (Fig. 3), but their impact was apparently not simply determined by their density. Availability of rice pollen as alternate food probably affects their predation rates on insects. In cage experiments, predation on rice leaffolder eggs by *Micraspis* sp. was strongly reduced on flowering rice plants (Chapter 4).

Including the effect of prey density on the search rate of *M. vittaticollis* adults did not improve model predictions, while the effect of predator density on the search rate of adult crickets seemed quite important (Table 5). As the latter mechanism is still poorly understood and modelled only descriptively, detailed studies on predator interference would improve our insight in the predation potential of the crickets.

Model comparison with field observed predation rates showed that only the predatory crickets *M. vittaticollis* and *A. longipennis*, both adults and nymphs, contributed positively to model performance (Table 5). This result is consistent with the field observations on rice leaffolder egg predation during two seasons (Chapter 4). It appears that predatory crickets are the major predators of rice leaffolder eggs due to their superior searching ability. As the search rate of adult crickets is about 10 - 30 times higher than that of coleopteran predators (*Micraspis* sp., *Ophionea* spp.), the crickets will play a relatively important role even when their densities are low compared to other predator species. Their high search rate and the wide variety of pest species they attack (Rothschild 1971, Rubia & Shepard 1987a, Canapi et al. 1988, van den Berg et al. 1992, Chapter 4) make *M. vittaticollis* and *A. longipennis* important targets for natural enemy conservation measures.

Model testing

With the simplified model the trend in the observations could be predicted: for the 'core' data set the regression line of observed vs. predicted was not significantly different from the 1:1 line, and predictions were not significantly different from observations in 80% of the cases. However, the predictions were not very accurate (relative error of 40%) nor precise (standard error of predictions 30% of mean). Both for the 'core' and the 'additional' data set, predation rates were usually underpredicted (Fig. 4).

A possible cause of this underprediction may be heavy rainfall, as removal of observations with high rainfall improved model performance (Table 6). Heavy rainfall may have caused additional disappearance of eggs by physical dislodgement from the leaf surface. Rain is known to cause considerable mortality of other insect eggs, such as *Heliothis* spp. (Kyi et al. 1991, Nuessly et al. 1991). The impact of rain on egg disappearance is complex however, and not easy to incorporate in a model, while extrapolations with such a model will be hampered by the erratic nature of rainfall. Numerous factors, such as location of the eggs, density of the crop canopy, intensity and duration of rainfall, and wind speed influence the relationship between rainfall and egg disappearance (Nuessly et al. 1991). Furthermore, rainfall or leaf wetness can also reduce egg disappearance by limiting the predation rate of predatory crickets (Chapter 5).

Errors in the input data, in particular the predator densities, may be another or perhaps additional cause of frequent underprediction. Predator densities were estimated using a suction sampler, which is not likely to have extraction rates of more than 80-90% (Southwood 1978, Perfect et al. 1983). Hence, absolute densities may have been underestimated, in particular those of the nymphs in a dense rice crop.

Limitations and applications

Both the predator types included in the preliminary model and subsequent model simplification were based on the conditions in irrigated lowland rice in Laguna Province, Philippines, and the model should therefore not be extrapolated to other geographic areas without further evaluation. This would involve checking for the presence of other major egg predators and model simplification based on local data sets. As the five predator types included in the preliminary model are at genus level representative of the leaffolder egg predators reported from irrigated rice in South- and Southeast Asia (cf. Chapter 4: Table 1), this model provides a good starting point for research, and a set of hypotheses on the impact of the local predator fauna on rice leaffolder eggs that can be tested with field data.

Environmental factors are not accounted for in the model. However, as pointed out before, rain may affect egg disappearance and could be important in areas where the intensity of rainfall is high. No relationship was found between temperature and rates of egg predation in Laguna Province (Chapter 3 and 5), but in areas where temperatures are more variable it may be necessary to include this factor. This would require quantification of the effect of temperature on the search rate.

For Laguna Province, the trends in egg predation rate could be estimated reasonably well, although the model predictions were not very accurate. Considering the simplicity of the model and the integration level at which the input relations are defined, it is not likely that the accuracy will greatly improve in other locations or seasons. However, with its ability to predict the general trend, the model can be useful in two ways: (1) it enables an approximate assessment of the impact of a predator complex on rice leaffolder eggs, once predator species and densities in the field are known; (2) it can also be used to explore the potential impact of enhanced densities of predators. For example, with the cricket population densities as observed in the field experiments in Laguna the maximum predicted daily rates of predation are 20-25% and the observed predation rates rarely exceed this range (Fig. 4). This daily rate would result in a mortality of 60-75% over the entire duration of the egg stage (4-5 days). When we consider only the major period of leaffolder oviposition (40-70 days after transplanting), the average predicted egg predation rate is 10-15% per day. The model can now be used to study the effect of natural enemy conservation measures, which may, for instance, enhance the peak density or advance the start of crop colonization by the predatory crickets (Fig. 5). It appears that predation rates of more than 20% are difficult to obtain within realistic boundaries for the peak density (40 crickets per m^2) or the start of colonization (10 days after transplanting). The predicted effect of enhanced cricket abundance is mainly limited by the effect of interference on the individual search rate, included in the model. For both types of application, the predation model could be integrated with a model

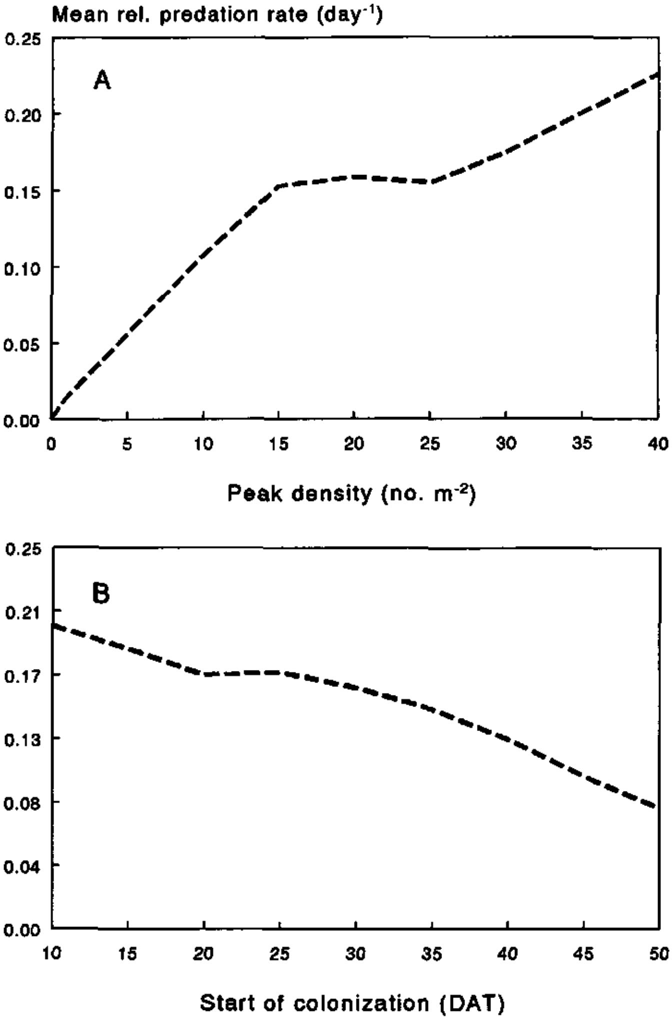


Figure 5. Predicted effect on the egg predation rate of changes in the population dynamics of predatory crickets. Predation rates are calculated with the simplified egg predation model, linked with descriptive functions for cricket density and crop leaf area during the growing season. Cricket density increases linearly from the 'colonization date' until a fixed 'population peak date' (70 days after transplanting, DAT), and then decreases linearly till harvest. The proportion of nymphs in the population is a function of time since colonization. A mean value for the daily predation rate is calculated over the period 40-70 DAT.

A. Effect of changing the peak density (colonization date fixed at 30 DAT).

B. Effect of changing the start of crop colonization (peak density fixed at 20 m^{-2}).

of leaffolder-rice crop interaction, to assess how the impact of rice field predators on leaffolder egg mortality translates into reduced rice leaffolder damage (cf. Chapter 8).

In conclusion, predatory crickets were the only predator type that helped to explain the observed predation levels of rice leaffolder eggs. Interference among these predators appeared to be an important mechanism and might limit the impact of enhancing cricket populations through conservation measures. At the observed densities, the effect of alternative prey on the predation rate of leaffolder eggs seemed negligible.

The presented model has the advantage over a regression model that it is based on functional relationships and independent parameters, established in cage predation experiments. An advantage over more complex, behaviour-based models, is that the input values needed for field testing and prediction can be obtained relatively easy. The simplified predation model can be applied within its 'validation domain' to explore the effect of enhanced predator abundance, and elsewhere the preliminary model can be used to test hypotheses on the impact of the local complex of egg predators.

Chapter 8

Do natural enemies prevent rice leaffolder damage ? A simulation study for Laguna Province, the Philippines

Abstract The development and partial validation of a combined pest population-crop growth simulation model of leaffolders in rice is described. This mechanistic model is used to test the hypothesis that in unsprayed rice fields in Laguna Province natural enemies can suppress leaffolder populations to below economic damage levels.

Simulated yield losses due to the larval infestations observed in unsprayed rice fields were less than 5% in a well-fertilized crop. An unfertilized crop was more sensitive to leaffolder injury, due to the smaller crop leaf area. Yield losses started to exceed 10% in a well-fertilized crop when the peak density was about 5 larvae per hill, and in an unfertilized crop at about 1-2 larvae per hill. However, very high levels of N-fertilization may result in a strong increase in leaffolder infestation and higher yield losses, despite the reduced sensitivity to injury. The impact of natural enemies on rice leaffolder infestation levels and damage was explored by introducing field observed mortality due to egg predation and parasitism of eggs and larvae into the population model. Yield losses simulated with an average egg recruitment pattern exceeded the economic damage level, when no natural enemy action was included. However, with all three natural enemy-related mortality factors included, larval density was strongly suppressed and the simulated yield loss was reduced to less than 5%. The contribution of egg predators to this reduction was relatively large. To study the impact of egg predation by the crickets *M. vittaticollis* and *A. longipennis*, the fixed egg predation rate was replaced by a simple egg predation sub-model, which calculated predation rates from the observed densities of these predatory crickets. Simulated peak larval densities were on average reduced by about 25% and yield losses by more than 30% due to egg predation by crickets (range: 5-60%).

This study confirms the importance of conservation of natural enemies and good crop management practices such as judicious use of N-fertilizers as the principle components of rice IPM. The combination of both principles will make chemical control of rice leaffolder in Laguna Province unnecessary most of the time.

Introduction

Rice leaffolders, *Cnaphalocrocis medinalis* and *Marasmia* spp. (Lepidoptera: Pyralidae), are considered major pests in many Asian countries (Reissig et al. 1986, Khan et al. 1988). The larvae injure the rice plants by folding the leaves and scraping off the green mesophyll tissue inside the folds (Fraenkel & Fallil 1981, Fraenkel et al. 1981). Leaffolder injury is highly visible, and rice farmers usually respond by applying insecticides, even at very low infestation levels (Heong et al. 1994). Farmers tend to overvalue pests with well-observable symptoms (Bentley & Andrews 1991, Escalada & Heong 1993), and most sprays targeted against rice leaffolder are probably not profitable, because modern rice varieties can tolerate high levels of defoliation (e.g. Hu et al. 1993, IRRI 1993c). In tropical rice fields, a large complex of natural enemies has been identified, which may keep the leaffolders below damaging levels most of the time (Khan et al. 1988, Barrion et al. 1991a). By killing these natural enemies, insecticide applications may even promote infestations of rice leaffolder (Bandong & Litsinger 1986, Nadarajan & Skaria 1988, Panda & Shi 1989) or other rice pests, such as brown planthopper (Stapley 1978, Heinrichs & Mochida 1984, Kenmore et al. 1984).

To determine whether natural enemies suppress rice leaffolder to below economic damage levels, the relationship between leaffolder larval densities and damage should be known, as well as the impact of natural enemies on these larval densities. Many empirical studies in various countries have been conducted to establish the relationship between leaffolder larval density or injury level and yield loss (Japan: Miyashita 1985, Mikuriya et al. 1988, Kuchiki et al. 1988; China: Anonymous 1993; India: Murugesan & Chelliah 1983a, 1983b, 1986; and the Philippines: Bautista et al. 1984, Barrion et al. 1991a). In most studies, a linear relationship was found between the percentage of injured leaves and yield loss. In others, where injury levels were below 10% (Budhasamai et al. 1992, Kuchiki et al. 1988, Fabellar et al. 1992), or where injury occurred only during the ripening stage (Miyashita 1985), no significant effect of leaf injury on yield was found. All these studies are difficult to compare or to generalize due to the specific experimental conditions, such as location or scale, rice variety, crop stage and climate. Furthermore, many studies were conducted in cages or greenhouses, where light intensity is reduced, while others were carried out with potted plants with few tillers. These experiments do not necessarily reflect the field situation.

The limitations of empirical damage functions can be overcome with eco-physiological crop growth models, in which the effect of pest organisms on crop growth processes is included in a mechanistic way (Rossing et al. 1993). With such a simulation model of rice leaffolder damage, it was shown that yield loss due to rice leaffolder injury was dependent on the growing conditions of the rice crop and the development stage during which injury occurred. Yield losses for a given injury level were lower at higher attainable yield levels, i.e. when radiation and supply of water and nutrients were optimal for crop growth (de Jong & Daamen 1992). Leaffolder infestations occurring before flowering caused far more yield loss than infestations during the ripening stage (de Jong, unpublished).

In Laguna Province, the Philippines, the impact of indigenous natural enemies on rice leaffolder populations, in particular of egg predators and egg and larval parasitoids, has been studied in detail (Kamal 1981, Guo 1990, Arida & Shepard 1991, Chapter 1-7). The leaffolder natural enemy complex is diverse and causes substantial mortality. However, in these studies the impact of natural enemies on yield loss due to rice leaffolder was not assessed. Simulation modelling provides the opportunity to investigate the effect of leaffolder mortality due to natural enemies on rice yields. A crop model that includes leaffolder damage mechanisms can be coupled with a leaffolder population model to simulate yield losses for varying infestation levels. Natural enemy-related mortality factors can be included in the leaffolder population model.

In this chapter such a combined pest-crop model of leaffolders in rice is described and used to test the hypothesis that in unsprayed rice fields in Laguna Province natural enemies can suppress leaffolder populations to below economic damage levels. Data on leaffolder population densities and mortality factors from eight unsprayed rice crops are used as input to the model to simulate rice leaffolder damage and the impact of various biotic mortality factors on yield loss. Particular attention is paid to the contribution of egg predation by the crickets *Metioche vittaticollis* and *Anaxipha longipennis* (Orthoptera: Gryllidae).

A model of rice leaffolder population dynamics and damage

Model structure and parameters

Rice leaffolder population model The simulation model of rice leaffolder population dynamics was based on life history data of *C. medinalis*, compiled from literature and

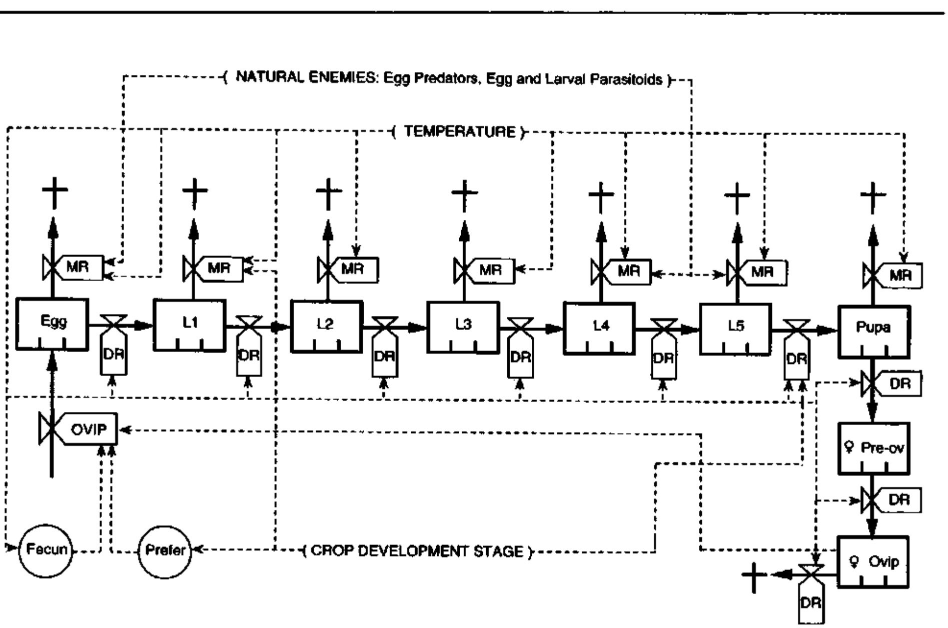


Figure 1. Relational diagram of the rice leaffolder population model. Leaffolders enter the rice field in the egg stage, and develop through the egg, larval (L1-5) and pupal stages to adults. Depending on the crop development stage, the females moths lay all or part of their eggs in the same field. Mortality caused by natural enemies is represented by egg predation, egg parasitism, and larval parasitism.
Symbols: rectangles, state variables (numbers of leaffolders in certain stage); valves, rates of change; circles, auxiliary variables; underlined, parameters; parentheses, driving variables; solid arrows, flow of material; broken arrows, flow of information. Small bars inside a rectangle indicate a series of integrals (boxcar train). MR = mortality rate; DR = development or ageing rate; OVIP = oviposition rate; Fecun = Daily Fecundity; Prefer = Preference, proportion of eggs laid within rice field; ♀ Pre-Ov = Female moths in pre-oviposition stage; ♀ Ovip = Female moths in oviposition stage. additional experiments.

The model simulates the development from egg to adult, mortality and egg production of a rice leaffolder population in a single rice field (Fig. 1). Development and relative mortality rate per stage and adult fecundity are dependent on temperature (Fig. 2a-d). Temperature-dependent development and ageing is simulated with the 'boxcar train'-method (Goudriaan & van Roermund 1989), which also mimics the dispersion in time resulting from variation in development rate between individuals. The relative dispersion during each developmental stage, i.e. the coefficient of variation of the development rate, is introduced as a function of temperature (data from Cheng 1987). The model also includes the effects of crop development stage on larval development, larval mortality, and oviposition (Fig. 2e).

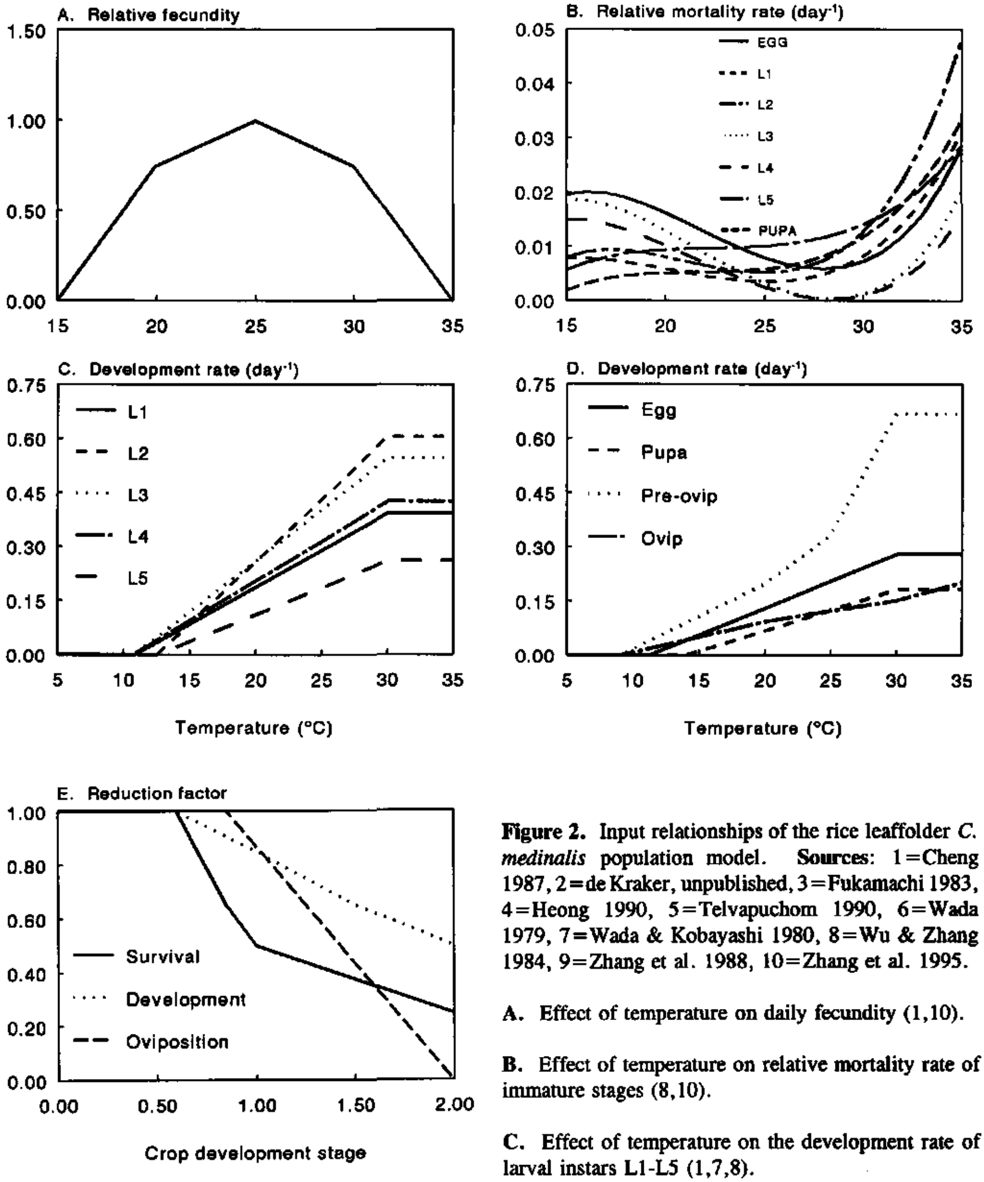


Figure 2. Input relationships of the rice leaffolder *C. medinalis* population model. **Sources:** 1=Cheng 1987, 2=de Kraker, unpublished, 3=Fukamachi 1983, 4=Heong 1990, 5=Telvapuchorn 1990, 6=Wada 1979, 7=Wada & Kobayashi 1980, 8=Wu & Zhang 1984, 9=Zhang et al. 1988, 10=Zhang et al. 1995.

A. Effect of temperature on daily fecundity (1,10).

B. Effect of temperature on relative mortality rate of immature stages (8,10).

C. Effect of temperature on the development rate of larval instars L1-L5 (1,7,8).

D. Effect of temperature on the development rate of egg, pupa, and female adult in pre-oviposition and oviposition stage (1,7,8). Note: under field conditions female longevity is reduced, see text.

E. Effect of crop development stage on: the survival rate of the 1st larval instar (4,5,9); the development rate of the last larval instar (1,6); the proportion of eggs laid within the crop (2,3).

Mortality due to natural enemy action can be introduced as location-specific input. In case several mortality factors act during one life stage, these factors are assumed to be independent and multiplicative. The density of each larval instar of rice leaffolder, calculated by the population model for each day of the crop season, is input to the damage model.

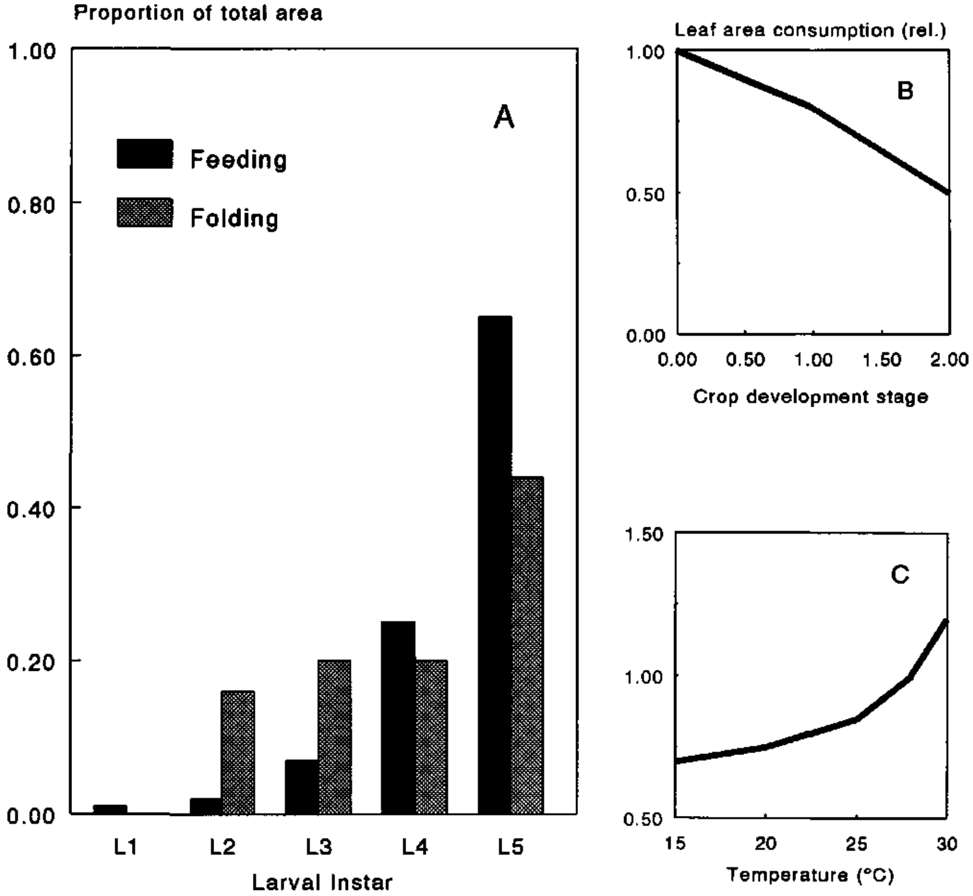


Figure 3. Factors affecting rice leaffolder folding and feeding rates. **Sources**: 1 = Cheng 1987, 2 = de Kraker, unpublished, 3 = Heong 1990, 4 = IRRI 1990, 5 = Ma & Hu 1993.

A. Relative folding and feeding rate per larval instar, as a proportion of the total area consumed or folded during the entire larval stage (1,2,3,5)

B. Effect of crop development stage on leaf area consumption (1,3,4).

C. Effect of temperature on leaf area consumption, with 28°C as reference temperature (1).

Rice leaffolder damage model The effects of leaffolder larvae on the rice crop were modelled by introducing damage mechanisms in an existing model of rice crop growth (ORYZA1), using an approach similar to De Jong & Daamen (1992). ORYZA1 simulates the time course of dry matter production by integrating the daily growth rate, which is based on canopy assimilation and respiration rates. The total daily rate of canopy CO_2 assimilation is calculated from the incoming radiation, temperature, and leaf cover (Kropff et al. 1994b). Rice leaffolder larvae affect crop growth by folding leaves and by scraping off the green mesophyll tissue. Removal of green leaf tissue reduces the total green leaf area and leaf weight of the crop. Folding of leaves reduces the light interception of these leaves, while photosynthesis in the remaining green tissue of folded leaves may be reduced as well (de Jong 1992). Larval leaf feeding and folding rates differ per instar, and feeding rates are dependent on plant age and temperature (Fig. 3). Several authors reported that the vertical distribution of the injured leaves within the canopy is not homogeneous, but concentrated in the upper leaf layers (Hirao 1982, Ma et al. 1991). By introducing three leaf layers in the ORYZA1 model, it was possible to include a non-homogeneous injury distribution.

The parameters used to describe rice leaffolder injury mechanisms in the damage model are listed in Table 1. Observed and reported values for these parameters showed a large variation, which is represented in three parameter sets for low, standard and high leaffolder injury capacity. The standard injury capacity set is based on calculated or estimated means. The reported variation in total leaf area scraped per leaffolder larva depends amongst others on rice variety (IRRI 1990b, Ma & Hu 1993, Chen et al. 1993). The total area folded per larva is quite variable as well (Zhang et al. 1989, de Kraker unpublished), and is probably inversely related to the residence time of the larva per leaffold. Each time a larva is disturbed and moves to another leaf, it will make a new leaffold (Fraenkel & Fallil 1981). After the leaffold is abandoned by the larva, it may 'unfold' again, perhaps due to weathering of the silk strands that tie the leaf margins together. The relative unfolding rate, i.e. the inverse of the average life-span of a leaffold, was low under greenhouse conditions (de Kraker unpublished), but may be higher in the field. Therefore, a large range in life-span values was included. The reduction of the photosynthesis rate in folded leaves measured by De Jong (1992) was 50%, but others claim that this reduction is compensated by enhanced photo-

Table 1. Parameters of rice leaffolder injury: standard values, and two alternative combinations, representing low and high leaffolder injury capacity. See text for explanation.

Injury parameter	Units		Low	Standard	High
Total leaf area scraped per larva (at 28°C)	[cm^2]		10	20	30
Total leaf area folded per larva	[cm^2]		30	50	60
Average life-span leaffold	[days]		10	30	∞
Relative senescence of injured leaves (compared to healthy leaves)	[-]		2.0	1.5	1.0
Vertical distribution of injured leaves in a 3-layered canopy (fractions)	[-]	upper	0.33	0.33	0.75
		middle	0.33	0.33	0.25
		lower	0.33	0.33	0.00
Reduction of maximum rate of leaf photosynthesis in folded area	[%]		0	50	50

synthesis in adjacent healthy leaves (Jin 1984, Zhang & Chen 1991). Therefore a minimum value of 0% (no reduction of photosynthesis) was included in the low injury parameter set. Parameter values for the vertical distribution of folded leaves in the canopy and the effects of folding and feeding on leaf senescence were estimated from own unpublished experiments.

Validation

Rice leaffolder population model The part of the model describing the development of immature stages was validated with a study of two subsequent leaffolder generations under semi-field conditions in a screenhouse. In the screenhouse natural enemies were excluded and rice leaffolder recruitment could be controlled. The experiment started with the infestation of two screenhouse compartments (300 m^2) with c. 1,000 female leaffolder moths at 35 days after transplanting (DAT). Samples were taken over a 2-month period after infestation to determine the stage of the immature leaffolders. Larval instars were determined by measurement of the head capsule widths. The number of leaffolders collected per sampling

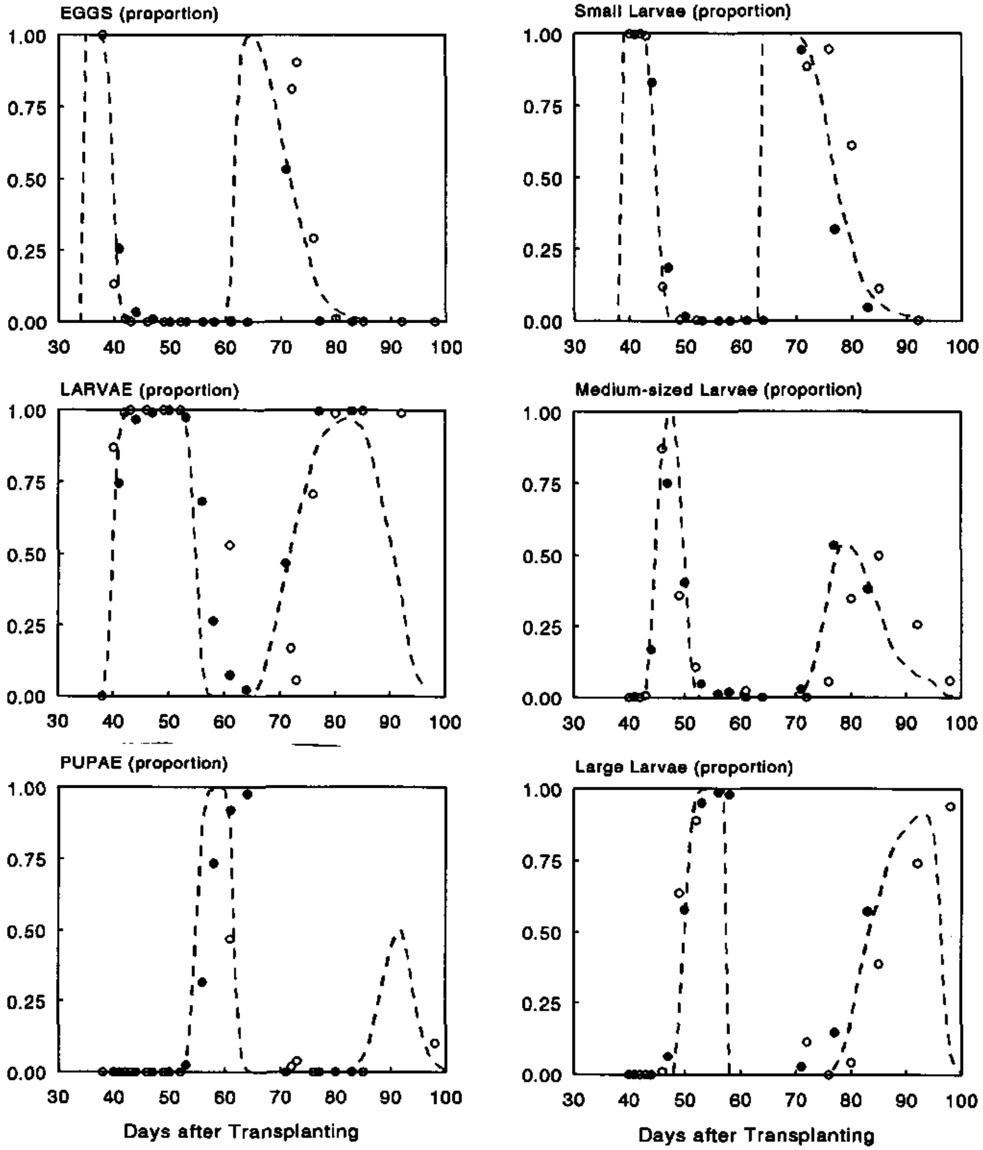


Figure 4. Simulated and observed development of rice leaffolder immature stages under semi-field conditions. Development is represented by the time course of the proportion in each stage. Open and filled circles: observations from two different screenhouse compartments; broken line: simulation. Small larvae = L1+2, Medium larvae = L3+4, Large larvae = L5.

date ranged from 100 to over 1,000 during the second generation. For validation, the simulation model was initialized with the data on egg recruitment from the two compartments, and run with temperature data measured in the screenhouse. Visual comparison of simulated and observed immature leaffolder development showed that the time course of simulation resembles the observations closely (Fig. 4).

Rice leaffolder damage model Validation of the damage model requires detailed information on leaffolder injury and crop growth throughout the growing season. A field experiment was conducted with rice variety IR72 under three levels of leaffolder infestation, replicated three times in a randomized complete block design. The different infestation levels were created by insecticide applications and artificial infestation with leaffolders eggs in the black-head stage (Table 2). At maximum tillering, flowering, mid-ripening and maturity, crop samples were taken to measure leaf N-content, leaf area, and dry weights of stems, leaves, and panicles. Also, the number and position of healthy and injured leaves, length of leaffolds, and leaf area scraped by the leaffolder larvae were determined. At maturity, yield

Table 2. Rice leaffolder injury levels in field validation experiment. Peak levels at mid-ripening stage. Averages of three replications. Treatments: control, Thiodan foliar spray at 68 and 73 DAT (days after transplanting); double infestation, at 60 and 64 DAT; triple infestation, at 57, 60 and 64 DAT.

Treatment	Injured leaves (%)	Area scraped/ injured leaf (%)	Mean length leaffold (cm)	Crop leaf area folded+scraped (%)
Control: 2 x insecticide	2.1	7.3	4.9	0.32
Double infestation: 2 x 10 eggs/hill	11.7	10.3	6.5	2.03
Triple infestation: 3 x 20 eggs/hill	20.6	11.0	6.0	3.73
Treatment effect [a]	**	n.s.	n.s.	**

[a] F-test, percentage data $\sqrt{}$-transformed: n.s. = non-significant, $p > 0.05$; ** = $p < 0.01$

components were measured and the plots were partially harvested to estimate grain yield. The three treatments resulted in significantly different levels of leaffolder injury (Table 2). Differences were large in terms of percentage injured leaves, but the total area folded and scraped was very low in all treatments, less than 5% of the crop leaf area. No treatment effect was found on the green leaf area index and weight of stems, leaves and panicles. Yield components and grain yield per hill did also not differ between the treatments.

Two aspects of the leaffolder damage model were validated: the simulation of injury (leaf area scraped and folded), using the observed larval densities as input, and the simulation of yield reduction, using the observed injury levels as input. Injury was simulated with low, standard and high parameter values (Table 1). The value for the senescence rate of injured leaves, twice the rate of healthy leaves, was estimated directly from counts of healthy and injured leaf numbers in the validation experiment and used as model input. Comparison of simulated and observed injury showed that the total leaf area scraped was overestimated with the standard value of 20 cm^2, but underestimated when the lower value for the area scraped per larva (10 cm^2) was used (Fig. 5a). Total leaf area folded was overestimated by the model (Fig. 5b), even when using the lowest values for the larval folding rate (30 cm^2) and the life-span of a leaffold (10 days). The overestimation of the fraction folded injured leaves prior to 80 DAT (Fig. 5c), indicates that the life-span of a leaffold may sometimes even be shorter than the lower value of 10 days. Up to 80 DAT rain showers were frequent, and high rainfall or humidity possibly accelerates the weathering of the silk strands that tie the leaf margins together.

To test the simulation of yield loss due to injury, the ORYZA1 model was first calibrated with data from the control treatment, in which the peak percentage of injured leaves was about 2%. The calibrated model was then run with the observed leaf area and the leaffolder injury levels and distribution from the three treatments. As phenology, dry matter distribution, specific leaf area and leaf N-content did not differ between treatments, common values were used in the simulations. The simulations of total dry matter production and yield (panicle weight) corresponded well with the observations (Fig. 6). Total dry matter and panicle weights were lower in the control treatment than in the treatments with artificial infestation, because crop leaf area was smallest in the control. The simulated differences in

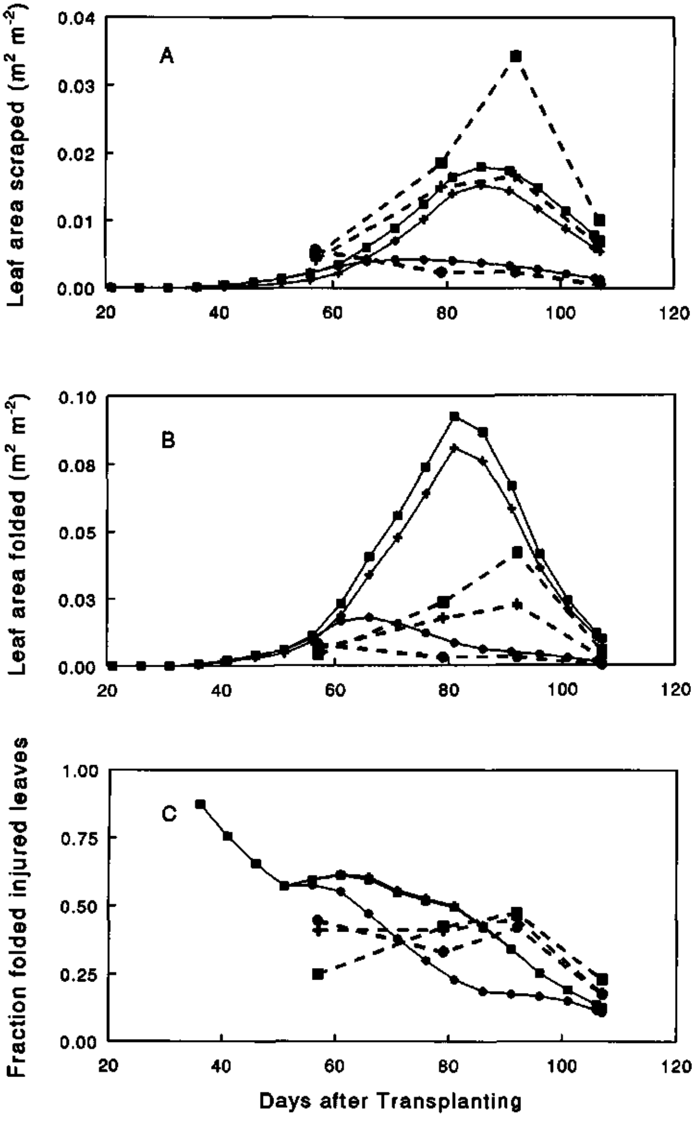


Figure 5. Simulated and observed time course of the total leaf area scraped (A) and folded (B), and the fraction of injured leaves still folded (C), in three treatments of the field validation experiment: control (●) double infestation (+) and triple infestation (■). Drawn line: simulations; broken line: observations.

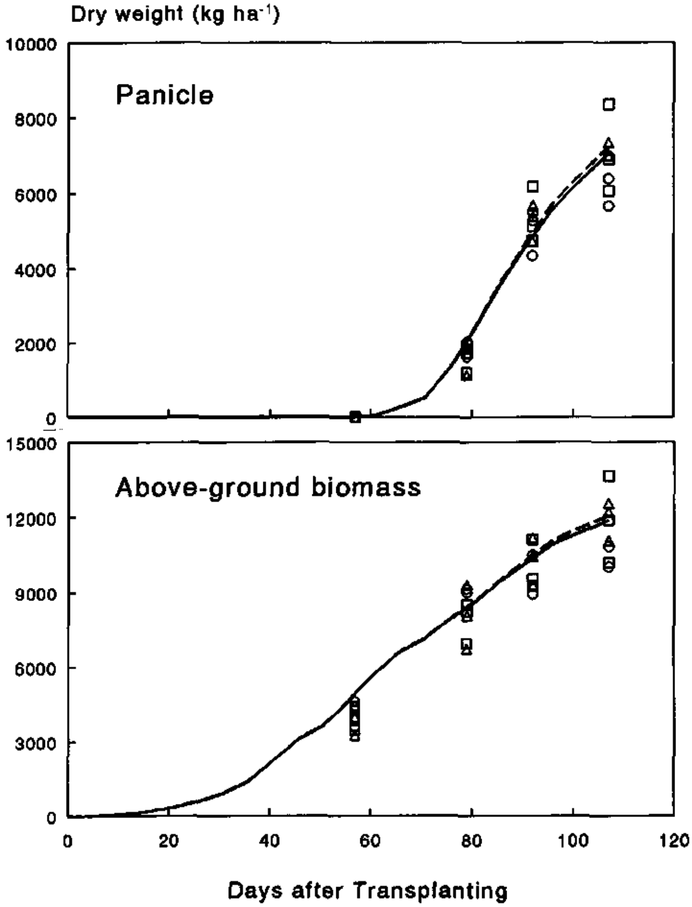


Figure 6. Simulated and observed time course of dry weight of panicles and total above-ground biomass in the field validation experiment. Drawn line: simulation of control treatment, broken line: simulation of triple infestation (double infestation not shown). Symbols: control (□), double infestation (○), triple infestation (△).

panicle weight were less than 3%. In simulations with common values for the crop leaf area for all treatments, the simulated yield reduction due to rice leaffolder injury was not more than 1% at the highest infestation level, even with a 50% reduction of the maximum rate of photosynthesis in folded leaves included. The simulations were thus in agreement with the observations, which also showed no significant effect on yield. Due to the low injury levels, however, the validation experiment could not be used to test hypotheses on the relative importance of the components of leaffolder injury to yield loss.

Simulation of rice leaffolder damage in Laguna Province

Simulations

The rice leaffolder damage model, simulating rice growth and yield in the presence of leaffolder larvae, was used to test the hypothesis that in unsprayed rice fields in Laguna Province natural enemies can suppress leaffolder populations to below economic damage levels. Depending on the objective of the simulation, forcing functions (fixed input relations) or dynamic sub-models were used to simulate leaffolder density (Fig. 7). First, to assess the effect of larval densities in unsprayed fields on rice yield, the leaffolder damage model was run with the observed larval densities introduced as forcing functions. Then, to study the impact of three natural enemy-related mortality factors, the forcing function for leaffolder larval density was replaced by the dynamic leaffolder population model. Now, the mortality factors derived from field observations were introduced as forcing functions into the population model. Finally, to assess specifically the impact of one group of natural enemies, the predatory crickets, the fixed value for egg predation was replaced by a sub-model of egg predation, with field observed cricket densities as forcing functions.

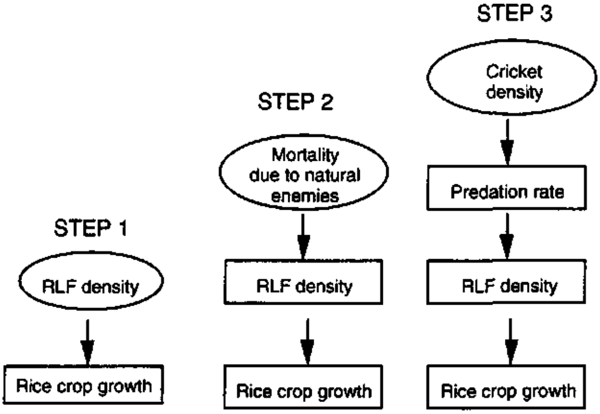


Figure 7. Simulation of damage due to rice leaffolders (RLF): oval indicates forcing function and rectangle indicates dynamic model. Step 1: simulation of damage with observed larval densities; Step 2: simulation of damage with observed mortality rates included in the rice leaffolder population model; Step 3: same as 2, but now with the egg predation rate calculated from observed densities of crickets.

1. Damage by rice leaffolders at observed infestation levels

Simulating yield loss with independent crop data To assess damage caused by rice leaffolder populations in Laguna Province, the observed larval densities from four crop seasons (Chapter 1) were used as input for simulations with independent crop data. Input data for the crop model were obtained from experiments by Kropff et al. (1994b) with IR72, conducted at the International Rice Research Institute (IRRI) in Los Baños under pest-free conditions and optimal water supply. The effect of crop management on the relationship between leaffolder infestation and yield reduction was studied by comparing simulated yield losses at two levels of nitrogen fertilization: no N and high N. The amount of N applied in the high N treatment was 110 kg ha^{-1} in the wet season, and 225 kg ha^{-1} in the dry season experiment. The N-fertilization levels represent two extremes in crop condition, with a maximum leaf area index (LAI) of about 2 in the unfertilized crop, and 5-6 in the well-fertilized crop. Leaffolder density data were combined with crop data sets for either wet or dry season, depending on the season the observations were made. The impact of variation in the parameter values describing leaffolder injury (Table 1), was determined by running each season × fertilizer combination with the three sets of injury parameters. To determine at what infestation levels yield losses would exceed a detection level of 10%, the simulations were repeated with a larger range of infestation levels, obtained by multiplying the observed larval densities 2, 5 and 10 times.

Interaction between N-fertilization and leaffolder infestation Simulating yield reduction due to rice leaffolder at observed densities with independent crop data from two extremes in fertilization level, ignores the possible interaction between leaffolder infestation and fertilization. Yet, many researchers have reported increased leaffolder infestation at higher N-fertilization levels (see Chapter 2). To assess how this interaction may influence the effect of N-fertilizer on leaffolder damage, observations from a field experiment with IR70 (Chapter 2) were used to simulate crop growth and leaffolder injury and damage. In this field experiment (Pila 1991 wet season), leaffolder population dynamics were studied in detail at three levels of N-fertilization: 0, 75, and 150 kg N ha^{-1}. Crop phenology, leaf area, leaf N-content, and final grain yield were recorded as well. The observed larval density at the highest N-level was eight times higher than in the plots without N-fertilization, while grain yield was highest at the medium N-level. For the simulations the observed phenology and the treatment means of leaf area index and leaf N-content were used, while the remaining crop parameters were obtained from Kropff et al. (1994b). Crop growth and yield was simulated for each N-fertilization level with 1991 weather data, either in the absence of rice leaffolders, or with the observed larval densities. Yield loss due to rice leaffolder was simulated for low, average, and high leaffolder injury capacity (Table 1).

2. Impact of natural enemies on leaffolder infestation levels and related damage

Field observed mortality rates The impact of natural enemies on rice leaffolder damage was explored by introducing field observed mortality rates due to egg predation and parasitism of eggs and larvae into the population model. Other biotic mortality factors, such as predation on larvae, pupae and adults, were not included. For egg predation a simple seasonal average of 45% mortality was taken (Chapter 3), while for the percentage egg parasitism a curvilinear relationship with crop development stage was fitted to the pooled field observations (Fig. 8). The seasonal average percentage parasitism of L2 and L3 larvae was 30%, and of L4 and L5 40% (recalculated from Chapter 1). Parasitized L2 and L3 larvae were assumed to die all during the L4 stage, parasitized L4 and L5 larvae die during the L5 stage. Density dependence was not included, as this effect was not evident or at least ambiguous in the field data on these mortality factors (Chapter 1, 2, 3 and 7). In the model, percentage mortality per stage was converted to a daily relative mortality rate, based on the stage duration.

For leaffolder population parameters that may be highly variable under field conditions, conservative values were chosen. For example, female longevity and fecundity are strongly related to the availability of sugars (Waldbauer et al. 1980). Observations from field cages (Kamal 1981) indicate that a 50% reduction of the values for oviposition period and daily egg production measured in the laboratory with sugar supply, provides reasonable estimates for field conditions. The effect of crop development stage on the proportion of females laying eggs outside the crop, is probably strongly related to distance and development stage of neighbouring fields (Fukamachi 1983, de Kraker unpublished). Here also a conservative relationship was included in the model (Fig. 2e), based on an oviposition preference

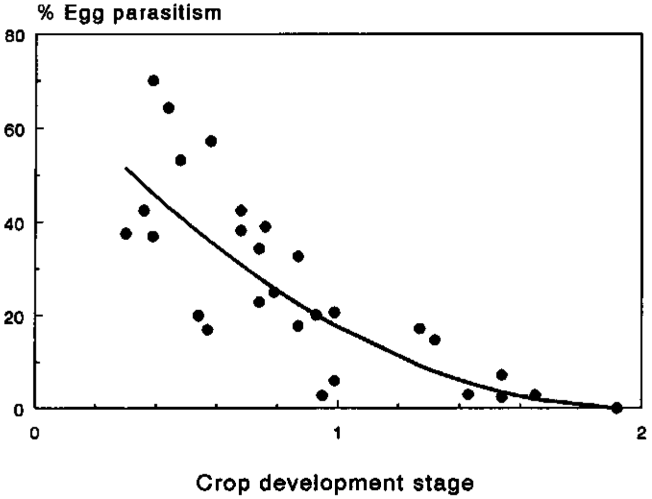


Figure 8. Relationship between percentage egg parasitism and crop development stage. Data points represent the observations (Chapter 1), drawn line is the fitted input relation for the leaffolder population model. Crop development stage is expressed in a numerical scale, where 0 = emergence, 1 = flowering, 2 = maturity.

experiment where plots in the preferred stages were present at only a few meters distance. This approach results in conservative levels of yield loss in simulations where all natural enemy-related mortality was excluded.

From the observations in eight irrigated rice crops (Chapter 1), a simplified peak-shaped pattern of leaffolder egg recruitment was derived. This represents the total number of eggs laid in the crop each day by immigrating females, from the start of colonization till the moment the next generation of female moths reaches the oviposition stage, about 30-35 days later. The average peak recruitment was 17.5 eggs day^{-1} m^{-2}, with a range from 5 to 40. Larval infestation levels and yield loss percentages were simulated for various combinations of the natural enemy-related mortality factors. By omitting all these mortality factors, or one at the time, their joint and individual impact can be assessed. Simulations were conducted with both wet and dry season crop data from the high N treatment only. Each combination of mortality factors and growing season was simulated for low, average and high leaffolder injury capacity.

Egg predation by crickets Earlier studies showed that the predatory crickets *M. vittaticollis* and *A. longipennis* are responsible for the major part of field predation of rice leaffolder eggs in Laguna Province (Chapter 3 and 4). Based on cage predation experiments, a model to calculate daily egg predation rates from predator densities was developed and evaluated with independent field data (Chapter 5 and 7). The model described the observed trends in field predation rates reasonably well, and can now be used to determine the impact of observed densities of predatory crickets on leaffolder infestation levels and related yield losses. Predator density data were collected in sufficient detail in seven irrigated rice crops (Chapter 1): three wet season crops (Pila 1991, 1993, IRRI 1992), and four dry season crops (Victoria 1991, Pila 1991, 1992, 1993). In the combined leaffolder rice model, the average value for egg predation was replaced with the sub-model of egg predation based on cricket densities. Simulations were conducted for two conditions: presence or absence of egg and larval parasitism. For both conditions the model was run with all input combinations of cricket density pattern, growing season, and leaffolder injury capacity.

Results

1. Damage by rice leaffolders at observed infestation levels

Simulating yield loss with independent crop data The observed levels of rice leaffolder infestation in unsprayed crops caused less than 5% yield loss in the well-fertilized crop, according to the simulations (Table 3). Exceptions occurred only when the peak larval density was more than 2 per hill, and the injury parameters were set at their maximum values. The unfertilized crop with a small leaf area (LAI $\leq$ 2), was much more sensitive to leaffolder injury: the percentage yield loss was three times higher than in the well-fertilized crop at the same infestation level. Absolute yield losses are probably more relevant to farmers, and these were also larger in the unfertilized crop (Table 3). The simulations with the larger range of infestation levels again demonstrate the importance of crop condition (Fig. 9). In the well-fertilized crop, yield losses start to exceed 10% when peak larval densities are around 5 per hill. For the unfertilized crop this already occurs at 1-2 larvae per hill.
The different values for the leaffolder injury parameters resulted in large differences in

simulated yield losses. Simulated losses at high injury capacity were 5 to 10 times larger than at low injury capacity (Table 3).

Table 3. Yield losses simulated with observed rice leaffolder larval densities, for two N-fertilization levels. Lower and upper bound of range based on low and high injury capacity (see Table 1).

Crop season	Larval peak (no. hill^{-1})	Yield loss (kg ha^{-1})		Yield loss (%)	
		zero N	high N	zero N	high N
Pila 1992-DS	1.2	248 (84-507)	114 (34-290)	4.5 (1.5-9.3)	1.2 (0.3-3.0)
Pila 1993-DS	0.4	109 (36-242)	43 (11-126)	2.0 (0.7-4.4)	0.4 (0.1-1.3)
IRRI 1992-WS	0.5	104 (41-197)	55 (21-126)	2.7 (1.1-5.1)	0.9 (0.4-2.2)
Pila 1993-WS	2.3	446 (163-886)	244 (83-522)	11.5 (4.2-22.8)	4.1 (1.4-8.8)

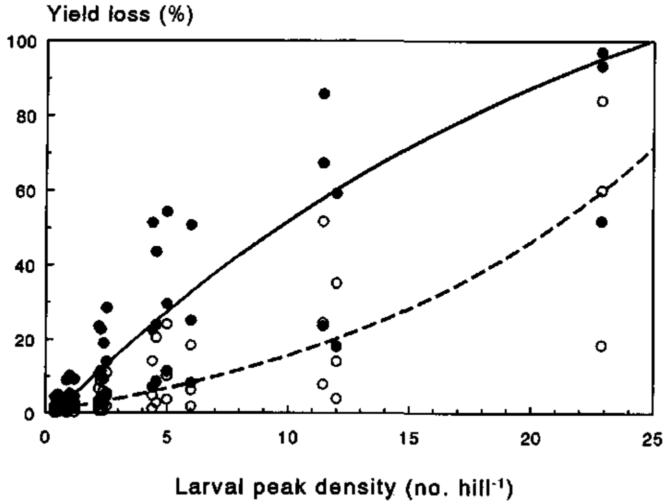


Figure 9. Simulated yield loss (%) due to rice leaffolder injury, as a function of larval peak density in an unfertilized (●) and a well-fertilized rice crop (○). Simulations were conducted with three levels of injury capacity (see Table 1) and with larval densities based on multiplied observed densities (see text for details). Curves represent average trend per fertilizer level: solid line, zero N; broken line, high N.

Interaction between N-fertilization and leaffolder infestation In the absence of pests and other stresses, simulated yields increased with N-fertilization level (Fig. 10a). This simulated effect is mainly determined by the larger crop leaf area, and to a minor extent by the higher

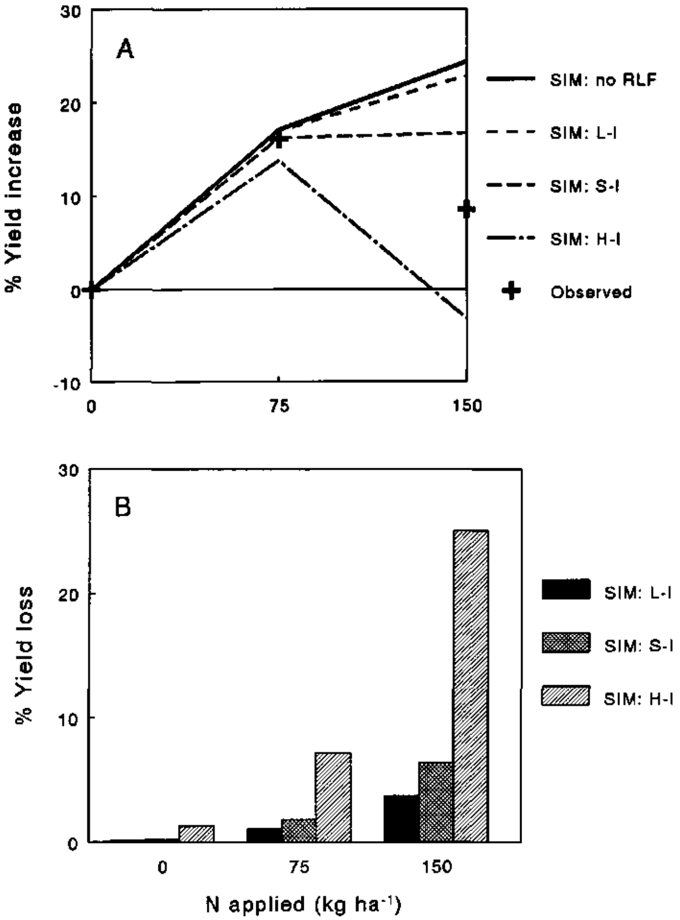


Figure 10. Effect of N-fertilization on yield and yield loss, simulated at three levels of injury capacity (H-I = high, S-I = standard, and L-I = low injury capacity respectively, see Table 1), and with crop parameters and leaffolder densities as observed in the experiment described in Chapter 2.
A. Yield increase of IR70 in response to N application rate, in the absence or presence of rice leaffolder. Yield increase was calculated as a percentage of the yield without N applied.
B. Yield loss (%) at three levels of N application. Yield loss was calculated as a percentage of the yield without leaffolder infestation, for each N level.

leaf N-content at higher N-application levels. The yield response to N-fertilizer changed when the observed leaffolder larval densities were introduced into the model: with standard injury capacity yield differences between 75 kg and 150 kg N ha^{-1} disappeared, while at high injury capacity the simulated yield at 150 kg N ha^{-1} was even lower than without fertilizer (Fig. 10a). The observed yield response lies in between the simulated responses at standard and high injury capacity. At all three levels of leaffolder injury capacity, the simulated yield losses increased with N-fertilization level (Fig. 10b).

2. Impact of natural enemies on leaffolder infestation levels and related damage

Field observed mortality rates The simulated percentage yield loss due to leaffolder infestation in a well-fertilized crop ranged from about 3 to 30%, when no natural enemy action was included (Table 4a). Differences between wet and dry season are mainly due to the smaller leaf area of the wet season crop. When all three natural enemy related mortality factors were included, larval density was strongly suppressed and simulated yield loss was reduced to less than 5% (Fig. 11a,b, Table 4a). Omitting one mortality factor at the time, showed that their individual contributions in absolute terms were similar in magnitude (Table 4a). In relative terms differences in impact were more pronounced: omitting egg predation, egg parasitism, or larval parasitism resulted in an increase in yield loss of about 115, 60, or 70% respectively (calculated from Table 4a).

Egg predation by crickets Predatory crickets, at observed density levels, contributed substantially to the suppression of leaffolder larval densities. In the presence of parasitism, egg predators reduced peak larval densities on average by 25%, and the area under the density curve by nearly 40% (Fig. 11c,d), while yield losses were reduced by 33% (Table 4b). Their impact was, of course, more pronounced in the absence of parasitism. Under that condition, the average reduction of larval peak density and area under the density curve was 50 and 55% respectively (Fig. 11e,f). The reduction in yield loss due to cricket egg predation increased to 40% (Table 4b). There was a large variation in cricket impact on yield loss between the seven rice crops: the simulated reduction in yield loss was at least 6-9%, and at most 60-70% (Table 4b).

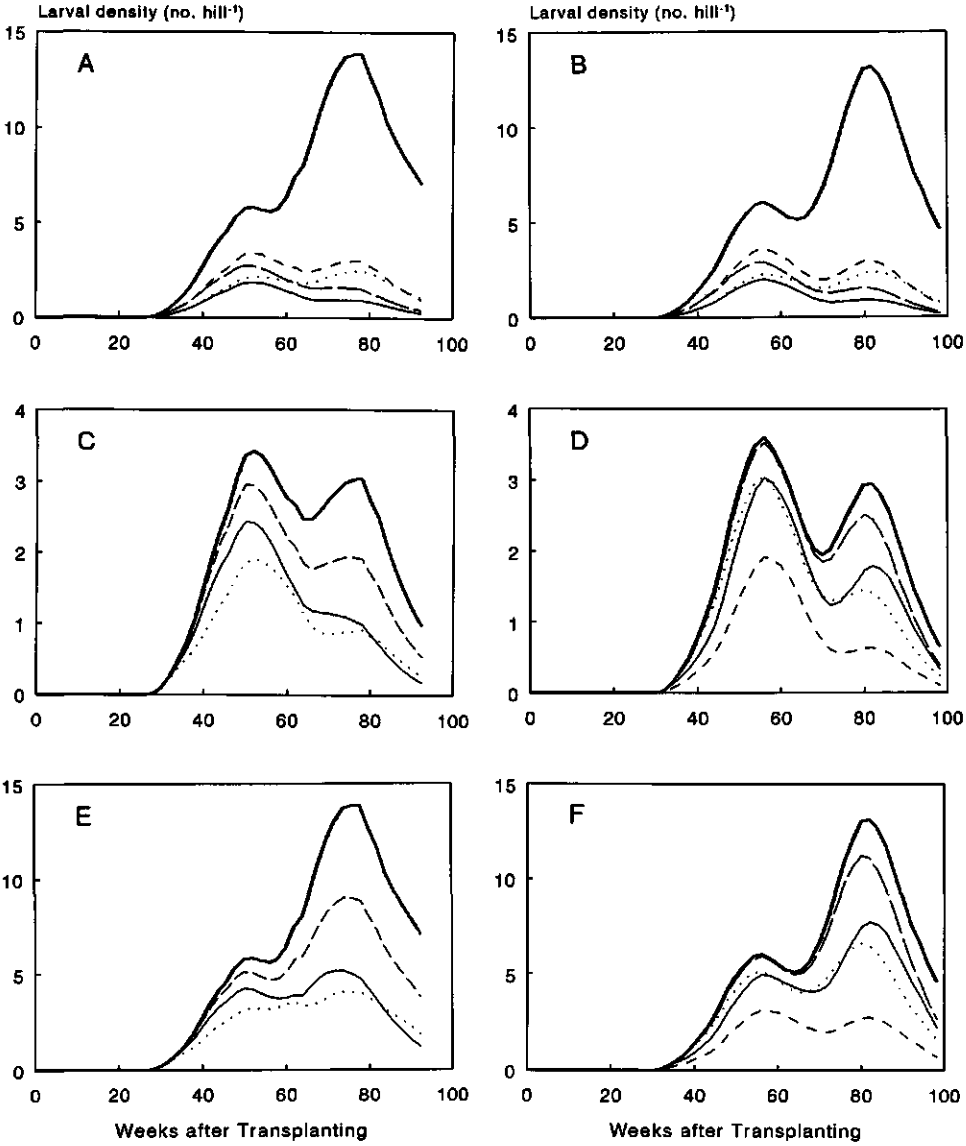


Figure 11. Effect of natural enemy-related mortality on leaffolder infestation.

A,B Simulated rice leaffolder infestation curves under wet (A) and dry (B) season conditions, for five combinations of natural enemy-related mortality factors:

—— no natural enemies; — — — egg and larval parasitism; ······· egg parasitism and predation

— — egg predation and larval parasitism; —— egg predation and parasitism, and larval parasitism.

Table 4. Rice leaffolder larval density and associated percentage yield loss, simulated with various combinations of natural enemy related mortality factors. Rice leaffolder input data: average egg recruitment level. Crop input data: IR72 at high N level, under wet and dry season conditions.

a. All mortality factors are forcing functions, averaged from observations. Simulations with standard leaffolder injury capacity, plus ranges based on low and high injury capacity.

Combination of mortality factors			Larval peak density (no. hill^{-1})	Yield loss (%)	
Egg predation	Egg parasitism	Larval parasitism		wet season	dry season
1. no	no	no	13.6	13.1 (4.9 - 29.7)	7.3 (2.7 - 9.8)
2. no	yes	yes	3.5	3.9 (1.5 - 8.7)	2.3 (0.8 - 2.9)
3. yes	no	yes	2.9	2.9 (1.1 - 6.5)	1.7 (0.6 - 2.1)
4. yes	yes	no	2.4	3.1 (1.2 - 6.6)	1.8 (0.7 - 2.1)
5. yes	yes	yes	2.0	1.8 (0.7 - 4.1)	1.1 (0.4 - 1.3)

b. Egg predation is a function of observed cricket densities. Average and ranges of yield loss are based on seven seasonal density patterns of crickets. Reduction vs. 'control' is the relative difference between simulated yield loss with and without cricket egg predators.

Combination of mortality factors			Larval peak density (no. hill^{-1})	Yield loss (%)	Reduction vs. 'control' (%)
Egg predation	Egg parasitism	Larval parasitism			
1. crickets	yes	yes	2.7	2.0 (0.3 - 7.0)	33.0 (6.2 - 59.3)
2. crickets	no	no	6.8	5.7 (0.9 - 22.6)	39.7 (9.0 - 71.1)

Figure 11 (opposite page, ***continued*****)**

C,D Simulated rice leaffolder infestation curves with egg and larval parasitism included, and egg predation calculated from the observed density patterns of predatory crickets from seven crops,
wet season (C): —— no egg predators; ····· Pila 1991; - - - IRRI 1992; —— Pila 1993;
dry season (D): —— no egg predators; - - - Victoria 1991; — — Pila 1991; ····· Pila 1992, —— Pila 1993
E,F Same as C and D, but now simulated without egg and larval parasitism.

Discussion and Conclusions

Damage by rice leaffolders

The simulation results show that both crop condition and the presence of natural enemies have a large impact on rice leaffolder population dynamics and, consequently, yield loss. Growth limiting or reducing factors other than nitrogen and rice leaffolders were not included in the simulations. To establish absolute damage thresholds, insight in the effect of these other factors would be required. However, the simulations served well to give insight in the relative importance of various factors affecting yield loss due to rice leaffolders. In this way, it can contribute to the identification and development of effective options for leaffolder management.

Crop condition In the simulations crop condition was varied with input data from different N-fertilizer levels. N-fertilization affected strongly the crop leaf area, and hence its sensitivity to leaffolder infestation (Table 3, Fig. 9). Due to the increased shading of lower leaf layers, canopy photosynthesis increases at a decelerating rate with crop leaf area index (LAI) (Penning de Vries et al. 1989). A reduction in leaf area in a crop with a high LAI has therefore less effect on canopy photosynthesis than in a crop with a low LAI. While N-fertilization can reduce the sensitivity of the crop to rice leaffolder injury, the opposite effect can be expected from water limitations (cf. de Jong & Daamen 1992) or biotic stresses, such as weeds (Canapi 1992), resulting in crops with a small leaf area.

Very high levels of N-fertilization, however, may result in such a strong increase in leaffolder infestation level, that yield losses also increase in spite of the reduced sensitivity to injury (Fig. 10b). Thus, the increase in yield loss resulting from the leaffolder density response to crop N-status can negate, at least partially, the yield response to N-fertilizer at high application levels (Fig. 10a). The increase of a number of other pests, e.g. yellow stemborer, will further contribute to the reduction in yield response to N-fertilization. In the presented case, the optimum level of N-fertilization without insecticide use would have been lower than the agronomic optimum (Fig. 10: 75 vs. 150 kg N ha^{-1}). Optimization of N-application considering agronomic as well as pest effects can reduce the need for insecticides.

This should not necessarily result in N-fertilization levels that are agronomically sub-optimal, because the effect on leaffolder infestation level can be strongly reduced by the method and timing of fertilizer application (Saroja et al. 1981, Swaminathan et al. 1985).

Natural enemies The importance of the biotic mortality factors acting in Laguna rice fields can be demonstrated by comparing the simulated yield losses due to observed larval densities in unsprayed fields (Table 3), and the losses simulated with a standard egg recruitment pattern and without any natural enemy action at all (Table 4). The larval densities in unsprayed fields reflect the impact of the entire complex of natural enemies of rice leaffolder, thus including more biotic mortality factors than the three studied here in detail (Table 4). For a well-fertilized crop the yield losses due to observed leaffolder densities ranged from 0.1 - 9% (Table 3), while when simulated without any natural enemy action the range in losses was 3-30% (Table 4). According to calculations by Smith et al. (1989), the economic threshold for insecticide applications against rice leaffolder in Philippine irrigated rice is approximately 300 kg of rice, equivalent to about 5% yield loss at the simulated yield levels. Considering the simulated ranges in yield loss, unacceptable losses of more than 5% would be rare at infestation levels as observed in unsprayed fields but can be expected to occur frequently when natural enemies are absent. The simulated losses for this situation are probably even underestimated, due to the conservative choice of parameter values determining leaffolder reproduction within the crop.

Impact of observed mortality rates on leaffolder infestation and damage

Combined mortality rates Peak larval densities simulated with an average egg recruitment level and observed predation and parasitism rates included, were about 2 per hill (Fig. 11a,b). Field observed larval peak densities are usually lower than 2 per hill, but the shape of the larval infestation curve is very similar (cf. Chapter 1). It could be expected that the simulated densities would be higher than observed, as all other biotic mortality factors but egg predation and parasitism of eggs and larvae were omitted in the model. Yet, simulated yield losses were already less than 5%, with only these three biotic mortality factors included (Table 4). In the simulations with natural enemy action, the size of the second larval generation is small, similar to observed leaffolder populations. The simulations indicate that this second generation is strongly suppressed only when natural enemy action at observed levels and the effect of crop stage on leaffolder oviposition preference are combined. This supports the hypothesis that these factors are crucial to the low leaffolder infestation levels observed in Philippine irrigated rice fields (Chapter 1).

Egg predation The contribution of egg predators to the suppression of rice leaffolder populations was larger than the contributions of egg or larval parasitoids, at the observed mortality levels. However, the role of the larval parasitoids will gain in importance when their impact is considered over a spatial and temporal scale larger than just a single crop, because only part of the mortality due to larval parasitism has a direct, within-crop effect on larval density and injury.

According to the simulations, the predatory crickets *M. vittaticollis* and *A. longipennis* could reduce yield losses by about 30-40%. At the highest observed densities, this reduction was 60-70% (Table 4b). Thus, these predators play an important role in preventing yield losses due to rice leaffolder, a role that might be further enhanced if their populations could be kept at high levels. To identify management opportunities for cricket conservation and enhancement, further research is required to reveal the principal factors governing their population densities.

Injury capacity of rice leaffolders

Field validation of the damage model showed that injury (area scraped and folded, life-span leaffold, relative senescence) was overestimated with the 'high injury capacity' as well as with the 'average injury capacity' set of parameters. This suggests that the lower values of the loss ranges, simulated with the 'low injury capacity' parameters, will usually be the most realistic. However, further investigation of these injury parameters under field conditions is required, as their values may vary strongly according to weather and crop conditions.

In the validation experiment, the incidence of leaffolder injury, i.e. the percentage injured leaves, was over 20% in the triple infestation treatment, while the severity, i.e. the proportion of leaf area that was scraped and folded, was less than 5% and had no significant effect on yield. The relationship between incidence and severity of leaffolder injury probably varies with the values of injury parameters, such as the feeding and folding rates and the life-span of leaffolds. Incidence, the percentage injured leaves, is easy to assess and therefore commonly used to define the injury-loss relationship and economic injury level for rice leaffolders. However, severity, the percentage injured leaf area, is probably a better predictor of yield loss (de Jong & Daamen 1992), and the variability of the incidence-severity relationship therefore further limits the usefulness of the published empirical injury-loss relationships. Superficial estimation of the leaffolder injury level is probably determined by the incidence rather than the severity of injury: e.g. an infestation of 20% injured leaves looks rather serious. This could (partly) explain why farmers tend to overestimate the importance of leaffolder injury. In IPM training, exercise in closer inspection of leaffolder injury by assessment of the proportion of leaf area actually scraped and folded may help farmers to improve their taxation of leaffolder injury.

In the present simulation study, the values of injury and population parameters were based on the leaffolder species *C. medinalis*. In Laguna rice fields the leaffolder complex consists of at least three species, with *C. medinalis* and *M. patnalis* being the most abundant (Chapter 1). Differences between both species are quite small however, both in terms of life history and injury parameters (Barrion et al. 1991a, de Kraker unpublished). It can therefore be assumed that the simulation results will not significantly differ for a mixture of the species.

Conclusions

The leaffolder densities observed in unsprayed rice fields in Laguna Province did not have a significant effect on the rice yield of a well-fertilized crop, according to the simulations. Introduction of three natural enemy related mortality factors (egg predation, egg and larval parasitism) into a leaffolder population model, suppressed larval densities to below damaging levels (<5% yield loss). Without any natural enemy action at all, yield losses of more than 5-10% can be expected to occur frequently.

The study confirms the importance of the so-called key principles of rice IPM, as formulated by the FAO (Gallagher 1992): grow a healthy crop and conserve natural enemies. Adequate nutrient supply, an important part of good crop management, makes the rice crop less sensitive to leaffolder injury. Excessively high levels of N-fertilization should be avoided, as these may result in a strong increase of leaffolder infestation. By conserving important natural enemies, such as egg predators and egg and larval parasitoids, leaffolder population levels can be strongly reduced. This simulation study shows that the combination of both principles will make chemical control of rice leaffolder in Laguna Province unnecessary most of the time. This may just as well apply to other Southeast Asian countries, such as Thailand and Malaysia, with a similar rice arthropod fauna (Tan 1981, Yasumatsu et al. 1981) and similar leaffolder infestation levels (Rurkviree 1981, Yuen 1982).

General Discussion

The study presented in this thesis concerned the potential of natural enemies to suppress rice leaffolder populations to below economic damage levels. The need for such a study was prompted by concern over the wide-spread applications of broad-spectrum insecticides against rice leaffolders and other leaf-feeding insects. The actual damage caused by leaffolders often seemed not to justify chemical control, which at the same time disrupts the control of this and other rice pests by indigenous natural enemies.

To determine whether natural enemies can suppress rice leaffolder populations to below economic damage levels, the effect of leaffolder densities on yield loss should be known, as well as the impact of natural enemies on these densities. Both issues were addressed with a systems analytical approach, by studying experimentally the processes that underlie natural enemy related mortality and leaffolder damage and by integrating these processes in models, to explain field level observations and to explore the consequences of changes in the natural enemy-pest-crop system. The emphasis in the experimental work was on the relationship between predator abundance and rice leaffolder egg mortality.

The field research was carried out in Laguna Province, Philippines, a tropical lowland area where rice is grown year-round under irrigated conditions. Rice leaffolder populations in unsprayed transplanted rice fields were characterized by an egg peak at maximum tillering, and a broad larval peak at booting stage, with peak densities ranging from 0.2 to 2.0 larvae per hill. These relatively low larval densities may be due to leaffolder ovipositional preference that allows for only one major generation, and to high immature mortality caused by the abundant and diverse complex of natural enemies. High levels of N-fertilization resulted in a strong increase in leaffolder larval density and injury, due to a positive effect on egg recruitment and survival of medium-sized larvae. The increase in larval survival was associated with decreasing predator-prey ratios. The generalist predators increased less in density with N-fertilizer level than leaffolder eggs and larvae, probably resulting in relatively lower predation rates of leaffolders.

Egg mortality in the field averaged about 60%, and was mainly due to disappearance of eggs and to a lesser extent to parasitism by *Trichogramma* spp. Non-hatching was of minor importance. The level of egg disappearance correlated positively with the densities of the predatory crickets *Metioche vittaticollis* and *Anaxipha longipennis*. Direct observations confirmed unambiguously the major role of these crickets. The egg predation rate of the crickets in cages was described adequately with a linear functional response model, indicating that predation was limited only by the search rate. Increasing the predator density per cage led to a decrease in the egg predation rate per capita. Field testing of a model of predation of leaffolder eggs based on cage experiments showed that the observed trend in egg predation could be described as a function of cricket densities and crop leaf area. The evaluation also indicated that predator interference may limit the egg predation rate of the crickets, while the presence of alternative prey did not.

A simulation study with a combined model of leaffolder population dynamics and rice crop growth highlighted the importance of natural enemies as well as crop growing conditions. The simulations indicated that larval densities as observed in the unsprayed fields would not cause significant yield loss in a well-fertilized crop. Yield losses simulated with an average leaffolder immigration pattern exceeded economic damage levels when no natural enemy action was included. Introduction of three field-observed natural mortality factors (egg predation, egg and larval parasitism) reduced losses to below these levels. Over their observed range in seasonal abundance, the predatory crickets could reduce leaffolder damage by 5 to 60% (average 35%).

Three broader issues of the study will be discussed below: (1) the methodology, (2) the implications for rice IPM, and (3) the possible impact of changes in rice cultivation on natural control of rice leaffolders.

1. An evaluation of the methodology

The main line of the approach followed in this thesis was to identify major natural enemies of rice leaffolder, to quantify their ability to kill rice leaffolders, and to integrate these quantitative relationships into a combined leaffolder-rice model. This model, covering three trophic levels, was used to assess to what extent the natural enemies can prevent high leaffolder densities, and consequently yield loss. The advantages and limitations of this approach are outlined.

1.1 Identification of major natural enemy species

Extensive field sampling of populations of rice leaffolders and their natural enemies yielded useful information on the diversity and abundance of the natural enemy complex. However, no clear correlations were found between the abundance of natural enemy groups and leaffolder survival rates per field (Chapter 1). Only within a single rice field, larval survival per treatment plot was closely correlated with the ratio of natural enemies to leaffolder immatures (Chapter 2). It was, therefore, concluded that to determine quantitative relationships between natural enemy abundance and leaffolder mortality, a distinction needs to be made within the large complex of natural enemies between species responsible for most of this mortality and species that only occasionally kill a leaffolder. Also, mortality rates needed to be assessed more precisely. This was done for leaffolder egg mortality (Chapter 3 and 4). The discovery that predation of leaffolder eggs could be attributed almost completely to only two species of predatory crickets (*A. longipennis* and *M. vittaticollis*) enabled detailed quantification of the predation rates (Chapter 5-7). This would not have been feasible if a multitude of predator species had been discovered.

Direct observations of egg predation in the field were crucial to the discovery of the major egg predators (Chapter 4). The other indirect techniques, such as regression analysis of field data on egg disappearance and predator density, ranking of species according to their predatory potentials, and modelling of predation, complemented and confirmed the direct observations. In some cases, however, direct observation is not feasible. For example, it will be difficult to observe the major predators involved in disappearance of young leaffolder larvae due to the mobility and cryptic behaviour of these larvae. Here, the most suitable approach may be to rank the known predator species using relatively simple predation tests, and then do a regression analysis of densities of a few high ranking predator species on field measured disappearance rates. Development and testing of a predation model would also be troublesome because of the interactions between the predation rate and larval behaviour (e.g. IRRI 1988), and the difficulties in partitioning larval disappearance into predation, abiotic mortality, dispersal, and host plant-induced mortality.

1.2 Use of modelling

In their reviews of methods to evaluate natural enemies in rice, Shepard & Ooi (1991, 1992) payed little or no attention to the use of models. They appear to adhere to the highly experimental and empirical approach proposed by Luck et al. (1988). In this approach the emphasis is on field assessment of mortality caused by the complex of natural enemies, and identification of the most important species within this complex. Luck et al. (1988) suggest to use this information to establish predator-prey ratios as treatment criteria in an empirical, iterative process, rather than trying to determine realistic predation rates. This empirical approach has the disadvantage that little insight is gained into how various factors determine the level and variability in pest mortality rates. Such factors are first of all the abundance of the major natural enemy species, but also the leaf area of the crop, and the density of the target pest and alternative prey species. Quantifying the relationships with these factors and integrating them in models (Chapter 7), enables explanation of the observed mortality levels. Models can be used to generate quantitative hypotheses and predictions of the potential impact of natural enemies under different conditions. These can serve to focus further experimental research on the impact of natural enemies in other areas, or to assess the effect of changes in predator abundance. Modelling can thus make the evaluation of indigenous natural enemies and the development of strategies to maximize natural control more efficient than in a purely empirical approach. However, as indicated above, this modelling approach is only feasible when there are only a few major natural enemy species.

Predation model The field predation rate of a species can be modelled descriptively, by relating measured predation rates to predator density and other independent variables, such as prey density, search area and temperature. Alternatively, predation rates can be modelled in an explanatory way, by calculating predation rates on the basis of underlying behavioural processes. Although measurements of predation rates at a low degree of complexity (cages) were used to model predation under far more complex conditions (field), the approach taken in this study was in essence descriptive. Behavioural components were not considered explicitly, but summarized in the search rate. This descriptive approach has the advantage that both estimation of parameters and field validation of the model were feasible. However, measuring predation rates in cages has the disadvantage that cage artifacts can be included. This study attempted to avoid such artifacts by using cages of various sizes and by conducting behavioural observations (Chapter 5 and 6). Yet, field evaluation of the predation model indicated the need for additional behavioural studies, because interference between the predatory crickets was identified as a potentially important mechanism, limiting their impact on rice leaffolder eggs. Thus far, interference was described with a biologically unrealistic, discontinuous function, based on cage predation experiments. Behavioural studies are needed to increase insight in the occurrence, mechanism and importance of interference among the crickets.

Pest-crop model The combined pest-crop simulation model of leaffolders in rice provided a useful framework to integrate knowledge on mortality factors and to assess the indirect impact of natural enemies on yield loss. It allowed study of the effect of removal or addition of mortalities, assessment of the effect of different patterns of predator abundance under similar crop conditions, and measurement of relatively small effects on yield (<10%). All this is either impossible or very difficult to achieve with field experiments. Moreover, crop yields in the field will always be affected by other pests as well. However, such a model can only be developed on the basis of extensive experimentation. In this study, the development of the combined pest-crop model was greatly facilitated by the availability of a well-validated model of rice crop growth (Kropff et al. 1994b) and the considerable amount of published data on rice leaffolder life history. Yet, the development of the model revealed major uncertainty about the values of parameters, particularly those describing injury, thus indicating the need for further investigations. Considering the current uncertainty about model parameters and the exclusion of other growth limiting or reducing factors, the model should not be used to establish decision rules, such as economic injury levels or predator-prey ratios, in quantitative detail. Nevertheless, the simulations can give a good insight into the relative importance of various factors affecting yield loss due to rice leaffolders (Chapter 8).

2. Implications for rice IPM research, training and implementation

2.1 Issues for further research

This study found that natural enemies can prevent rice leaffolder damage under good growing conditions, and that predatory crickets are important species within the complex of natural enemies. These findings raise three further issues for investigation. The first is whether the *predatory crickets* play a major role in egg predation over a wider geographic area. The second concerns how the impact of natural enemies can be maximized by *conservation*. The third issue to be investigated is how *nitrogen management* can be optimized for rice cultivation based on natural biological control.

Egg predators In Laguna Province egg predation was found to be the main factor in leaffolder egg mortality, and the crickets *M. vittaticollis* and *A. longipennis* were identified as the major egg predators. Their role could be explained by their search rate and consumption capacity, which are much higher than for the other species observed to feed on leaffolder eggs. *Metioche* and *Anaxipha* species are distributed throughout the Indo-Australian region, and the minor egg predator species found in Laguna Province, or close relatives, are also common throughout South and South-east Asia. As there are no reports of other egg predators as voracious as the two cricket species, it seems likely that the major role of the predatory crickets can be extrapolated to a larger geographic area, e.g. to irrigated lowland rice in South and South-east Asia. However, this should be verified locally in two steps. Firstly, the local species preying on rice leaffolder eggs should be identified and their relative importance assessed. Direct observations by IPM trainees has proved to be a very effective and efficient method for this purpose (van den Berg 1992, 1993). This first step will reveal whether there is a need to study the predation rates of species not included in the egg predation model (Chapter 7). Secondly, the validity of the quantitative description of the impact of the crickets and other predators, the egg predation model, must be evaluated with local data sets. These can be obtained in leaffolder egg exposure experiments and sampling of predator populations, covering a range of fields, seasons and crop development stages.

Conservation of natural enemies Natural enemies were shown to play an important role in suppressing rice leaffolder populations to below damaging levels. Of the three mortality factors explicitly measured and evaluated for Laguna Province, egg predators contributed most to the reduction in leaffolder larval density and damage within a growing season. Egg and larval parasitism contributed less, although larval parasitoids probably have a more prominent role when their impact on carry-over of leaffolder populations to other crops is considered. Census studies indicated that other mortality factors not studied here in detail are also important, such as predation of young larvae. Conservation of naturally-occurring predators and parasitoids must thus be given high priority in sustainable management of rice leaffolders. In general, reduced pesticide use will favour the build-up of diverse and abundant natural enemy communities. However, the impact of this increased diversity and abundance on rice leaffolder density and survival will largely depend on the species composition of the natural enemy complex. The identification of *M. vittaticollis* and *A. longipennis* as major egg predators makes it possible to focus further research on the development of more specific conservation measures. The consequences of enhanced cricket densities for leaffolder egg predation and damage can be explored with the combined leaffolder-rice model. As these crickets are also important egg predators of many other rice insect pests, their conservation is of broader significance than the control of rice leaffolders only.

The use of insecticides less harmful to the crickets is one obvious way to conserve these important predators. Studies on the toxicity of insecticides to the crickets have indicated that both species are highly susceptible to common broad-spectrum insecticides, but a few less harmful chemicals have also been identified (Bandong & Litsinger 1986, Rubia & Shepard 1987b). These selective chemicals are, however, generally too expensive for large-scale adoption by farmers (Litsinger 1989, Heong et al. 1994). Bio-pesticides based on insect pathogens and produced locally could provide competitive alternatives, but are as yet not available (Litsinger 1989). The toxicity of herbicides urgently needs further investigation because their use is rapidly increasing in Asian rice cultivation (Moody 1993), and many herbicides have a negative effect on natural enemies (Hassan 1984).

The population density of the predatory crickets in unsprayed rice fields in Laguna Province varied considerably between seasons and locations (Chapter 1 and 8). Further studies are needed to determine the principal factors affecting these variations. This will help in identifying options to sustain high cricket densities. One such option may be management of the habitats of the crickets outside rice fields. Rubia & Shepard (1987a) found that *M. vittaticollis* in a free-choice test laid as many eggs on several plant species common to rice field borders as on rice plants. Surveys of the arthropod fauna in the vegetation surrounding rice fields showed that the predatory crickets can be very abundant in grassy habitats (R.C. Joshi, pers. comm.). This vegetation may act as source and refuge of the rice field cricket populations, and careful management of these non-rice habitats could be an effective component of a conservation strategy. Circumstantial evidence of the importance of these habitats is provided by the low densities of predatory crickets and the concurrent severe rice leaffolder infestations in an area in Malaysia where large-scale destruction of all vegetation is practised prior to crop establishment (Klein Beekman & Lamour 1993). Thus, further research into the effects of agro-ecosystem architecture and management on the abundance of natural enemies, in particular of crickets, appears fully justified.

Nitrogen management Apart from raising the attainable yield level, an adequate supply of nitrogen can also increase the crop's tolerance to pests. A well-fertilized crop is less sensitive to leaffolder injury, mainly because of its larger leaf area. However, leaffolders have a strong oviposition preference for heavily fertilized crops. Very high levels of N-fertilization may thus result in such a high increase in leaffolder density that yield losses also increase in spite of the reduced sensitivity to injury. In areas where leaffolders are common, farmers applying much higher levels of N-fertilizer than their neighbours risk losing this investment due to heavy leaffolder attack. N-fertilization thus has a dual effect on rice leaffolder damage, which has also been observed for a number of other rice pests (Litsinger 1994). Optimization of N-application should aim at maximizing the positive effects on yield formation and tolerance to injury, while minimizing its stimulating effect on pest density so that chemical control is not needed. Rather than attempting to establish an optimal N-application strategy by trial and error, institutional research should first focus on the central, underlying relationship between N-application level and leaffolder ovipositional preference. Two aspects of N-application - timing and spatial scale - require particular attention.

The timing of fertilizer application affects the density response of leaffolders (e.g. Saroja et al. 1981). Studies are needed to clarify how N-application and uptake at various rice growth stages affects leaffolder ovipositional preference. Knowledge of these relations can be integrated with recent insights into the effects of level and timing of N-fertilization on crop growth and yield (ten Berge et al. 1996a,b) in a combined leaffolder-rice simulation model. With this model, interactions can be studied between growth stage-dependent effects of N-application on leaffolder density, crop tolerance and yield formation. Such a model may serve to generate hypotheses and general principles for optimal N-application strategies, which can be field tested and adapted to local conditions, for example in the context of participatory training of farmers in IPM.

As the strong effect of N-fertilization on leaffolder infestation in small-scale field trials appears mainly based on preference, increasing fertilizer rates over a larger area may have a less dramatic effect. Studies on the dispersal range of leaffolder females during the oviposition period can provide a more quantitative insight into the relationship between the spatial scale of N-application and the level of egg recruitment as a result of ovipositional preference. The long-term effects of a large-scale increase of fertilizer rates on leaffolder population dynamics, however, are difficult to test empirically. The unpredictable response of the natural enemy complex does not allow extrapolation of laboratory-defined relationships between crop N-level and leaffolder fitness.

2.2 Rice IPM Training and implementation

The location-specific nature of natural biological control prevents the design of general solutions to local pest problems (Waage 1994). Farmers will have to be empowered with the skills to assess their own pest problems and decide on appropriate action (Kenmore 1991, Matteson et al. 1994). Waage (1994) therefore defined the role of institutional research on natural control as supplier of information and methods to train farmers to be IPM experimenters and implementers. What inputs to farmer training could the present research project provide to help farmers improve their management of rice leaffolders ? Possible inputs concern three aspects of integrated pest management: correct assessment of damage potential, appropriate crop management, and appreciation of the role of natural enemies.

Rice leaffolder damage potential Model simulations indicated that a well-fertilized, irrigated rice crop is not very sensitive to leaffolder injury. Larval densities below 5 per hill are unlikely to cause significant yield loss. The studies in Laguna Province, and reports from other areas in South and South-east Asia indicate that this level is rarely exceeded. Yet, many Asian rice farmers perceive rice leaffolders as a serious threat to their crops and apply insecticides even at very low infestation levels (IRRI 1993c, Heong et al. 1994). Farmer training, therefore, should strive to bring about a change in perception of leaffolder injury. Defoliation experiments can be very useful in conveying the concept of crop tolerance to leaf injury. As farmers tend to overestimate the conspicuous injury symptoms of leaffolders, it may be quite instructive to include exercises on assessment of the proportion of total leaf area folded and scraped. These assessments can then be coupled to the design and interpretation of their defoliation experiments to get a feel for the level of injury that can be tolerated.

Crop management The model simulations clearly indicated that a crop adequately supplied with water and nutrients is far less sensitive to rice leaffolder injury than a crop with a low leaf area due to poor growing conditions. The importance of good water and nutrient supply to prevent economic damage by leaffolders may be demonstrated in learning experiments combining levels of defoliation and water or nutrient supply. This can encourage farmers to invest in fertilizer rather than in pesticides, which will probably also enhance the economic benefits of IPM through a more favourable rate of return (Waibel & Meenakanit 1988).

Several researchers have proposed applying additional fertilizer instead of an insecticide in response to stemborer or foliar injury to improve the compensatory ability of the crop (IRRI 1991a, Way & Heong 1994). This is probably not a good concept. Rice plants are least sensitive to leaffolder injury when adequately supplied with nitrogen, but N-fertilizer will be most effective and efficient when applied according to the physiological need of the crop (ten Berge et al. 1996a,b). This timing does not necessarily coincide with the occurrence of pest injury, and application according to injury thresholds may even have a negative effect. For example, when 20 kg additional N was applied in response to early leaf injury by the whorl maggot, it either had no effect on yield, or caused lodging of the crop (IRRI 1991a).

As already indicated, N-fertilizer application may also lead to increased leaffolder infestation.

In areas where high infestations of leaffolders on heavily fertilized crops are common, farmers may conduct experiments to assess how timing of N-fertilizer application may reduce leaffolder infestation. Ideally, this should be combined with experimentation on the optimum timing of fertilizer for yield formation.

Appreciation of natural enemies Shepard (1989) suggested to take the beneficial impact of natural enemies into account before deciding on spraying, by using thresholds that depend on the abundance of a few major natural enemy species (e.g. Shepard et al. 1988). In current IPM training in farmer field schools, integration of natural enemies in pest management decisions is a central concept, but the use of fixed, quantitative monitoring procedures and thresholds has been abandoned. Farmers conduct a broad, more qualitative assessment of the condition of their fields ('agro-ecosystem analysis', Matteson et al. 1994), in which the balance between pests and major natural enemy species is the basis for decision making. By rearing field-collected pest stages and doing small predation experiments, farmers learn about presence and impact of these natural enemies. As the predatory crickets are fairly big and well-visible, and quite voracious feeders on a range of pest insect eggs, they are ideal for such predation experiments. This is even more urgent as most cricket species are not predatory but herbivorous (Reissig et al. 1986), and farmers are likely to consider all species as pests. Subsequently, crickets can be included in field monitoring and accounted for in the beneficial-pest balance in the agro-ecosystem analysis. Little impact can be expected from cricket densities less than 1 per 10 hills, while high egg mortality will be caused when densities exceed 1 per 3 hills. The predatory crickets may further be used in pesticide toxicity trials, which could convince farmers of the need to avoid harmful broad-spectrum insecticides, and to apply the selective chemicals even though more expensive, once intervention is inevitable.

Awareness of crop tolerance to leaffolder injury and of crop management practices to enhance this, and appreciation of the presence and impact of natural enemies and their sensitivity to broad-spectrum insecticides will enable farmers to make better informed decisions about the need for chemical control once leaffolder infestations occur in their fields.

This will certainly reduce insecticide use against this pest, which in turn will lead to enhanced and more effective populations of natural enemies.

3. Impact of new crop management practices and rice plant types on rice leaffolder populations and damage

The study presented in this thesis was conducted in transplanted irrigated rice, with current high yielding varieties. However, crop management practices change, and new rice varieties are developed and introduced. Currently, an important change is the shift from transplanting to direct seeding, mainly because of the shortage and cost of labour for transplanting (De Datta & Nantasomsaran 1991). In the major irrigated lowland rice areas of South- and South-east Asia, direct seeding is practised by a large proportion of the farmers (>50%; IRRI 1991b, 1993c) and the adoption rate is likely to increase further.

The ever-increasing demand for rice calls for a further increase in production level. Various ways have been put forward to increase the yield potential of rice beyond that of the current high yielding varieties. An important prerequisite is an extended green leaf area duration during the grain filling period. This may be achieved through a combination of additional late applications of N-fertilizer and rice varieties with reduced leaf senescence during grain-filling (Kropff et al. 1994a).

The population dynamics of rice leaffolders in Laguna Province appeared mainly affected by the relationship between egg recruitment and crop development stage, and immature mortality caused by natural enemies. How will direct seeding and an extended green leaf area duration affect the egg recruitment pattern and natural enemy impact ?

3.1 Direct seeding

An increase in rice leaffolder infestation associated with a shift to direct seeding of rice has been reported from Malaysia (Hirao & Ho 1987, Chang 1991) and Thailand (Waibel & Meenakanit 1988). The major difference between direct seeded and transplanted rice crops is the larger leaf area during the early crop stages in direct seeded rice (Dingkuhn et al. 1993). In a screenhouse experiment with *C. medinalis*, the number of eggs laid per m^2 depended positively on both crop leaf area and leaf N-content (de Kraker unpublished). *C.*

medinalis laid few eggs in transplanted plots in the early tillering stage, but in direct seeded plots of the same age many eggs were laid. Luo (1989) observed in a field experiment that leaffolder moths arrived earlier in direct seeded plots than in transplanted plots. However, the major egg predators *A. longipennis* and *M. vittaticollis* colonized the direct seeded plots earlier as well, and reached higher peak densities than in transplanted plots. This probably resulted in the relatively high predation rates of yellow stemborer eggs, observed in the direct seeded rice plots during the early crop stages. At the same time, the parasitism rates of these eggs were higher in the more open transplanted plots, as was also found by Shepard & Arida (1986). During the later crop stages, parasitism and disappearance rates of rice leaffolder eggs did not differ between direct seeded and transplanted rice (Arida & Shepard 1990).

The balance between the various factors, viz. the time and rate of colonization of the crop by leaffolders and their natural enemies, and the effectiveness of the natural enemies will determine whether the leaffolder infestations is higher in direct seeded rice. There is no a-priori reason why natural enemies will not be as effective as in transplanted rice fields. The reported problems of rice leaffolder in direct seeded rice appear primarily related to *other* management practices that are directly detrimental to natural enemies. In a large direct seeded area in Malaysia very high injury levels were indeed observed during the first month after crop establishment (>50% injured leaves). This could be attributed, however, to a delayed build-up of natural enemies as a result of large-scale destruction of vegetation prior to crop establishment (Klein Beekman & Lamour 1993). In Thailand, the association between high rice leaffolder infestations and direct seeding was confounded by a correlation with high insecticide use in the same area (Waibel & Meenakanit 1988). Whether the intensive use of herbicides that is commonly associated with direct seeding also has a negative impact on the natural enemy complex is not known and should be a high priority issue for further investigation.

3.2 Extended green leaf area duration

Thus far no experiments have been carried out on the effects of an extended green leaf area duration during the grain filling phase on rice leaffolder population dynamics or the impact of its natural enemies. We can assume, however, that enhancing leaf N-content and delaying senescence will prolong the suitability of the host plant, which normally decreases quickly after flowering (Telvapuchom 1990). Positive effects on oviposition and young larval survival will result in a potentially larger second generation of leaffolder larvae in transplanted rice fields. Whether this will cause higher yield losses depends on the response of natural enemies to the prolonged availability of their prey or host, and the effects of an extended green leaf area duration on the crop's sensitivity to leaffolder injury.

In general, changes in crop leaf area and leaf N-content lead to increased rice leaffolder egg recruitment. However, natural enemies often increase in abundance as well, while at the same time a crop with a large green leaf area is less sensitive to leaf injury. As was demonstrated for the comparable effect of enhanced N-fertilization (Chapter 2 and 8), the implications of these changes for crop damage depend on the balance of these processes.
The combined leaffolder-rice simulation model offers a suitable framework to explore the consequences of these changes at the crop level. It can also serve to guide further experimental research by focusing on the underlying processes of leaffolder damage and by providing quantitative hypotheses on the impact of these processes at crop level. Better insight into how crop management practices can affect yield directly through crop growth processes, as well as indirectly through their effects on rice pests and natural enemies, will contribute to the development of rice production techniques that combine high productivity with sustainable management of rice pests, based on the action of naturally-occurring predators and parasitoids.

Summary

Introduction

Rice leaffolders *Cnaphalocrocis medinalis* and *Marasmia* spp. (Lepidoptera: Pyralidae) occur in all rice environments throughout Asia. The larvae injure the rice plants by folding the leaves and scraping off the green mesophyll tissue inside the folds. The study presented in this thesis concerned the potential of natural enemies to suppress rice leaffolder populations to below economic damage levels. The need for such a study was prompted by concern over the wide-spread applications of broad-spectrum insecticides against rice leaffolders and other leaf-feeding insects. The damage caused by leaffolders seemed not to justify chemical control, which at the same time disrupts the control of this and other rice pests by indigenous natural enemies. To determine whether natural enemies can suppress rice leaffolder populations to below economic damage levels, the effect of leaffolder densities on yield loss should be known, as well as the impact of natural enemies on these densities. A quantitative understanding of the mechanisms that underlie the (system-level) relationships between populations of natural enemies and rice leaffolders, and the rice crop, is needed to explain how these relationships change under different conditions. In this study such a systems analytical approach was followed, with the objectives:

(1) to quantify the impact of natural enemies on rice leaffolder populations, and

(2) to assess the potential of natural enemies to prevent rice leaffolder damage,

on the basis of the underlying ecological and crop physiological mechanisms.

The main line of research was to identify major natural enemies of rice leaffolder, to quantify their ability to kill rice leaffolders, and to integrate these quantitative relationships into a combined leaffolder-rice model. This combined simulation model, covering three trophic levels, was used to assess to what extent the natural enemies can prevent high leaffolder densities and consequently yield loss. The emphasis in the experimental work was on rice leaffolder egg mortality, and in particular the role of egg predators. Field studies were conducted in Laguna Province, Philippines, a tropical lowland area where rice is grown year-round under irrigated conditions. Experiments in screenhouse, greenhouse and laboratory were all carried out at the International Rice Research Institute (IRRI) in Los Baños, also located in Laguna Province.

Rice leaffolder population dynamics

For a descriptive analysis of pest population dynamics and the natural enemy complex, populations of rice leaffolders and their natural enemies were sampled in eight unsprayed rice crops **[Chapter 1]**. The rice leaffolder complex consisted of three species: *Cnaphalocrocis medinalis*, *Marasmia patnalis*, and *Marasmia exigua*. Either *C. medinalis* or *M. patnalis* was dominant, or both were equally abundant. The populations were characterized by an egg peak at maximum tillering and a broad larval peak around booting stage. Larval infestation levels were quite variable, but never exceeded a density of more than two per hill and the number of injured leaves was always below 10 per hill. During the first month after transplanting leaffolder populations were always very low. Most larvae originated from immigrant moths and there was no substantial second generation. Eleven species of hymenopterous parasitoids were reared from the field-collected leaffolder eggs, larvae and pupae. The seasonal percentage egg parasitism by *Trichogramma* sp. (Hymenoptera: Trichogrammatidae) ranged from 0 to 50%, and percentage larval parasitism from 14 to 56%. *Macrocentrus philippinensis* (Hymenoptera: Ichneumonidae) was the most commonly reared parasitoid. Forty taxa of natural enemies that may attack rice leaffolders were identified from field samples: 24 predator taxa and 16 parasitoid taxa. The number of taxa found per crop ranged from 28 to 36. Predator populations were numerically dominated by hemipteran species. The most common taxa of parasitoids were *Cotesia* spp., *Opius* spp. and *Tetrastichus* spp. The average estimated survival rate from eggs to large larvae (14%) was much lower than published values for natural enemy-free conditions. To explore the impact of the natural enemy complex, correlations between leaffolder abundance and survival, and parasitism rates and (relative) abundance of natural enemy groups were investigated. However, at this level of aggregation no clear relationships were found, except for a negative correlation between survival of medium-sized larvae and parasitism of young larvae. The generally low infestation levels of rice leaffolders in Philippine transplanted rice are probably caused by their ovipositional preference for the maximum tillering stage, allowing for only one generation, and high immature mortality caused by the abundant and diverse complex of natural enemies. The impact of the natural enemy complex on rice leaffolder will be determined by its composition.

N-fertilization is often reported to cause an increase in rice leaffolder infestation levels. To determine how N-fertilization affects the population dynamics and natural control of rice leaffolders, a field experiment was conducted with three levels of N (0, 75, and 150 kg ha^{-1}) in a randomized block-design **[Chapter 2]**. N-fertilization had a very strong effect on rice leaffolder population dynamics and injury level. The average density of rice leaffolder larvae at the highest N level was eight times the density at zero N 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 N-fertilization on oviposition, and on survival of medium-sized larvae. The percentage egg and larval parasitism was not affected by N-fertilization. The increase in survival of medium-sized larvae with N level is probably due to the lower predator-leaffolder ratios. The generalist predators increased less in abundance with N-fertilizer level than did leaffolder immatures, resulting in lower levels of natural control. The strong increase in infestation of rice leaffolders and other pests with N-fertilization was probably the cause of the lower yield at the highest N-level, as compared with the medium N-level.

Egg mortality and egg predation

The population studies showed that mortality due to natural enemies was important in suppressing leaffolder densities, but it was difficult to predict the stage mortality levels from parameters based on large groups of natural enemies. To understand how leaffolder mortality relates to the presence and abundance of natural enemies, stage mortalities should be analyzed in more detail, and the natural enemy species responsible for the major part of the mortality should be identified. With this purpose, mortality of rice leaffolder eggs was studied in detail in the field. Mortality was assessed by field exposure of laboratory-laid eggs for two days and by monitoring naturally-laid eggs **[Chapter 3]**. Egg disappearance, the major mortality factor, was low during the first four weeks after transplanting and then increased. Eggs were parasitized by *Trichogramma japonicum* Ashmead (Hymenoptera: Trichogrammatidae). Parasitism was highest at the start of the crop and decreased to a low level towards maturity. Non-hatching was of minor importance. Over the total duration of the egg stage, the average disappearance of exposed laboratory-laid eggs was 40% (6 crops), and of naturally-laid eggs 46% (4 crops). Egg mortality due to parasitism averaged 15% and

18% respectively. The potential impact of egg parasitism is probably partly obscured by disappearance of parasitized eggs. A high level of egg disappearance was correlated with high densities of the predatory crickets *Metioche vittaticollis* (Stål) and *Anaxipha longipennis* (Serville) (Orthoptera: Gryllidae). Percentage disappearance of naturally-laid eggs was also positively correlated with average leaffolder egg density and total rainfall. Percentage parasitism of exposed leaffolder eggs was positively correlated with the total host egg density in the field, and negatively correlated with crop leaf area and wind speed.

As correlations are no proof of causal predator-prey relationships, laboratory and field studies on predation of rice leaffolder eggs were conducted to identify the major predator species **[Chapter 4]**. In petri-dish tests the consumption of leaffolder eggs by the predatory crickets *Metioche vittaticollis* and *Anaxipha longipennis* was far greater than that of other predators. Female cricket adults consumed at least 80 eggs per day, and all individuals accepted leaffolder eggs as food. According to daily egg consumption and acceptance rates, the predators ranked as follows: *M. vittaticollis*, *A. longipennis* > *Micraspis* sp. > *Ophionea nigrofasciata* > *Paederus fuscipes, Conocephalus longipennis*. Choice tests with alternative food showed that the cricket *M. vittaticollis* preferred insect eggs over the usually very abundant brown planthopper *Nilaparvata lugens* nymphs, and had a slight but stable preference for green hairy caterpillar *R. atimeta* eggs over leaffolder eggs. The leaffolder egg consumption of *Micraspis* sp. decreased drastically when rice pollen were available, while *C. longipennis* preferred to feed on rice plant tissues rather than on leaffolder eggs.

Direct observations of predation on field-exposed eggs made clear that during two seasons *M. vittaticollis* and *A. longipennis* were the major predators of leaffolder eggs. Together these crickets took the largest part of all eggs consumed during observation (92%), and had the highest ratio of visits with predation to their total visits observed (0.43). Furthermore, their activity pattern correlated best with the daily pattern of egg disappearance, and their seasonal trends in abundance correlated best with the seasonal trends in egg disappearance. Other, minor predators observed feeding were: *O. nigrofasciata, Micraspis* sp., and *C. longipennis*. The latter species was the most common egg predator, but had a negligible share in the observed egg predation. Predator ranking according to the ratio of visits with predation to total visits observed in the field, was identical to the one based on the petri-dish tests.

The egg predation capacity of the crickets *M. vittaticollis* and *A. longipennis* was quantified with a series of cage experiments **[Chapter 5]**. Egg predation was measured in response to changes in egg density, predator density and leaf surface area per cage. The predator types included were nymphs, females, and males of *M. vittaticollis* and females of *A. longipennis*. The functional response to prey density of all predator types could be adequately described by the linear Nicholson-Bailey model, with the effect of leaf area included. This indicates that the response to egg density was not limited by egg handling time or satiation, but by the search rate. The search rate can be interpreted as the leaf surface area effectively searched by a single predator in one day. The estimated search rates for leaffolder eggs ranged from 0.05 m^2 day^{-1} for *M. vittaticollis* nymphs to 0.13 m^2 day^{-1} for *M. vittaticollis* females. Search rates of *M. vittaticollis* females, males, and *A. longipennis* females were not significantly different. The search rate of *M. vittaticollis* females increased significantly with prey density, but the density dependent model explained only an additional 3% of the total variation in search rate. Increasing predator density per cage led to a decrease in the per capita egg predation rate when the predator density was more than two per m^2 leaf area.
To check the results of the cage experiments and the assumptions of the functional response model, the searching behaviour of the crickets *M. vittaticollis* and *A. longipennis* was studied in the laboratory **[Chapter 6]**. Predators were observed during 1.5 or 2.5 h periods on isolated rice plants or in 30-plant cages, with rice leaffolder *M. patnalis* eggs as prey. Movement of the predators over and between plants was close to random and the predators seemed to detect leaffolder eggs only by direct physical contact. The time needed to consume a single egg was short (20 s), supporting the assumption that prey handling time can be neglected. After egg consumption the walking activity and speed of the predator *M. vittaticollis* did not change markedly, but locations where eggs had been consumed were revisited more often than locations where the eggs had not been detected and consumed. This apparently area-restricted searching behaviour contradicts the assumptions of completely random search and constant search rate, but had little effect on the overall walking pattern. The predators spent 25-50% of their time walking and were more active in the early morning and the evening than during daytime. On isolated plants the predators covered 12-20 cm^2 leaf area per minute walking time, but failed to find and consume the leaffolder eggs in this area

in nine out of ten times. The walking activity of *A. longipennis* and *M. vittaticollis* was similar, but *A. longipennis* covered less area and visited fewer plants per unit walking time. Estimates of the daily search rate, based on observed walking activity, encounter rate and probability of consumption, ranged from 0.01 m^2 for *A. longipennis* to 0.12 m^2 for *M. vittaticollis*. These values are lower than calculated from the cage predation experiments and may be underestimated due to the circadian rhythm in cricket predation activity.

With the results of the cage predation experiments a deterministic model of field predation of rice leaffolder eggs was developed and evaluated with independent field data **[Chapter 7]**. The model included the functional response of five predator types: three types of predatory crickets (*Metioche vittaticollis* adults, *Anaxipha longipennis* adults, nymphs of both species), a coccinellid (*Micraspis* sp.) and carabids (*Ophionea* spp.). In the model the search rates of the adult crickets were affected by prey density and mutual interference. Evaluation of this model showed that it could be simplified to a large degree. Predictions of field predation rates improved after removing predation by *Micraspis* sp. and *Ophionea* spp., the effect of prey density on the search rate of *M. vittaticollis*, and the distinction between *M. vittaticollis* and *A. longipennis* adults. The resulting simplified model included only the functional response of cricket nymphs and adults, and a 50% reduction of adult cricket search rates when their density exceeds 1.5 m^{-2}. The evaluation confirmed field observations on the major role of predatory crickets in leaffolder egg predation, and indicated that predator interference may be an important mechanism limiting their predation rates, while the effect of alternative prey on the egg predation rate seemed negligible. The simplified model described the observed trend in egg predation rates reasonably well, and can be applied to explore the effect of changes in predator abundance on rice leaffolder survival.

A simulation study on the impact of natural enemies on leaffolder damage

A combined pest population-crop growth simulation model of leaffolders in rice was developed and partially validated **[Chapter 8]**. This mechanistic model was used to test the hypothesis that in unsprayed rice fields in Laguna Province natural enemies can suppress leaffolder populations below economic damage levels. Data on leaffolder population densities and mortality factors from the field studies were used as input to this model. Particular attention was paid to the contribution of egg predation by the crickets *M. vittaticollis* and *A. longipennis*.

Simulated yield losses due to the larval infestations observed in unsprayed rice fields were less than 5% in a well-fertilized crop. An unfertilized crop was more sensitive to leaffolder injury, mainly because its smaller leaf area. Yield losses started to exceed 10% in a well-fertilized crop when larval peak density was about 5 larvae per hill, and in an unfertilized crop at about 1-2 larvae per hill. However, very high levels of N-fertilization may result in a strong increase in leaffolder density and, consequently, in higher yield losses, despite the reduced sensitivity to injury.

The impact of natural enemies on the level of rice leaffolder infestation and damage was explored by introducing field-observed mortality due to egg predation and parasitism of eggs and larvae into the population model. The model was initialized with an average egg recruitment pattern, based on observations from eight unsprayed rice crops. In the absence of natural enemies, the simulated percentage yield loss in a well-fertilized crop ranged from 3 to 30%. When all three natural enemy-related mortality factors were included, larval density was strongly suppressed and the simulated yield loss was reduced to less than 5%. The contribution of egg predators to this reduction was relatively large. To study the impact of egg predation by the crickets *M. vittaticollis* and *A. longipennis*, the fixed egg predation rate was replaced by the simple egg predation sub-model, which calculated predation rates from the observed densities of these predatory crickets. Simulated peak larval densities were on average reduced by about 25%, and yield losses by more than 30% due to cricket predation.

The simulation study confirmed the importance of conservation of natural enemies and good crop management practices such as judicious use of N-fertilizers as the principle components of rice IPM. The combination of both principles will make chemical control of rice leaffolder in Laguna Province unnecessary most of the time.

Implications for rice IPM research and training

Three major research questions are prompted by the conclusions that natural enemies can prevent rice leaffolder damage under good growing conditions, and that predatory crickets are important species within this complex of natural enemies. The first is whether the major role of the predatory crickets in leaffolder egg predation can be extrapolated to a wider geographic area. This should be verified locally, first qualitatively through direct observation and then quantitatively by evaluation of the egg predation model. The second question concerns how the impact of natural enemies on leaffolder populations can be maximized by conservation of species of major importance. Options to conserve the predatory crickets demanding further study concern the use of selective pesticides and management of non-rice habitats. As the crickets are also important egg predators of many other rice insect pests, their conservation will be of broader significance than just the control of rice leaffolders. The third issue to be investigated is optimization of nitrogen management: how can we maximize the positive effects of N-fertilizer on yield formation and tolerance to injury, while minimizing its effects on leaffolder density such that chemical control will not be needed. Study of the underlying mechanisms, in particular concerning the effect of timing and spatial scale of N-application on leaffolder ovipositional preference, should receive priority over an empirical approach.

Institutional research on these topics should be conducted in interaction with rice IPM training and implementation in the 'Farmer Field School' system. In this context researchers should concentrate on the mechanisms underlying rice field ecology, such as the feeding relationships, the factors determining the abundance of natural enemy species, and the effects of N-fertilization on crop growth and arthropod abundance referred to above. These insights can then be acquired and applied locally by farmers through observation and experimentation, as part of their training in IPM.

Possible inputs of the present research project to help farmers improve their management of rice leaffolders concern three aspects of IPM: correct assessment of damage potential, appropriate crop management, and appreciation of the role of natural enemies. As farmers tend to overvalue leaffolder injury symptoms, the emphasis in farmer training must be placed on a change in perception of leaf injury. Defoliation experiments have proved to be very useful to convey the concept of crop tolerance to leaf injury. Such experiments may be linked with exercises in assessment of the proportion of leaf area actually folded and scraped by leaffolders, to get a feel for the level of injury that can be tolerated. By combining the defoliation experiments with different levels of fertilization, the farmers can learn how favourable growing conditions reduce the sensitivity of the crop to leaf injury. In field schools, farmers conduct small predation experiments to learn about the identity and impact of natural enemies. Due to their size and voracity, the predatory crickets are ideal insects for such experiments. The predatory crickets may further be used in pesticide toxicity trials to demonstrate their sensitivity to broad-spectrum insecticides.

Impact of changes in rice cultivation

The study presented in this thesis dealt with transplanted irrigated rice and current high yielding varieties. However, crop management practices change, and new rice varieties are developed and introduced. Currently, an important change is the shift from transplanting to direct seeding. While leaffolders tend to colonize direct seeded fields at an earlier stage than transplanted fields, their natural enemies, e.g. the predatory crickets, do so as well. There seems to be no a-priori reason why natural enemies will not be as effective in direct seeded as in transplanted rice fields. The reported problems of rice leaffolder in direct seeded rice appear primarily related to *other* management practices, that are directly detrimental to natural enemies, such as destruction of non-rice habitats and insecticide use. Whether the intensive use of herbicides that is commonly associated with direct seeding, also has a negative impact on the natural enemy complex, should be a high priority issue for further investigation.

To meet the ever-increasing demand for rice, researchers have suggested to increase the yield potential of rice by extending the green leaf area duration during the grain filling period. This may be achieved through a combination of additional, late applications of N-fertilizer and rice varieties with delayed leaf senescence. Enhancing leaf N-content and delaying leaf senescence during grain filling will prolong the suitability of the host plant to rice leaffolder, mainly expressed in oviposition preference and young larval survival. In transplanted rice fields this results in a potentially larger second generation of leaffolder larvae. Whether this will cause higher yield losses depends on the balance between the density response of the leaffolders, the response of natural enemies to the prolonged availability of their prey or host species, and the change in crop tolerance to injury with the extension of its green leaf area.

Concluding remarks

The main line of the research presented in this thesis was to identify major natural enemies of rice leaffolder, to quantify their ability to kill rice leaffolders, and to integrate these quantitative relationships into a combined leaffolder-rice model. This approach is most effective (1) when the pest stage or species is relatively immobile, allowing for direct observations, (2) when it has only few major natural enemy species, enabling detailed quantification of attack rates, and (3) with extensive prior knowledge of pest biology and its effect on crop growth and yield, facilitating the development of a combined pest-crop model. Under such conditions this explanatory approach has considerable advantages over a descriptive one. Insight into the identity of major natural enemy species and the factors determining their impact on the pest offers possibilities to predict the effect of changing agro-ecological conditions on pest survival, and to identify options that enhance natural enemy effectiveness. The combined leaffolder-rice simulation model provides a suitable framework to integrate the effects of natural enemies on leaffolder survival and the effects of leaffolder density on crop growth. With the model the consequences of changes in these relationships can be explored at the crop level. A better insight in how crop management practices can affect yield directly through crop growth processes, as well as indirectly through their effects on rice pests and natural enemies, will contribute to the development of rice production techniques that combine high productivity with sustainable management of rice pests, based on the action of naturally-occurring predators and parasitoids.

Samenvatting

Rijst, plagen en bladrollers

Rijst is, na tarwe, het belangrijkste voedselgewas ter wereld. Alleen al in Azië is rijst het hoofdvoedsel voor meer dan 2 miljard mensen. In dit continent wordt ongeveer 90% van 's werelds rijst verbouwd. Daarvan wordt ruim driekwart, zo'n 360 miljoen ton, geproduceerd met behulp van irrigatie.

Rijst biedt niet alleen voedsel aan de mens, het is ook een gastvrije waard voor meer dan 800 soorten plantenetende insekten. Van deze menigte aan planteneters worden echter in tropisch Azië minder dan 20 soorten als belangrijke plaaginsekten beschouwd. In de geïrrigeerde rijstbouw zijn deze te verdelen over een drietal hoofdgroepen: stengelborende rupsen, sapzuigende cicaden en een diverse groep van bladvreters. Binnen deze laatste groep zijn de rijstbladrollers het belangrijkst. De voornaamste bladrollersoorten zijn *Cnaphalocrocis medinalis*, *Marasmia patnalis* en *Marasmia exigua*. Het zijn motjes die alle tot de Pyralidae familie behoren. Zowel de motjes als de rupsen van deze soorten lijken uiterlijk sterk op elkaar en ze komen vaak tegelijkertijd voor in hetzelfde rijstveld.

Evenals veel andere plaaginsekten zijn de bladrollers in belang toegenomen sinds de rijstteelt in Azië in het midden van de jaren zestig sterk veranderde met de introduktie van nieuwe, hoogopbrengende rijstrassen. Deze zogenaamde 'Groene Revolutie' behelsde onder meer het verbouwen van meerdere rijstgewassen per jaar en een sterke toename in het gebruik van irrigatie, kunstmest en bestrijdingsmiddelen. Door de gelijktijdigheid van al deze veranderingen is er geen precieze oorzaak van de toename van de bladrollers aan te wijzen, waarschijnlijk is het een samenspel van faktoren.

De rupsen van de bladroller beschadigen de rijstplanten door de bladeren tot een buisje op te rollen en het groene bladweefsel tussen de nerven weg te vreten, wat resulteert in opvallende witte strepen. Door deze beschadigingen kan de plant minder licht opvangen en wordt bovendien het oppervlak aan aktief assimilerend bladweefsel gereduceerd, zodat een bladrolleraantasting tot een verminderde rijstopbrengst kan leiden.

Bestrijding van bladrollers

Rijstboeren in Azië zien bladetende insekten veelal als een ernstige bedreiging voor het gewas. De in het oog springende beschadiging door bladrollers is daarom vaak al bij een lage aantastingsgraad voldoende aanleiding om naar de gifspuit te grijpen. Een enquête onder Vietnamese en Filippijnse rijstboeren wees uit dat 30 tot 40% van al hun bespuitingen met insecticiden gericht waren op bestrijding van bladetende insekten. Deze bespuitingen werden hoofdzakelijk binnen één maand na overplanten uitgevoerd. Dit patroon van op grote schaal en vroeg in het gewasseizoen inzetten van breedwerkende insecticiden baart ernstig zorgen, want het verstoort de populaties van natuurlijke vijanden in de rijstvelden. Het succes van de geïntegreerde plaagbestrijding (IPM) in rijst berust namelijk voor een groot deel op een goede biologische bestrijding door het in stand houden van deze vijanden. Insecticiden gericht op bestrijding van bladrollers doden ook de natuurlijke vijanden, en kunnen daarom het optreden van bladrollers en andere plaaginsekten juist versterken.

De risico's die de huidige chemische bestrijding van rijstbladrollers met zich mee brengt nopen tot een kritisch onderzoek naar de noodzaak van dit ingrijpen met insecticiden. Het lijkt er sterk op dat veel rijstboeren het schadelijke effekt van een bladrolleraantasting overschatten, en te snel hun toevlucht tot chemische bestrijdingsmiddelen zoeken. Onder gunstige groeiomstandigheden kan een rijstgewas namelijk heel wat bladbeschadiging verdragen zonder dat dit de opbrengst vermindert. Bovendien wordt de bladroller belaagd door talloze natuurlijke vijanden, zoals predatoren en parasieten, die een al te grote aantasting kunnen helpen voorkomen.

Doel en aanpak van dit onderzoek

Om vast te kunnen stellen of natuurlijke vijanden de bladrollers op een (economisch) aanvaardbaar niveau kunnen houden, moeten we allereerst het verband kennen tussen het aantal bladrollers in een gewas en het opbrengstverlies, en vervolgens ook de invloed van natuurlijke vijanden op de bladrollerdichtheid. Beide relaties zijn al redelijk vaak onderzocht, maar hoofdzakelijk op een empirische, beschrijvende manier. De uitkomsten van deze studies zijn afhankelijk van de proefomstandigheden en lopen daarom nogal uiteen. Ze zijn dus ook niet algemeen toepasbaar. Een systeem-analytische benadering van het probleem kan hier uitkomst bieden. In de systeemanalyse wordt getracht waarnemingen op een bepaald niveau, bijvoorbeeld het veld of de populatie, te verklaren uit relaties die bepaald zijn op een lager, zogenaamd 'onderliggend' niveau, zoals bijvoorbeeld het effekt van omgevingsfaktoren op de groeiprocessen van de plant of op de lotgevallen van individuen.

In het hier beschreven onderzoek werd deze verklarende, systeem-analytische benadering toegepast met het doel inzicht te krijgen in het effekt van natuurlijke vijanden op bladrollerpopulaties, en vast te stellen in hoeverre natuurlijke vijanden bladrollerschade kunnen voorkomen. Door de mechanismen die hieraan ten grondslag liggen kwantitatief te beschrijven en te integreren in modellen, is het mogelijk te bepalen of onder gegeven omstandigheden natuurlijke vijanden de bladrollers afdoende bestrijden, en welke faktoren daarbij verhoudingsgewijs het belangrijkst zijn. Is eenmaal bekend welke faktoren het meeste bijdragen tot een effektieve biologische bladrollerbestrijding, dan kan ook beter bepaald worden welke maatregelen voor bestrijding van bladrollers kansrijk zijn. Dit zouden bijvoorbeeld maatregelen voor het in stand houden en bevorderen van specifieke natuurlijke vijanden kunnen zijn, of bepaalde teeltmaatregelen die het gewas minder gevoelig maken voor bladrolleraantasting.

Het onderzoek werd uitgevoerd in Laguna Province, in de Filippijnen. Dit is een tropisch laagland gebied waar rijst met behulp van irrigatie het hele jaar door verbouwd wordt, zowel in de natte als in de droge tijd. De veldproeven werden deels uitgevoerd in boerenvelden en deels op het International Rice Research Institute (IRRI, internationaal rijst onderzoeks-instituut). Daar werden ook de kas- en laboratoriumexperimenten gedaan.

Het onderzoek naar het effekt van natuurlijke vijanden op de bladrollerdichtheid en -schade is uitgevoerd in een aantal stappen. In eerste instantie werd de populatiedynamiek (=aantalsverloop) van de rijstbladrollers en hun natuurlijke vijanden bestudeerd, om inzicht te krijgen in de faktoren die de dichtheid van bladrollers bepalen **(Hoofdstuk 1 en 2)**. Voor dat doel werden onbespoten rijstvelden bemonsterd in diverse seizoenen en lokaties en onder verschillende niveaus van stikstofbemesting. Het aantal bladrollerrupsen per plant verschilde sterk per veld, maar bleek onder de gangbare bemestingsniveaus nooit hoger te zijn dan twee per plant. Twee faktoren spelen waarschijnlijk een belangrijke rol in deze verhoudingsgewijs lage bladrollerdichtheden. Ten eerste blijken de motjes bij voorkeur eitjes te leggen gedurende één bepaald groeistadium van het gewas, waardoor er in hoofdzaak slechts één generatie bladrollers per gewasseizoen voorkomt. Ten tweede waren in de rijstvelden tientallen soorten natuurlijke vijanden te vinden in vaak hoge dichtheden, die verantwoordelijk leken te zijn voor een hoge mortaliteit (=sterfte) van bladrollereitjes en -rupsen.

Bij een stikstofgift tweemaal zo hoog als gangbaar nam het aantal rupsen en de aantasting van het gewas sterk toe. Dit kwam omdat een zware bemesting de eileg van bladrollers in het gewas stimuleerde en de overlevingskans van de rupsen vergrootte. Deze overlevingskans hing samen met de verhouding tussen de aantallen predatoren en bladrollers. Doordat er zoveel meer eitjes werden gelegd in het zwaar bemeste gewas waren er relatief minder predatoren per prooi en werden er waarschijnlijk ook relatief minder prooien opgegeten.

Onderzoek aan bladrollerpopulaties door bemonstering gaf niet voldoende inzicht in het oorzakelijke verband tussen het vóórkomen van natuurlijke vijanden en bladrollermortaliteit. Om een beter inzicht te krijgen in deze relatie werd de mortaliteit in het eistadium nader onderzocht. Dit werd gedaan door het lot te bepalen van bladrollereitjes die in het veld waren uitgezet en van 'natuurlijk' gelegde eitjes (**Hoofdstuk 3**). Van de bladrollereitjes bleek gemiddeld 60% het nooit tot rups te brengen. De hoofdoorzaak was 'verdwijning' en in mindere mate parasitering door sluipwespjes (*Trichogramma*). Het niet uitkomen van ogenschijnlijk gezonde eitjes kwam weinig voor. De mate waarin eitjes verdwenen leek samen te hangen met het voorkomen van twee krekelsoorten (*Metioche vittaticollis* en *Anaxipha longipennis*).

Vervolgens werd, om de oorzaken van de 'eiverdwijning' duidelijk boven tafel te krijgen, in het veld dag en nacht de wacht gehouden bij de daar geplaatste eitjes. Deze zogenaamde 'direkte observatie' werd aangevuld met laboratoriumproefjes waarin het ei-predatievermogen van een aantal algemeen voorkomende soorten roofinsekten werd vergeleken (**Hoofdstuk 4**). De veldwaarnemingen bevestigden de belangrijke rol van de krekels in de eipredatie. Andere predatoren, zoals lieveheersbeestjes, loopkevers en sprinkhanen speelden slechts een bescheiden rol. Ook uit de laboratoriumproeven kwamen de krekels als meest vraatzuchtige van alle onderzochte soorten te voorschijn.

In een reeks van kooiexperimenten werd daarna het zoek- en vraatvermogen van de belangrijkste predatorsoorten nader bepaald en hun gedrag in detail bestudeerd **(Hoofdstuk 5 en 6)**. De resultaten van deze experimenten dienden als bouwstenen voor een (eenvoudig) model van de predatie van bladrollereitjes in het veld, wat vervolgens met onafhankelijke veldgegevens op z'n kwaliteiten beproefd werd **(Hoofdstuk 7)**.

De kooiproeven met de krekels lieten zien dat hun eiconsumptie recht evenredig toeneemt met het aantal eitjes per plant. Dit geeft aan dat bij de gangbare ei-dichtheden in het veld, de predatie door krekels afhangt van de snelheid waarmee ze de eitjes vinden en niet van hun vraatvermogen. Een volwassen krekel kan per dag ongeveer één rijstplant afzoeken op bladrollereitjes. Deze zoeksnelheid nam sterk af wanneer het aantal krekels per kooi een bepaalde grens overschreed.

Uit de bestudering van het zoekgedrag van de krekels bleek dat deze min of meer lukraak hun prooi zoeken en vinden. Dit maakt het mogelijk het predatieproces met een eenvoudig model te beschrijven. De evaluatie van het model van eipredatie in het veld wees uit dat de waargenomen trend in predatie redelijk goed verklaard kon worden met gegevens over de aantallen krekels en het totale bladoppervlak per veld. De toetsing gaf ook aan dat het onderling storen van krekels de predatie in belangrijke mate kan beperken. De aanwezigheid van andere prooien bleek geen effekt te hebben.

Als laatste stap werd een gecombineerd plaag-gewasmodel voor bladrollers in rijst ontwikkeld. Dit model werd gebruikt om het effekt van natuurlijke vijanden op bladroller-dichtheid en -schade te evalueren, onder de omstandigheden van Laguna Province **(Hoofdstuk 8)**. Daartoe werd allereerst bekeken wat het effekt op de opbrengst zou zijn van de in onbespoten velden waargenomen bladrollerdichtheden. De simulaties gaven aan dat in een goed bemest gewas deze plaagdichtheden geen schade van belang aanrichten. Een onbemest gewas bleek veel gevoeliger voor bladrolleraantasting, voornamelijk doordat zo'n gewas verhoudingsgewijs al weinig blad heeft.

Opbrengstverliezen gesimuleerd met een gemiddeld niveau van eileg per veld overschreden een economisch aanvaardbaar niveau wanneer in het model het effekt van natuurlijke vijanden op de bladrollerpopulatie genegeerd werd. Echter, de opbrengstverliezen werden gereduceerd tot onder dit niveau, wanneer de mortaliteit veroorzaakt door eipredatoren en parasieten van eitjes en rupsen in de berekeningen werd meegenomen. Daarbij ging het om gemiddelden van de waargenomen mortaliteit. De afzonderlijke bijdrage van de krekels aan het onderdrukken van de bladrollers werd geëvalueerd door het ei-predatiemodel in te voegen in het gecombineerde plaag-gewasmodel. Het opeten van bladrollereitjes door de krekels leidde, volgens het model, tot een afname van de bladrollerschade ten opzichte van velden zonder krekels. Deze vermindering variëerde van 5% in velden met lage aantallen krekels, tot zo'n 60% bij de hoogst waargenomen krekeldichtheid.

De simulatiestudie bevestigde dat het behouden en bevorderen van natuurlijke vijanden, bijvoorbeeld krekels, en een goede gewasverzorging, zoals door voldoende bemesting, de belangrijkste ingrediënten zijn van een geïntegreerde strategie voor plaagbestrijding in rijst. In Laguna Province zal de combinatie van beide de chemische bestrijding van bladrollers in de regel overbodig maken.

Conclusies en nieuwe vragen

Bestudering van populaties van rijstbladrollers liet zien dat ze in onbespoten rijstvelden in relatief lage aantallen voorkomen, onder andere als gevolg van een hoge sterfte door natuurlijke vijanden. Verdwijning van eitjes was een belangrijke mortaliteitsfaktor en bleek voor het overgrote deel toe te schrijven aan een tweetal krekelsoorten. Hun belang als eipredator kon verklaard worden uit hun eigenschappen. Simulaties met een plaag-gewasmodel gaven aan dat natuurlijke vijanden onder gunstige omstandigheden voor gewasgroei in staat waren economische schade door bladrollers te voorkomen. Zowel het behoud van natuurlijke vijanden, als een goede gewasverzorging zijn dus van groot belang voor een effektieve plaagbestrijding.

Deze conclusies roepen drie nieuwe hoofdvragen voor verder onderzoek op. De eerste is of deze krekels ook zo'n belangrijke rol spelen in andere delen van Azië. Dit zou ter plaatse getoetst moeten worden. Allereerst kwalitatief door direkte observatie van eipredatie in het veld, en vervolgens kwantitatief door toetsing van het predatiemodel dat het effekt van de in het veld aanwezige aantallen predatoren beschrijft.

De tweede vraag betreft hoe we door het in stand houden van belangrijke soorten het effekt van natuurlijke vijanden op bladrollerpopulaties zo groot mogelijk kunnen maken. Wat het behoud en bevorderen van de krekels betreft is verder onderzoek gewenst naar de toepassing van krekelvriendelijke bestrijdingsmiddelen en naar het beheer van de plantengroei rondom de rijstvelden. Die begroeiing kan namelijk een belangrijke broedplaats en toevluchtsoord voor de krekels zijn. Aangezien de krekels ook veel eitjes van andere plaaginsekten eten, zal hun behoud van grotere waarde zijn dan enkel de bestrijding van rijstbladrollers.

Het derde onderwerp voor verder onderzoek is de optimalisering van de stikstofbemesting binnen een teeltwijze die zoveel mogelijk gebruik maakt van natuurlijke biologische bestrijding. Hoe kunnen we de gunstige effekten van stikstofbemesting op de opbrengstvorming en de tolerantie voor bladbeschadiging zo groot mogelijk maken, terwijl het stimulerende effekt op de bladrollerpopulatie zo gering mogelijk wordt gehouden, zonder dat we daarbij een beroep hoeven doen op bestrijdingsmiddelen ? Het onderzoek hiernaar zou zich vooral moeten richten op de mechanismen die hieraan ten grondslag liggen, met name de relaties tussen het tijdstip en de ruimtelijke schaal van stikstofbemesting en de eileg in het gewas door bladrollers.

Training van boeren

Wanneer de bovenstaande onderwerpen door onderzoeksinstituten opgepakt zouden worden, kan dat het best gebeuren in samenspel met de training van boeren in de toepassing van geïntegreerde plaagbestrijding, zoals die nu in Azië plaats vindt in de zogenaamde 'veldscholen'. Binnen dit verband moeten onderzoekers zich richten op de ecologische basis van de rijstteelt, zoals de mechanismen en relaties die hierboven werden genoemd. Boeren kunnen zich de nieuwe ecologische inzichten eigen maken en zelf lokaal toepassen door het verrichten van waarnemingen en proeven in de veldscholen.

Hoe kan het hier beschreven onderzoek de boeren behulpzaam zijn bij het verbeteren van hun bestrijding van rijstbladrollers ? De bijdragen hebben betrekking op drie aspekten van geïntegreerde gewasbescherming: het juist inschatten van de kans op opbrengstverlies, het aanpassen van teeltmaatregelen en het onderkennen van de rol van natuurlijke vijanden.

Omdat boeren de neiging hebben de kwalijke gevolgen van bladbeschadiging te overdrijven, moet in de trainingen de nadruk liggen op een vergroting van hun inzicht in het effekt van bladrolleraantasting op de opbrengst. De ervaring leert dat ontbladeringsproeven, door de boeren zelf uitgevoerd, heel bruikbaar zijn om het begrip over te dragen dat bladbeschadiging pas op een bepaald niveau tot opbrengstverlies leidt. Zulke proeven kunnen gekoppeld worden aan oefeningen in het goed schatten van het percentage beschadigd bladoppervlak bij verschillende niveaus van bladrolleraantasting. Op deze wijze kunnen boeren gevoel ontwikkelen voor welke graad van aantasting nog te tolereren is.

De ontbladeringsproeven kunnen ook uitgevoerd worden in combinatie met verschillende bemestingsniveaus, waardoor de boeren leren hoe gunstige groeiomstandigheden niet enkel de opbrengst verhogen, maar ook de gevoeligheid van het gewas voor bladbeschadiging verminderen. Dit kan er toe leiden dat boeren hun geld liever uitgeven aan kunstmest dan aan bestrijdingsmiddelen, wat hun hoogstwaarschijnlijk een beter rendement zal opleveren. In gebieden waar zwaar bemeste velden vaak lijden onder een hoge bladrolleraantasting, zouden de boeren in veldscholen kunnen experimenteren met verschillende tijdstippen van bemesting.

In de veldscholen doen boeren kleine predatieproefjes met insekten die ze in het rijstveld vinden. Daardoor leren ze de nuttige insekten kennen en ook hoeveel plaaginsekten deze kunnen eten. De krekels zijn ideale beestjes voor zulke experimenten omdat ze redelijk groot en goed hanteerbaar zijn, en doordat ze forse hoeveelheden eitjes van diverse plaagsoorten verslinden. Verder is het belangrijk dat boeren de nuttige 'roof'krekels leren herkennen en niet over één kam scheren met andere, plantenetende krekels, die ook in rijstvelden voorkomen. Tenslotte zouden de krekels ook nog gebruikt kunnen worden in giftigheidsproefjes met insecticiden, om hun gevoeligheid voor veel van de gangbare middelen te demonstreren.

Wanneer boeren ervaringskennis bezitten van het vermogen van het rijstgewas om bladbeschadiging te tolereren en van teeltmaatregelen die deze tolerantie kunnen vergroten, en zich terdege bewust zijn van de aanwezigheid en nuttige effekten van natuurlijke vijanden en hun gevoeligheid voor breedwerkende bestrijdingsmiddelen, zal hun dat in staat stellen beter geïnformeerde beslissingen te nemen met betrekking tot de noodzaak van chemische bestrijding van bladrollers. Dit zal vrijwel zeker leiden tot minder insecticidebespuitingen tegen bladrollers, wat op z'n beurt weer grotere en effektievere populaties van natuurlijke vijanden tot gevolg heeft.

Vooruitblik

De conclusies van dit onderzoek hadden betrekking op overgeplante, geïrrigeerde rijst, met gangbare hoogopbrengende rijstrassen. De wijze waarop rijst verbouwd wordt is echter aan veranderingen onderhevig en bovendien worden er steeds nieuwe rassen gekweekt en op de markt gebracht. Bijvoorbeeld, als gevolg van de toenemende schaarste en kostprijs van arbeid vindt er momenteel in Zuid- en Zuidoost Azië op grote schaal een overgang plaats van het arbeidsintensieve overplanten naar het direkt zaaien van geïrrigeerde rijst. Naar verluidt zou deze overgang geleid hebben tot grotere problemen met rijstbladrollers. In direkt gezaaide rijst beginnen bladrollers eerder met eitjes leggen dan in overgeplante rijst, en dat zou kunnen leiden tot meerdere bladrollergeneraties per gewas en een voorsprong op hun natuurlijke vijanden. Echter, ook veel van deze nuttige insekten arriveren sneller in direkt gezaaide rijstvelden, en er is dan ook geen reden om bij voorbaat aan te nemen dat natuurlijke vijanden daar minder effektief zouden zijn dan in overgeplante rijst. Het lijkt er sterk op dat de gerapporteerde bladrollerproblemen in direkt gezaaide rijst meer verband houden met andere teeltmaatregelen, die schadelijk zijn voor de natuurlijke vijanden van de bladrollers. Voorbeelden van zulke praktijken zijn het op grote schaal doodspuiten van alle vegetatie rondom de rijstvelden en het veelvuldig gebruik van insecticiden. Mogelijk heeft ook het intensieve gebruik van onkruidbestrijdingsmiddelen in direkt gezaaide rijst schadelijke neveneffekten op de natuurlijke vijanden. Onderzoek naar deze laatste mogelijkheid is dringend gewenst, want chemische onkruidbestrijding neemt hand over hand toe in Zuidoost-Azië.

Om in de voortdurend toenemende behoefte aan rijst te kunnen voorzien hebben onderzoekers onlangs voorgesteld het opbrengstvermogen van rijst te vergroten door het gewas langer groen te laten blijven. Wanneer het gewas tijdens de korrelvullingsfase nog veel aktief, groen blad heeft, worden er meer en zwaardere korrels gevormd. Dit zou bereikt kunnen worden door een combinatie van extra, late stikstofgiften en rijstvariëteiten met een van nature tragere bladafsterving. Een langer groen gewas blijft echter ook langer aantrekkelijk voor bladrollers en meer stikstof in het blad kan bovendien de overlevingskansen van bladrollerrupsen vergroten. In overgeplante rijst zou de tweede bladrollergeneratie dus aanzienlijk groter kunnen worden. Of 'langer groen' ook daadwerkelijk tot een toename van de schade zal leiden, hangt af van de balans tussen de effekten op de bladrollerpopulatie, op de natuurlijke vijanden en op de gevoeligheid van het gewas voor bladbeschadiging.

Ter afsluiting

De hoofdlijn van het hier beschreven onderzoek liep van de identificatie van belangrijke natuurlijke vijanden van de rijstbladroller, via het kwantitatief bepalen van hun vermogen om bladrollers te doden, naar het integreren van deze kwantitatieve relaties in een gecombineerd plaag-gewasmodel, waarmee het effekt van natuurlijke vijanden op opbrengstverlies door bladrollers verklaard en geëvalueerd kon worden. Deze benadering is het meest geschikt en effektief wanneer aan de volgende voorwaarden kan worden voldaan:

- het plaaginsekt (of één van de stadia) moet niet al te beweeglijk zijn, zodat direkte observatie in het veld mogelijk is om te kunnen bepalen welke de belangrijkste vijanden zijn;
- het aantal echt belangrijke soorten natuurlijke vijanden moet beperkt zijn, zodat een gedetailleerde bestudering van hun dodelijke vermogens mogelijk is;
- er moet al veel bekend zijn over de biologie van het plaaginsekt en z'n effekt op het gewas, wat de ontwikkeling van een gecombineerd plaag-gewasmodel vergemakkelijkt.

Onder dergelijke omstandigheden zal de gevolgde verklarende benadering aanzienlijke voordelen bieden boven een puur beschrijvende. Inzicht in de identiteit van de belangrijkste natuurlijke vijanden en de faktoren die hun effect op de plaag bepalen biedt de mogelijkheid tot voorspelling van het effekt van veranderende omstandigheden op de overleving van de plaag en tot het nader bepalen van maatregelen die de effektiviteit van natuurlijke vijanden kunnen vergroten. Het gecombineerde bladroller-rijst simulatiemodel levert een bruikbaar raamwerk op waarmee zowel de effekten van natuurlijke vijanden op de overleving van bladrollers, als die van bladrollers op de gewasgroei geïntegreerd kunnen worden. Met het model kunnen de gevolgen van veranderingen in deze relaties op gewasniveau verkend worden, zoals in de modelstudie voor Laguna Province. Een beter inzicht in hoe teeltmaatregelen de opbrengst beïnvloeden, enerzijds direkt door gewasgroeiprocessen en anderzijds indirekt via hun effekt op rijstplagen en hun natuurlijke vijanden, draagt bij aan de ontwikkeling van een rijstteeltwijze die een hoge produktiviteit combineert met een duurzame beheersing van rijstplagen, gebaseerd op natuurlijke biologische bestrijding.

References

Abenes, M.L.P.; Khan, Z.R. 1990. Biology of rice leaffolders (LF) on susceptible IR36 and resistant TKM6. International Rice Research Newsletter 15(3):14.

Aguda, R.M.; Rombach, M.C. 1987. Bioassay of *Beauveria bassiana* and *Nomuraea rileyi* (Deuteromycotina; Hyphomycetes) against the rice leaffolder (LF). International Rice Research Newsletter 12(3):36.

Ahmed, S.; Khan, M.R.; Ahmed, M.; Ghaffar, A. 1989. Natural enemies of paddy leaf-roller (*Cnaphalocrocis medinalis* Gn.). Journal of Agricultural Research 27: 71-76.

Alexander R.D. 1961. Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). Behaviour 17:130-223.

Altieri, M.A.; Letourneau, D.K. 1982. Vegetation management and biological control in agroecosystems. Crop Protection 1: 405-430.

Anonymous 1993. Research on rice leaffolder management in China. Proceedings of the International Workshop on Economic Threshold Level for Rice Leaffolder in China, March 4-6, 1992, Beijing, 111pp.

Arida, G.S.; Heong, K.L. 1992. Blower-Vac: a new suction apparatus for sampling rice arthropods. International Rice Research Newsletter 17(6):30-31.

Arida, G.S.; Shepard, M. 1986. Seasonal abundance of the rice leaffolder complex in Laguna Province, Philippines. Journal of Agricultural Entomology 3:382-383.

Arida, G.S.; Shepard, B.M. 1990. Parasitism and predation of rice leaffolders, *Marasmia patnalis* (Bradley) and *Cnaphalocrocis medinalis* (Guenée) (Lepidoptera: Pyralidae) in Laguna province, Philippines. Journal of Agricultural Entomology 7: 113-118.

Arida, G.S.; Shepard, M.B.; Almazan, L.P. 1990. Effect of crop age and leaf location on food consumption and development of rice leaffolder (LF) *Marasmia patnalis*. International Rice Research Newsletter 15(2):29.

Balasubramanian, P.; Palaniappan, S.P.; Gopalar, M. 1983. Effect of carbofuran and nitrogen on leaffolder incidence. International Rice Research Newsletter 8(5)13-14.

Bandong, J.P.; Litsinger, J.A. 1986. Egg predators of rice leaffolder (LF) and their susceptibility to insecticides. International Rice Research Newsletter 11(3):21.

Bandong, J.P.; Litsinger, J.A. 1988. Development of action control thresholds for major rice pests. In: P.S. Teng; K.L. Heong (Eds.), Pesticide Management and Integrated Pest Management in Southeast Asia. pp.95-102. Consortium for International Crop Protection, Maryland, U.S.A.

Barrion, A.T.; Litsinger, J.A. 1980. Ants - a natural enemy of *Cnaphalocrosis medinalis* larvae in dryland rice. International Rice Research Newsletter 5(4): 22-23.

Barrion, A.T.; Litsinger, J.A. 1985a. *Chlaenius* spp. (Coleoptera: Carabidae), a leaffolder (LF) predator. International Rice Research Newsletter 10 (1):21.

Barrion, A.T.; Litsinger, J.A. 1985b. Identification of rice leaffolder (LF) by wing markings. International Rice Research Newsletter 10(1):24.

Barrion, A.T.; Litsinger, J.A. 1987. Meadow grasshopper *Conocephalus longipennis* damage to rice spikelets. International Rice Research Newsletter 12:8.

Barrion, A.T.; Litsinger, J.A.; Medina, E.B.; Aguda, R.M.; Bandong, J.P.; Pantua, P.C. Jr.; Viajante, V.D.; dela Cruz, C.G.; Vega, C.R. 1991a. The rice *Cnaphalocrocis* and *Marasmia* (Lepidoptera: Pyralidae) leaffolder complex in the Philippines: taxonomy, bionomics and control. Philippine Entomologist 8:987-1074.

Barrion, A.T.; Litsinger, J.A.; Last, H. 1991b. A new species of *Hesperus* (Coleoptera: Staphylinidae) and other rove beetles associated with rice agroecosystems. Philippine Entomologist 8(4):1075-1080.

Bautista, R.C.; Heinrichs, E.A.; Rejesus, R.S. 1984. Economic injury levels for the rice leaffolder *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae): insect infestation and artificial leaf removal. Environmental Entomology 13:439-443.

Beddington, J.R. 1975. Mutual interference between parasites or predators and its effect on searching efficiency. Journal of Animal Ecology 44:331-340.

Bell, W.J. 1991. Searching behaviour. The behavioural ecology of finding resources. Chapman and Hall Animal Behaviour Series.

Bellows, T.S. Jr.; Van Driesche, R.G.; Elkinton, J.S. 1992. Life-table construction and analysis in the evaluation of natural enemies. Annual Review of Entomology 37:587-614.

Bentley, J.W.; Andrews, K.L 1991. Pests, peasants, and publications: anthropological and entomological views of an integrated pest management program for small-scale honduran farmers. Human Organizations 50: 113-124.

Bentur, J.S.; Kalode, M.B.; Rajendran, B.; Patel, V.S. 1994. Field evaluation of the egg parasitoid, *Trichogramma japonicum* Ash. (Hym., Trichogrammatidae) against the rice leaf folder, *Cnaphalocrocis medinalis* (Guen.) (Lep., Pyralidae) in India. Journal of Applied Entomology 117:257-261.

Bharati, L.R.; Kushwaha, K.S. 1988. Parasitoids of leaffolder (LF) pupae from Haryana, India. International Rice Research Newsletter 13(5):31.

Bharati, L.R.; Om, Hari; Kushwaha, K.S. 1990. Alternate plant hosts of rice leaffolder (LF). International Rice Research Newsletter 15(5):21-22.

Bhardwaj, D.; Pawar, A.D. 1987. Predators of rice insect pests. International Rice Research Newsletter 12(4):35.

Bhatnagar, Y.V. 1989. Occurrence of insect pests on rice crop and studies on the natural enemies of the rice leaffolder *Cnaphalocrocis medinalis* Guenée. M.Sc. thesis, G.B. Pant University of Agriculture & Technology, Pantnagar, India.

Bradley, J.D. 1981. *Marasmia patnalis* sp. n. (Lepidoptera: Pyralidae) on rice in S.E. Asia. Bulletin of Entomological Research 71:323-327.

Budhasamai, T.; Silapasorn, P.; Chantaraprapha, N. 1992. Effect of foliar insecticide sprays on rice leaffolder *Cnaphalocrocis medinalis* Guenée and rice yield. International Rice Research Newsletter 17:26.

Canapi, B.L. 1992. Effects of single and multiple pests and stresses on yield loss of rice. M.Sc. thesis, University of the Philippines at Los Baños, Philippines.

Canapi, B.L.; Rubia, E.G.; Litsinger, J.A.; Shepard, B.M.; and Rueda, L.M. 1988. Predation by sword-tailed cricket *Anaxipha longipennis* (Serville) (Gryllidae) on eggs of three lepidopterous pests of rice. International Rice Research Newsletter 13(4):40.

Carter, N.; Dixon, A.F.G.; Rabbinge, R. 1982. Cereal aphid populations: biology, simulation and prediction. Simulation Monographs, Pudoc, Wageningen.

Chandragiri, K.K.; Velusamy, R.; Janaki, I.P.; Ramakrishnan, M.S. 1974. Effect of different levels of nitrogen on rice leaf roller (*Cnaphalocrocis medinalis* Guenée) incidence. Madras Agricultural Journal 61:717.

Chandramohan, N.; Jayaraj, S. 1977. Effect of different levels of nitrogen and granular insecticides in the control of the rice leaf roller, *Cnaphalocrocis medinalis* (Guenée). Madras Agricultural Journal 64:544-548.

Chang, P.M. 1991. An integrated crop management approach for major rice pests in broadcast direct-seeded rice in Peninsular Malaysia. Paper presented at the Pest Surveillance and Forecasting Workshop, Department of Agriculture, 23-25 April 1991.

Chang, P.M. 1993. Rice leaffolder and brown planthopper occurrence in FELCRA Seberang Perak, Malaysia. In: Research on rice leaffolder management in China. Proceedings of the International Workshop on Economic Threshold Level for Rice Leaffolder in China, March 1-2, 1992, Beijing, pp.14-15.

Chang, S.S.; Lo, Z.C.; Keng, C.G.; Li, G.Z.; Chen, X.L.; Wu, X.W. 1980. Studies on the migration of rice leaf roller *Cnaphalocrocis medinalis* Guenée. Acta Entomologica Sinica 23:130-140. (In Chinese, English summary).

Chantaraprapha, N.; Katanyukul, W.; Semapetch, U. 1980. Influence of ammonium phosphate levels on rice leaf roller incidence. International Rice Research Newsletter 5(5):21.

Chatterjee, P.B. 1987. Rice leaffolder (LF) infestations in West Bengal. International Rice Research Newsletter 12(4):44-45.

Chen, C.C.; Chiu, S.C. 1983. A survey on natural enemies of the rice leaf roller in Taiwan. Journal of Agricultural Research China 32(3):286-291.

Chen, C.; Chiu, S. 1986. Studies on the field releases of *Trichogramma chilonis* and the factors affecting its activity [in Chinese, English summary]. Journal of Agricultural Research China 35(1):99-106.

Chen, C.M.; Zhang, J.P.; Dan, J.G. 1993. The effects of rice leaffolder (RLF) on rice yield - economic threshold in Hunan, China. In: Research on rice leaffolder management in China. Proceedings of the International workshop on Economic Threshold Level for Rice Leaffolder, March 4-6, 1992, Beijing. pp.83-87.

Cheng, C.H. 1987. Investigation on bionomics of the rice leaffolder, *Cnaphalocrocis medinalis* (Guenée) in the South of Taiwan. Plant Prot. Bull. (Taiwan) 29:135-146. (In Chinese, English abstract)

Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64: 1297-1304.

Chiranjeevi, Ch.; Rao, G.M. 1991. Population fluctuation of leaffolder (LF) at different planting times in some rice varieties. International Rice Research Newsletter 16(6):22.

Chiu, S.F. 1984. Recent advances in the integrated control of rice insects in China. Bulletin of the Entomological Society of America 30(3):41-46.

Chopard, L. 1969. The fauna of India and adjacent countries. Orthoptera, Vol. 2. Grylloidea. Baptist Mission Press, Calcutta.

Chu, Y.I. 1979. Some notes on the lepidopterous rice insect pests at Jawa Timur, Indonesia. Phytopathologist & Entomologist, NTU (1979):38-43.

Chu, Y.I.; Ho, K.Y.; Lee, Y.S. 1983. The effect of various host plants on growth and development of the rice leaf roller, (*Cnaphalocrocis medinalis* (Guenée)). Chinese Journal of Entomology 3:75-92. (In Chinese, English summary)

Cohen, J.E.; Schoenly, K.; Heong, K.L.; Justo, H.; Arida, G.S.; Barrion, A.T.; Litsinger, J.A. 1994. A food web approach to evaluating the effect of insecticide spraying on insect pest population dynamics in a Philippine irrigated rice ecosystem. Journal of Applied Ecology 31:747-763.

Craswell, E.T.; Vlek, P.L.G. 1979. Fate of fertilizer nitrogen applied to wetland rice. In: Nitrogen and rice. In: Nitrogen and rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Crawley, M.J. 1992. Overview. In: M.J. Crawley (Ed.) Natural enemies: the population biology of predators, parasites, and diseases. Blackwell Scientific Publications, Oxford, UK. pp.476-489.

Crawley, M.C. 1993. GLIM for ecologists. Blackwell Scientific Publications, Oxford.

Dale, D. 1994. Insect pests of the rice plant - Their biology and ecology. In: E.A. Heinrichs (Ed.) Biology and management of rice insects. Wiley Eastern Ltd., pp.363-485.

Dan, J.G.; Chen, C.M. 1990. The effects of feeding condition on the growth, development, and reproduction of rice leafroller. [In Chinese, English summary] Acta Phytophylacica Sinica 17:193-199.

de Jong, P.D. 1992. Effect of folding and feeding by *Cnaphalocrocis medinalis* on photosynthesis and transpiration of rice leaves. Entomologia experimentalis et applicata 63:101-102.

de Jong, P.D.; Daamen, R.A. 1992. Simulation of yield loss by the rice leaffolder *Cnaphalocrocis medinalis* under different growing conditions. Journal of Plant Protection in the Tropics 9:117-123.

De Datta, S.K.; Nantasomsaran, P. 1991. Status and prospects of direct seeded flooded rice in tropical Asia. In: Direct seeded flooded rice in the tropics. International Rice Research Institute, P.O. Box 933, Manila, Philippines, pp.1-16.

Dent, J.B.; Blackie, M.J. 1979. Systems simulation in agriculture. Applied Science Publishers, London.

Dhaliwal, G.S.; Shahi, H.N.; Gill, P.S.; Maskina, M.S. 1979. Field reaction of rice varieties to leaf folder at various nitrogen levels. International Rice Research Newsletter 4(3):7.

Dhaliwal, G.S. Raina, G.L.; Sidhu, G.S. 1985. Second generation rice insect and disease problems in Punjab, India. International Rice Communication Newsletter 34(1):54-65.

Dhaliwal, G.S.; Singh, J.; Malhi, S.S.; Sukhija, H.S. 1988. Effect of date of transplanting of rice on the incidence of leaf folder. Journal of Insect Science 1(2):191-192.

Dingkuhn, M.; Penning de Vries, F.W.T.; Miezan, K.M. 1993. Improvement of rice plant type concepts: systems research enables interaction of physiology and breeding. In: F.W.T. Penning de Vries; P.S. Teng; K. Metselaar (Eds.) Systems approaches for agricultural development. Kluwer Academic Publishers, pp.19-35.

Draper, N.R.; Smith, H. 1981. Applied regression analysis. Second edition. John Wiley & Sons.

Escalada, M.M.; Heong, K.L. 1993. Communication and implementation of change in crop protection. In: Crop Protection and Sustainable Agriculture, Ciba Foundation Symposium 177, (Cichester: J. Wiley & Sons), pp.191-207.

Escalada, M.M.; Lazaro, A.A.; Heong, K.L. 1992. Early spraying by rice farmers in Leyte, Philippines. International Rice Research Newsletter 17(6):27-28.

Evans, A.R. 1988. Mating systems and reproductive strategies in three Australian gryllid crickets - *Bobilla victoriae* Otte, *Balamaria gidya* Otte and *Teleogryllus commodus* (Walker) (Orthoptera, Gryllidae, Nemobiinae, Trigonidiinae, Gryllinae). Ethology 78:21-52.

Fabellar, L.T.; Heong, K.L. 1991. Leaf consumption of rice leaffolder *Cnaphalocrocis medinalis* larvae on different crop ages and N-levels. Poster presented at the 22nd Anniversary and Annual Convention of the PMCP, Manila, May 9-10, 1991.

Fabellar, L.T; Fabellar, N.G.; Heong, K.L. 1992. Effect of rice leaffolder feeding on plant biomass and yield. In: Proceedings Mid-term Research Review, Entomology Division, International Rice Research Institute, P.O. Box 933, Manila, the Philippines, pp.250-257.

Fraenkel, G.; Fallil, F. 1981. The spinning (stitching) behaviour of the rice leaf folder, *Cnaphalocrocis medinalis*. Entomologia experimentalis et applicata 29:138-146.

Fraenkel, G.; Fallil, F.; Kumarasinghe, K.S. 1981. The feeding behaviour of the rice leaf folder, *Cnaphalocrocis medinalis*. Entomologia experimentalis et applicata 29: 147-161.

Fransz, H.G. 1974. The functional response to prey density in an acarine system. Simulation Monographs, Pudoc, Wageningen.

Free, C.A.; Beddington, J.R.; Lawton, J.H. 1977. On the inadequacy of simple models of mutual interference for parasitism and predation. Journal of Animal Ecology 46:543-554.

Fuentes, C.; Shaw, K.C. 1986. Aggressive behavior in female field crickets, *Teleogryllus oceanicus* (Orthoptera: Gryllidae). Journal of the Kansas Entomological Society 59:687-698.

Fukamachi, S. 1980. Habitat and oviposition behavior of the rice leafroller moth, *Cnaphalocrocis medinalis*, Guenée. Proceedings of the Association for Plant Protection, Kyushu 26:93-96. (In Japanese)

Fukamachi, S. 1983. Nocturnal activity of the rice leafroller moth, *Cnaphalocrocis medinalis*, Guenée. Proceedings of the Association for Plant Protection, Kyushu 29:71-74. (In Japanese)

Gallagher, K.D. 1992. IPM development in the Indonesian National IPM Program. In: A.A.S.A. Kadiz; H.S. Barlow (Eds.), Pest management and the environment in 2000, pp.82-92.

Goudriaan, J; Roermund, H.J.W. van 1989. Modelling of ageing, development, delays and dispersion. In: Rabbinge, R.; Ward, S.A.; Laar, H.H. van (Eds.) Simulation and systems management in crop protection. Simulation Monographs, Pudoc, Wageningen, the Netherlands, pp.47-79.

Graf, B.; Lamb, R.; Heong, K.L.; Fabellar, L. 1992. A simulation model for the population dynamics of rice leaf-folders (Lepidoptera: Pyralidae) and their interactions with rice. Journal of Applied Ecology 29:558-570.

Gross, H.R.; Lewis, W.J.; Beevers, M.; Nordlund, D.A. 1984. *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae): effects of augmented densities and distributions of *Heliothis zea* (Lepidoptera:Noctuidae) host eggs and kairomones on field performance. Environmental Entomology 13:981-985.

Gu, D.X.; Zhou, C.Q.; Tang, J.Q.; Zhou. H.H. 1983. On the life tables of natural populations of rice leaf roller, *Cnaphalocrocis medinalis* Guenee. Acta Ecologica Sinica 3(3):229-238.

Guo, Y.J.; Zhao, J.H. 1993. Natural enemies of rice leaffolder and its effect on the economic threshold level in China [in Chinese, English summary]. In: Research on rice leaffolder management in China. Proceedings of the International Workshop on Economic Threshold Level for Rice Leaffolder in China, March 1-2, 1992, Beijing, pp.101-108.

Guo, Y.J. 1990. Larval parasitization of rice leaffolder (Lepidoptera: Pyralidae) under field and laboratory conditions. Ph.D. dissertation, University of the Philippines at Los Baños, Philippines.

Gutierrez, A.P.; Baumgaertner, J.U.; Summers, C.G. 1984. Multitrophic models for predator-prey energetics. Canadian Entomologist 116:923-963.

Gutierrez, A.P.; Neuenschwander, P.; Schulthess, F.; Herren, H.R.; Baumgaertner, J.U.; Wermelinger, B.; Loehr, B.; Ellis, C.K. 1988. Analysis of biological control of cassava pests in Africa. II. Casava mealybug *Phenacoccus manihoti*. Journal of Applied Ecology 25:921-940.

Hassan, S.A. 1984. Testing the side effects of pesticides on beneficial arthropods. In: Judicious and Efficient Use of Insecticides on Rice, International Rice Research Institute, P.O. Box 933, Manila, Philippines. p.117-126.

Hassell, M.P. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, USA.

Heinrichs, E.A.; Mochida, O. 1984. From secondary to major pest status: the case of insecticide-induced rice brown planthopper, *Nilaparvata lugens*, resurgence. Protection Ecology 7:201-218.

Heinrichs, E.A.; Camanac, E.; Romena, A. 1985. Evaluation of rice cultivars for resistance to *Cnaphalocrosis medinalis* Guenée (Lepidoptera: Pyralidae). Journal of Economic Entomology 78:274-278.

Heinrichs, E.A.; Rapusas, H.R.; Viajante, V.; Medrano, F.G.; Vega, C.R.; Medina, E.B. 1986. Development of insects (Homoptera, Lepidoptera) on traditional and modern rice cultivars. Environmental Entomology 15:147-421.

Heong, K.L. 1990. Feeding rates of the rice leaffolder, *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae), on different plant stages. Journal of Agricultural Entomology 7:81-90.

Heong, K.L. 1991. Management of the brown planthopper in the tropics. Proceedings of International Seminar on Migration and Dispersal of Agricultural Insects, Tsukubo, Japan, September 1991. pp.269-279.

Heong, K.L. 1993. Rice leaffolders: are they serious pests ? In: Research on rice leaffolder management in China. Proceedings of the International Workshop on Economic Threshold Level for Rice Leaffolder in China, March 1-2, 1992, Beijing, pp.8-11.

Heong, K.L.; Aquino, G.B.; Barrion, A.T. 1991. Arthropod community structures of rice ecosystems in the Philippines. Bulletin of Entomological Research 81:407-416.

Heong, K.L.; Aquino, G.B.; Barrion, A.T. 1992. Population dynamics of plant- and leafhoppers and their natural enemies in rice ecosystems in the Philippines. Crop Protection 11:371-379.

Heong, K.L.; Escalada, M.M.; Vo Mai 1994. An analysis of insecticide use in rice: case studies in the Philippines and Vietnam. International Journal of Pest Management 40:173-178.

Heuel-Rolf, B.; Vungsilabutr, P. 1988. Development of simple sampling methods for pest surveillance in rice. In: P.S. Teng; K.L. Heong (eds.) Pesticide Management and Integrated Pest Management in Southeast Asia. pp.113-122. Consortium for International Crop Protection, Maryland, U.S.A.

Hirai, K. 1988. The parasitism of *Trichogramma chilonis* T. on eggs of the soybean pod borer *Leguminovora glycinivorella* M. in soybean fields of Northern Japan. In: *Trichogramma* and other egg parasites (Ghangzhou 1-15 Nov. 1986). Colloques de l'INRA 43:489-497.

Hirao, J.; Ho, N.K. 1987. Status of rice pests and measures of control in the double cropping area of the Muda irrigation scheme, Malaysia. In: Int. Symp. on Technology for Double Cropping of Rice in the Tropics. pp.107-115. Oct. 3-30, 1987, Tsukuba, Japan. Tropical Agricultural Research Series No. 20.

Hirao, J. 1982. Ecology and chemical control of the rice leafroller. Japan Pesticide Information No. 41:14-17.

Hirose, Y. 1986. Biological and ecological comparision of *Trichogramma* and *Telenomus* as control agents of lepidopterous pests. Journal of Applied Entomology 101:39-47.

Holling, C.S. 1966. The functional response of invertebrate predators to prey density. Memoirs of the Entomological Society of Canada 48, 86pp.

Holt, J.; Wareing, D.R.; Norton, G.A. 1992. Strategies of insecticide use to avoid resurgence of *Nilaparvata lugens* (Homoptera: Delphacidae) in tropical rice: a simulation analysis. Journal of Economic Entomology 85: 1979-1989.

Hu, G.W.; Chen, Z.X.; Liu, G.J.; Ma, J.F.; Pan, Q.W. 1993. Dynamic modelling of compensation of late season hybrid to rice leaffolder (*Cnaphalocrocis medinalis*) defoliation. Scientia Agricultura Sinica 26:24-29.

Hu, J.Z.; Lu, Q.H.; Yang, J.S.; Yang, L.P. 1986. Influence of N fertilizer level and irrigation on population dynamics of the major insect pests in paddy fields and consequent rice yield. Acta Entomologica Sinica 29:49-55. (In Chinese, English summary).

Inoue, H.; Fukamachi, S. 1990. Infestation and yield losses caused by *Cnaphalocrocis medinalis* Guenée under differential fertilization and control procedure. Proceedings of the Association for Plant Protection Kyushu 36: 103-107. (In Japanese).

IRRI 1981. Annual report for 1980. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

IRRI 1988. Annual report for 1987. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

IRRI 1990a. Resistance of IR varieties to insect pests. International Rice Research Institute, Los Baños, Philippines. 1p.

IRRI 1990b. Program Report for 1989. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

IRRI 1991a. Program Report for 1990. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

IRRI 1991b. Direct seeded flooded rice in the tropics. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

IRRI 1992. Compilation of weather data for 1991. Climate Unit, International Rice Research Institute, P.O. Box 933, Manila, Philippines.

IRRI 1993a. IRRI Rice Almanac 1993-1995. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

IRRI 1993b. Program Report for 1992. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

IRRI 1993c. Rice IPM Network - Phase I. Final Report 1990-1993. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Jin, D.R. 1984. Ability of compensation of rice to the larval injury by the rice leaffolder, *Cnaphalocrocis medinalis* (Guenée). Acta Phytophylacica Sinica 11:1-7. [In Chinese, English summary]

Johnson, N.L.; Kotz, S. 1977. Urn models and their application. Wiley, New York.

Joshi, R.C.; Medina, E.; Heinrichs, E.A. 1985. Life cycle of *Marasmia patnalis*, a rice leaffolder in the Philippines. International Rice Research Newsletter 10(4): 15-16.

Kalode, M.B. 1985. Pest monitoring in rice. In: S. Jayaraj (Ed.) Integrated pest and disease management. Proceedings of the national seminar. Tamil Nadu Agricultural University, Coimbatore, India. pp.1-7.

Kamal, N.Q. 1981. Suppression of whitebacked planthopper, *Sogatella furcifera* (Horvath), and rice leaffolder, *Cnaphalocrocis medinalis* (Guenée), populations by natural enemies. Ph.D. dissertation, Gregorio Araneta University Foundation, Manila, Philippines.

Kamal, N.Q.; Karim, A.N.M.R.; Alam, S. 1987. Some common predators of rice insect pests. International Rice Research Newsletter 12(3):34.

Keller, M.A.; Lewis, W.J.; Stinner, R.E. 1985. Biological and practical significance of movement by *Trichogramma* species: a review. Southwestern Entomologist, Supplement 8:138-155.

Kenmore, P.E. 1991. Indonesia's Integrated Pest Management - A model for Asia. FAO Rice IPC Programme, FAO P.O. Box 1864 Manila, Philippines.

Kenmore, P.E.; Carino, F.O.; Perez, C.A.; Dyck, V.A.; Gutierrez, A.P. 1984. Population regulation of the rice brown planthopper (*Nilaparvata lugens* Stal) within rice fields in the Philippines. Journal of Plant Protection in the Tropics 1:19-37.

Khan, Z.R.; Joshi, R.C. 1990. Varietal resistance to *Cnaphalocrocis medinalis* (Guenée) in rice. Crop Protection 9:243-251.

Khan, Z.R.; Barrion, A.T.; Litsinger, J.A.; Castilla, N.P.; Joshi, R.C. 1988. Mini Review: a bibliography of rice leaffolders (Lepidoptera: Pyralidae). Insect Science and its Applications 9(2):129-174.

Klein Beekman, M.; Lamour, A. 1993. Population dynamics of *Cnaphalocrocis medinalis* and its natural enemies in paddy fields and surrounding vegetation. Internal Report, Dept. of Entomology, Wageningen Agricultural University.

Knipling, E.F.; McGuire, J.U. 1968. Population models to appraise the limitations and potentialities of *Trichogramma* in managing host insect populations. USDA Technical Bulletin 1387.

Kobayashi, M.; Wada, T. 1979. Hymenopterous parasites of the rice leaf roller, *Cnaphalocrocis medinalis* Guenee and their activities observed in the paddy fields of Chikugo. Proceedings of the Association for Plant Protection, Kyushu 25:64-66 (In Japanese, English abstract).

Krishnaiah, K.; Reddy, P.C.; Rao, C.S. 1986. Integrated pest control in rice in Krishna delta area of Andhra Pradesh. Indian Journal of Plant Protection 14:1-12.

Krishnasamy, N.; Chauhan, O.P.; Das, R.K. 1984. Some common predators of rice insect pests. International Rice Research Newsletter 9(2):15-16.

Kropff, M.J.; Cassman, K.G.; van Laar, H.H. 1994a. Quantitative understanding of the irrigated rice ecosystem and yield potential. In: Virmani, S.S. (ed.) Hybrid rice technology: new developments and future prospects. Selected papers from the International Rice Research Conference. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Kropff, M.J.; van Laar, H.H.; Matthews, R.B. (Eds.) 1994b. ORYZA1 - An ecophysiological model for irrigated rice production. SARP Research Proceedings - September 1994. AB-DLO/WAU-TPE/IRRI, 110pp.

Kuchiki, F.; Mikuriya, H.; Yamaguchi, J. 1988. Yield decrease of rice plants by injurious insects in Saga prefecture. I. Yield losses caused by the rice leaffolder, *Cnaphalocrocis medinalis* Guenée in early rice varieties. Proceedings of the Association for Plant Protection, Kyushu 34:100-102. (In: Japanese)

Kulshreshtha, J.P.; Kalode, M.B.; Prakasa Rao, P.S.; Misra, B.C.; Varma, A. 1970. High yielding varieties and the resulting changes in the pattern of rice pests in India. Oryza 7:61-64.

Kyi, A.; Zalucki, M.P.; Titmarsh, I.J. 1991. An experimental study of early stage survival of *Helicoverpa armigera* (Lepidoptera: Noctuidae) on cotton. Bulletin of Entomological Research 81:262-271.

Li, L.Y. 1982. Integrated rice insect pest control in the Guangdong Province of China. Entomophaga 27(Special Issue):81-88.

Liang, G.W.; Pang, X.F. 1987. Studies on the life system of rice leafroller. In: The developments in integrated control of rice diseases and insect pests in China. pp.214-237.

Liang, G.W.; Luo, G.H.; Li, C.F. 1984. Effects of fertilizer application on the adult and egg density of the rice leafroller. [In Chinese, English abstract] Guangdong Agricultural Science 2(14):34-35.

Liang, G.W.; Tao, F.L.; Pang, X.F. 1993. The relationship between control index and population structure of the rice leaffolder, *Cnaphalocrocis medinalis* in Guangdong. In: Research on rice leaffolder management in China. Proceedings of the International Workshop on Economic Threshold Level for Rice Leaffolder in China, March 1-2, 1992, Beijing, pp.69-74.

Lingappa, S. 1972. Bionomics of the rice leaffolder, *Cnaphalocrocis medinalis* Guenée (Lepidoptera: Pyralidae). Mysore Journal of Agricultural Sciences 6:123-134.

Litsinger, J.A. 1979. Major insect pests of rainfed wetland rice in tropical Asia. International Rice Research Newsletter 4(2):14.

Litsinger, J.A. 1989. Second generation insect pest problems on high yielding rices. Tropical Pest Management 35:235-242.

Litsinger, J.A. 1994. Cultural, mechanical, and physical control of rice insects. In: E. A. Heinrichs (Ed.) Biology and management of rice insects. Wiley Eastern Ltd., New Delhi, pp.549-584.

Litsinger, J.A.; Barrion, A.T.; Soekarna, D. 1987a. Upland rice insect pests: their ecology, importance, and control. IRRI Research Paper Series 123.

Litsinger, J.A.; Canapi, B.L.; Bandong, J.P.; Dela Cruz, C.G.; Apostol, R.F.; Pantua, P.C.; Lumaban, M.D.; Alviola III, A.L.; Raymundo, F.; Libetario, E.M.; Loevinsohn, M.E.; Joshi, R.C. 1987b. Rice crop loss from insect pests in wetland and dryland environments of Asia with emphasis on the Philippines. Insect Science and its Applications 8:677-692.

Loevinsohn, M.E. 1984. The ecology and control of rice pests in relation to the intensity and synchrony of cultivation. Ph.D. dissertation, University of London, U.K.

Loevinsohn, M.E.; Litsinger, J.A.; Heinrichs, E.A. 1988. Rice insect pests and agricultural change. In: M.K. Harris, M.K.; C.E. Rogers (eds.) The Entomology of indigenous and naturalized systems in agriculture. pp.161-182. Westview Studies in Insect Biology, Westview Press, Boulder, Colorado, U.S.A. 238 pp.

Luck, R.F.; Shepard, B.M.; Kenmore, P.E. 1988. Experimental methods for evaluating arthropod natural enemies. Annual Review of Entomology 33:367-391.

Luo, L.Z. 1989. Interaction and fluctuation of arthropod species in a tropical rice ecosystem. Ph.D. dissertation, University of the Philippines at Los Baños, Philippines.

Ma, J.F.; Hu, G.W. 1993. Review on the yield loss caused by rice leaffolder (*Cnaphalocrocis medinalis*) and control threshold in China. In: Research on rice leaffolder management in China. Proceedings of the International Workshop on Economic Threshold Level for Rice Leaffolder in China, March 4-6, 1992, Beijing, pp.18-23.

Ma, J.F.; Hu, G.W.; Zhu, D.F.; Chen, Z.X. 1991. Simulation of damage caused by leaffolder on rice crops. In: F.W.T. Penning de Vries, H.H. van Laar and M.J. Kropff (Eds). Simulation and systems analysis for rice production. Pudoc, Wageningen. pp.328-331.

Manley, G.V. 1985. The predatory status of *Conocephalus longipennis* (Orthoptera: Tettigoniidae) in rice fields of West Malaysia. Entomological News 96:167-170.

Manly, B.F.J. 1974. A model for certain types of selection experiments. Biometrics 30:281-294.

Manly, B.F.J. 1989. A review of methods for the analysis of stage-frequency data. In: L. McDowell (Ed.), Estimation and analyses of insect populations. Springer, New York. pp.3-69.

Matteson, P.C.; Gallagher, K.D.; Kenmore, P.E. 1994. Extension of integrated pest management for planthoppers in Asian irrigated rice: empowering the user. In: R.F. Denno; T.J. Perfect (Eds.) Planthoppers, their ecology and management. Chapman & Hall, pp.656-685.

Mattson, W.J. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics 11:119-161.

Mayer, D.G.; Butler, D.G. 1993. Statistical validation. Ecological Modelling 68:21-32.

McNeill, S.; Southwood, T.R.E. 1978. The role of nitrogen in the development of insect/plant relationships. In: J. Harborne (Ed.), Biochemical aspects of plant and animal coevolution. London: Academic. pp.77-98.

Michael, Raj, S.; Morachan, Y.B. 1973. Effect of fertilization and diazinon application on the incidence of stem borer and leaf roller on rice. Madras Agricultural Journal 60:431-435.

Mikuriya, H. 1988. Yield decrease of rice plants by injurious insects in Saga prefecture. II. Yield loss caused by the rice leaffolder. *Cnaphalocrocis medinalis* Guenée in late rice varieties. Proceedings of the Association for Plant Protection, Kyushu 34:103-105. (In: Japanese)

Miyahara, Y. 1981. Occurrence of the rice leafroller in Japan. JARQ 15(2):100-105.

Miyahara, Y. 1992. Habitats of the rice leafroller moth, *Cnaphalocrocis medinalis* Guenée. Proceedings of the Association for Plant Protection, Kyushu 38:78-81. (In Japanese)

Miyashita, T. 1985. Estimation of the economic injury level in the rice leafroller, *Cnaphalocrocis medinalis* Guenée (Lepidoptera: Pyralidae). I. Relation between yield loss and injury of rice leaves at heading or in the grain filling stage. Japanese Journal of Applied Entomology and Zoology 29:73-76 (In Japanese, English abstract).

Mochida, O.; Joshi, R.C.; Litsinger, J.A. 1987. Climatic factors affecting the occurrence of insect pests. In: Weather and rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines, 322pp.

Mols, P.J.M. 1988. Simulation of hunger, feeding and egg production in the carabid beetle *Pterostichus coerulescens* L (=*Poecilus versicolor* Sturm). Agricultural University Wageningen Papers 88-3.

Mols, P.J.M. 1993. Foraging behaviour of the carabid beetle *Pterostichus coerulescens* L. (= *Poecilus versicolor* Sturm) at different densities and distributions of the prey. Agricultural University Wageningen Papers 93-5.

Moody, K. 1993. Weed control in wet-seeded rice. Experimental Agriculture 29:393-403.

Morris, R.F. 1965. Contemporaneous mortality factors in population dynamics. Canadian Entomologist 97: 1173-1184.

Morrison, G. 1986. 'Searching time aggregation' and density dependent parasitism in a laboratory host-parasitoid interaction. Oecologia 68:298-303.

Morrison, G.; Lewis, W.J. 1981. The allocation of searching time by *Trichogramma pretiosum* in host-containing patches. Entomologia experimentalis et applicata 30:31-39.

Morrison, G.; Lewis, W.J.; Nordlund, D.A. 1980. Spatial differences in *Heliothis zea* egg density and the intensity of parasitism by *Trichogramma* spp.: an experimental analysis. Environmental Entomology 9:79-85.

Murdoch, W.W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecological Monographs 39:335-354.

Murugesan, S.; Chelliah, S. 1983a. Rice yield loss caused by leaffolder damage at tillering stage. International Rice Research Newsletter 8(4):13-14.

Murugesan, S.; Chelliah, S. 1983b. Rice yield losses caused by leaffolder damage to the flag leaf. International Rice Research Newsletter 8(4):14.

Murugesan, S.; Chelliah, S. 1986. Yield loss and economic injury by rice leaf-folder. Indian Journal of Agricultural Sciences 56(4):282-285.

Nadarajan, L.; Skaria, B.P. 1988. Leaffolder (LF) resurgence and species composition in Pattambo, Kerala. International Rice Research Newsletter 13(3):33-34.

Need, J.T.; Burbutis, P.P. 1979. Searching efficiency of *Trichogramma nubilale*. Environmental Entomology 8:224-227.

Nicholson, A.J.; Baily, V.A. 1935. The balance of animal populations. - Part I. Proceedings of the Zoological Society of London 3:551-598.

Noldus, L.P.J.J. 1989. Semiochemicals, foraging behaviour and quality of entomophagous insects for biological control. Journal of Applied Entomology 108: 425-451.

Nuessly, G.S.; Hartstack, A.W.; Witz, J.A.; Sterling, W.L. 1991. Dislodgement of *Heliothis zea* (Lepidoptera: Noctuidae) eggs from cotton due to rain and wind: a predictive model. Ecological Modelling 55:89-102.

O'Neil, R.J. 1989. Comparison of laboratory and field measurements of the functional response of *Podisus maculiventris* (Heteroptera: Pentatomidae). Journal of the Kansas Entomological Society 62:148-155.

O'Neil, R.J. 1990. Functional response of arthropod predators and its role in the biological control of insect pests in agricultural systems. In: R.R. Baker; P.E. Dunn (Eds.), New directions in biological control: Alternatives for suppressing agricultural pests and diseases. Alan R. Liss, Inc., New York. pp.83-96.

Panda, S.K.; Shi, N. 1989. Carbofuran-induced rice leaffolder (LF) resurgence. International Rice Research Newsletter 14(1):30.

Pang, X.F. 1988. Evaluation of *Trichogramma* and other natural enemies. In: *Trichogramma* and other egg parasites (Ghangzhou 10-15 Nov. 1986). Colloques de l'INRA 43: 443-449.

Pang, X.F.; Liang, G.W.; Zeng, L.L. 1984. Evaluation of the effectiveness of natural enemies [in Chinese, English summary]. Acta Ecologica Sinica 4(1): 1-11.

Patel, R.K.; Janoria, M.P.; Bhowmik, A.K. 1987. Leaffolder (LF) population on rice under drought. International Rice Research Newsletter 12(3):30.

Pena, J.E.; Waddill, V. 1983. Larval and egg parasitism of *Keiferia lycopersicella* (Walsingham) (Lepidoptera: Gelechiidae) in Southern Florida tomato fields. Environmental Entomology 12:1322-1326.

Peng, B.; Fu, S.; Chen, N.; Chang, S.; Liu, .; Wen, Q.; Yin, Y. 1984. Studies on the efficacy of *Bacillus thuringiensis* Var, Kurstaki (HD-1) in controlling the rice leaf roller, *Cnaphalocrocis medinalis* (Guenee). Acta Phytophylacica Sinica 11:9-16 (In Chinese, English summary).

Peng, S.B. 1993. Physiological processes of crop growth and production and their relationships to damage by stemborer, bacterial leaf blight and sheath blight. In: Rossing *et al.* (Eds.) Mechanisms of damage by stemborer, bacterial leaf blight and sheath blight, and their effects on yield. SARP Research Proceedings - December 1993. AB-DLO/TPE-WAU/IRRI. pp.7-21.

Perez, M.L.; Cadapan, E.P. 1986. The efficacy of *Trichogramma* species as biological control agents against some rice insect pests. Philippine Entomologist 6(5):463-470.

Perfect, T.J.; Cook, A.G.; Ferrer, E.R. 1983. Population sampling for planthoppers (Hemiptera: Delphacidae & Cicadellidae) and their predators in flooded rice. Bulletin of Entomological Research 73:345-355.

Price, P.W.; Bouton, C.E.; Gross, P.; McPheron, B.A.; Thompson, J.N.; Weis, A.E. 1980. Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. Annual Review of Ecology and Systematics 11:41-65.

Pu, T.S.; Liu, Z.J.; Zhang, Y.X. 1988. Studies on *Trichogramma*. In: *Trichogramma* and other egg parasites (Ghangzhou 10-15 Nov. 1986). Colloques de l'INRA 43:551-556.

Qadeer, G.A.; Arya, S.P.; Tomer, O.S. 1988. Leaffolder (LF) outbreak in Haryana. International Rice Research Newsletter 13(3):38.

Rabbinge, R. 1976. Biological control of the fruit-tree spider mite. Simulation Monographs, Pudoc, Wageningen.

Rajamma, P.; Das, N.M. 1969. Studies on the biology and control of the rice leaf roller, *Cnaphalocrocis medinalis* Guen. Agricultural Research Journal Kerala 7(2):110-112.

Rajapakse, R.H.S.; Kulasekare, V.L. 1982. Larval parasites of rice leaffolder in Southern Sri Lanka. International Rice Research Newsletter 7(1):11.

Rajendran, R. 1985. Influence of varieties, nitrogen and spacings on the infestation by rice leaffolder *Cnaphalocrocis medinalis* (Guenée). Madras Agricultural Journal 72:586-589.

Ramachandran, R.; Khan, Z.R. 1991a. Feeding site selection of first-instar larvae of *Cnaphalocrocis medinalis* on susceptible and resistant rice plants. Entomologia experimentalis et applicata 60:43-49.

Ramachandran, R.C.; Khan, Z.R. 1991b. Mechanisms of resistance in wild rice *Oryza brachyantha* to rice leaffolder *Cnaphalocrocis medinalis* (Guenée) (Lepidoptera: Pyralidae). Journal of Chemical Ecology 17:41-65.

Randriamananoro, J.J. 1990. Colonization of rice leaffolders *Cnaphalocrocis medinalis* (Guenée) and *Marasmia patnalis* Bradley (Lepidoptera: Pyralidae) in upland and irrigated rice fields. M.Sc. thesis, University of the Philippines at Los Baños, Philippines.

Reissig, W.H.; Heinrichs, E.A.; Litsinger, J.A.; Moody, K.; Fiedler, L.; Mew, T.W.; Barrion, A.T. 1986. Illustrated guide to integrated pest management in rice in tropical Asia. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Rekhi, R.S.; Singh, J.; Meelu, O.P. 1985. Effect of green manure and nitrogen on mole rat damage and leaffolder (LF) incidence in rice. International Rice Research Newsletter 10(1):26.

Roger, P.A.; Simpson, I.; Oficial, R.; Ardales, S.; Jimenez, R. 1994. Impact of pesticides on soil and water microflora and fauna in wetland ricefields. In: P.S. Teng; K.L. Heong; K. Moody (Eds.) Rice pest science and management. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Rogers, D. 1972. Random search and insect population models. Journal of Animal Ecology 41:369-383.

Rola, A.C.; Pingali, P.L. 1993. Pesticides, rice productivity, and farmers' health. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Rossing, W.A.H. 1991. Simulation of damage in winter wheat caused by the grain aphid *Sitobion avenae*. 2. Construction and evaluation of a simulation model. Netherlands Journal of Plant Pathology 97:25-54.

Rossing, W.A.H.; Rubia, E.G.; Heong, K.L.; Keerati-Kasikorn, M.; Reddy, P.R. (Eds.) 1993. Mechanisms of damage by stemborer, bacterial leaf blight and sheath blight, and their effects on rice yield. SARP Research Proceedings - December 1993. AB-DLO/TPE-WAU/IRRI.

Rothschild, G.H.L. 1970. Observations on the ecology of rice-ear bug *Leptocorisa oratorius* (F.) (Hemiptera: Alydidae) in Sarawak (Malaysian Borneo). Journal of Applied Ecology 7:147-167.

Rothschild, G.H.L. 1971. The biology and ecology of rice-stemborers in Sarawak (Malaysian Borneo). Journal of Applied Ecology 8:287-322.

Rubia, E.G.; Shepard, B.M. 1987a. Biology of *Metioche vittaticollis* (Stål) (Orthoptera: Gryllidae), predator of rice pests. Bulletin of Entomological Research 77:669-676.

Rubia, E.G.; Shepard, B.M. 1987b. Toxicity of five insecticides to the cricket *Metioche vittaticollis* (Stål) (Orthoptera: Gryllida), a predator of some insect pests of rice. International Rice Research Newsletter 12(6): 31.

Rubia, E.G.; Peña, N.B.; Almazan L.P.; Shepard B.M. 1990a. Efficacy of selected predators against some insect pests of rice. Journal of Plant Protection in the Tropics 7:69-76.

Rubia, E.G.; Ferrer, E.R.; Shepard, B.M. 1990b. Biology and predatory behavior of *Conocephalus longipennis* (de Haan) (Orthoptera: Tettigoniidae). Journal of Plant Protection in the Tropics 7: 47-54.

Rurkviree, S. 1981. Natural enemy complex of rice leaffolder, *Cnaphalocrocis medinalis* (Guenee) (Lepidoptera: Pyralidae) in Thailand. M.Sc. thesis, Kasetsart University, Bangkok, Thailand. 85p.

Sabelis, M.W. 1981. Biological control of two-spotted spider mites using phytoseiid predators. Part I (Modelling the predator-prey interaction at the individual level). Agricultural Research Report 910, Pudoc, Wageningen.

Sabelis, M.W. 1992. Predatory arthropods. In: M.J. Crawley (Ed.) Natural enemies. The population biology of predators, parasites, and diseases. pp.225-264.

Saroja, R.; Raju, N. 1982. Effect of nitrogen fertilizer levels and spacing on rice gall midge and leaffolder damage. International Rice Research Newsletter 7(4):10.

Saroja, R.; Peeran, S.N.; Raju, N. 1981. Effects of methods of nitrogen application on the incidence of rice leaffolder. International Rice Research Newsletter 6(4):15-16.

Saroja, R.; Jagannathan, R.; Raju, N. 1987. Effect of N nutrition and rice variety on leaffolder (LF), yellow stem borer (YSB), and grain yield. International Rice Research Newsletter 12(5):11-12.

Saunders, D.S. 1982. Insect clocks. 2nd edition, Pergamon Press.

Shepard, B.M. 1989. Integrated management of rice insect pests. In: Rice Farming Systems: New directions. International Rice Research Institute, P.O. Box 933, Manila, Philippines. pp.203-212.

Shepard, M.; Arida, G.S. 1986. Parasitism and predation of yellow stem borer, *Scirpophaga incertulas* (Walker) (Lepidopter: Pyralidae) eggs in transplanted and direct seeded rice. Journal of Entomological Science 21:26-32

Shepard, B.M.; Ooi, P.A.C. 1991. Techniques for evaluating predators and parasitoids in rice. In: E.A. Heinrichs; T.A. Miller (Eds.), Rice insects: management strategies, pp.205-214.

Shepard, B.M.; Ooi, P.A.C. 1992. Evaluating biocontrol in rice: present and future considerations. In: P.A.C. Ooi, G.S. Lim; P.S. Teng (Eds.), Biological control: issues in the tropics, pp.93-99.

Shepard, B.M.; Barrion, A.T.; Litsinger, J.A. 1987. Friends of the rice farmer. Helpful insects, spiders and pathogens. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Shepard, B.M.; Minnick, D.R.; Soriano, J.S.; Ferrer, E.R.; Magistrado, O.N. 1988. A simplified method for sampling leaffolders (LFs) and planthoppers. International Rice Research Newsletter 13(1):40-41.

Smith, J.; Litsinger, J.A.; Bandong, J.P.; Lumaban M.D. 1989. Economic thresholds for insecticide application to rice: Profitability and risk analysis to Filipino farmers. Journal of Plant Protection in the Tropics 6:67-87.

Southwood, T.R.E. 1978. Ecological methods - with particular reference to the study of insect populations. 2nd edition, Chapman & Hall.

Southwood, T.R.E.; Comins, H.N. 1976. A synoptic population model. Journal of Animal Ecology 45:949-965.

Stapley, J.H. 1978. The rice leaf roller in the Solomon Islands. International Rice Research Newsletter 3(1):13.

Stewart, L.; Dixon, A.F.G 1988. Quantification of the effect of natural enemies on the abundance of aphids: precision and statistics. In: E. Niemczyk; A.F.G. Dixon (Eds.), Ecology and effectiveness of aphidophaga, pp.187-197.

Subbaih, K.K.; Morachan, Y.B. 1974. Effect of nitrogen nutrition and rice varieties on the incidence of leaf roller (*Cnaphalocrocis medinalis* Guenee). Madras Agricultural Journal 61:716.

Suharto 1989. Abundance of *Heliothis armigera* and its natural enemies in cotton intercropped with cereals or legumes. M.Sc. thesis, University of the Philippines at Los Baños, Philippines.

Suharto, H.; Noch, I.P. 1987. Effect of transplanting date on leaffolder (LF) Cnaphalocrocis medinalis and rice bug (RB) *Leptocorisa oratorius* infestation at Kuningan, West Java. International Rice Research Newsletter 12(5):27.

Sunderland, K.D. 1988. Quantitative methods for detecting invertebrate predation occurring in the field. Annals of Applied Biology 112:201-224.

Swaminathan, K.; Saroja, R.; Raju, N. 1985. Influence of source and level of nitrogen application on pest incidence. International Rice Research Newsletter 10(1):24.

Tan, C.L. 1981. Natural enemies of the major insect pests of rice in Peninsular Malaysia. Crop Protection Branch Information Leaflet No. 1, MARDI.

Telvapuchom, W. 1990. Effects of sublethal doses of insecticides and host plant age on *Cnaphalocrocis medinalis* (Guenée). M.Sc. thesis, Kasetsart University, Bangkok, Thailand.

ten Berge, H.F.M. 1990. Heat and water transfer in the bare topsoil and the lower atmosphere. Simulation Monographs, Pudoc, Wageningen.

ten Berge, H.F.M.; Thiyagarajan, T.M.; Qinghua Shi; Wopereis, M.C.S.; Drenth, H.; Jansen, M.J.W. 1996a. Numerical optimization of nitrogen application to rice. Part I. Description of MANAGE-N. Field Crops Research, in press.

ten Berge, H.F.M.; Shi Qinghua; Zheng Zhiming; Rao, K.S.; Riethoven, J.J.M.; Zhong Xuhua 1996a. Numerical optimization of nitrogen application to rice. Part II. Field evaulations. Field Crops Research, in press.

Tevapuchom, W.; Heong, K.L. 1991. Effects of sublethal insecticide application on rice leaffolder (LF). International Rice Research Newsletter 16(2):23-24.

Thakur, R.B.; Mishra, S.S. 1989. Effect of different levels of nitrogen and some granular insecticides on stem borer and leaf folder incidence in rice. Journal of Entomological Research 13:121-124.

Thangamuthu, G.S.; Murugesan, C.; Subramanian, S. 1982. Effect of spacing on leaffolder *Cnaphalocrocis medinalis* Guenee infestation in rice. International Rice Research Newsletter 7(5):21.

Thiyagarajan, T.M.; ten Berge, H.F.M.; Wopereis, M.C.S. (Eds.) 1995. Nitrogen management studies in irrigated rice. SARP Research Proceedings - May 1995. AB-DLO/TPE-WAU/IRRI.

Trexler, J.C.; McCulloch, C.E.; Travis, J. 1988. How can the functional response best be determined ? Oecologia 76:206-214.

Tryon, E.H.; Litsinger, J.A. 1988. Feasibility of using locally produced *Bacillus thuringiensis* to control tropical insect pests. In: P.S. Teng; K.L. Heong (Eds.) Pesticide Management and Integrated Pest Management in Southeast Asia, Consortium for International Crop Protection, Maryland, USA. 473pp.

Upadhyay, R.K.; Diwakar, M.C. 1983. Natural enemies of rice insect pests. International Rice Research Newsletter 8(6):17-18.

Upadhyay, V.R.; Shah, A.H.; Desai, N.D. 1981. Influence of levels of nitrogen and rice varieties on the incidence of rice leaf folder *Cnaphalocrocis medinalis* Guenée. GAU Research Journal 6:115-117.

Uthamasamy, S. 1985. Problems and priorities in the management of rice leaffolder. In: S. Jayaraj (Ed.) Integrated pest and disease management. Proceedings of the national seminar. Tamil Nadu Agricultural University, Coimbatore, India. pp.54-61.

van den Berg, H. 1992, 1993. Studies on the impact of natural enemies on soybean pests, to support the National IPM Training Programme in Indonesia. Reports, International Institute of Biological Control, Kuala Lumpur, Malaysia.

van den Berg, H. 1993. Natural control of *Helicoverpa armigera* in smallholder crops in East Africa. PhD dissertation, Wageningen Agricultural University, Wageningen, the Netherlands.

van den Berg, H.; Shepard, B.M.; Litsinger, J.A.; Pantua, P.C. 1988. Impact of predators and parasitoids on the eggs of *Rivula atimeta, Naranga aenescens* (Lepidoptera: Noctuidae) and *Hydrellia philippina* (Diptera: Ephydridae) in rice. Journal of Plant Protection in the Tropics 5: 103-108.

van den Berg, H.; Litsinger, J.A., Shepard, B.M.; Pantua, P.C. 1992. Acceptance of eggs of *Rivula atimeta, Naranga aenescens* (Lep.: Noctuidae) and *Hydrellia philippina* (Dipt.: Ephydridae) by insect predators on rice. Entomophaga 37: 21-28.

van Driesche, R.G. 1983. Meaning of "Percent Parasitism" in studies of insect parasitoids. Environmental Entomology 12:1611-1622.

van Driesche, R.G.; Bellows, T.S.; Elkington, J.S.; Gould, J.R.; Ferro, D.N. 1991. The meaning of Percentage Parasitism revisited: solutions to the problem of accurately estimating total losses from parasitism. Environmental Entomology 20:1-7.

van Hamburg, H.; Hassell, M.P. 1984. Density dependence and the augmentive release of egg parasitoids against graminaceous stalkborers. Ecological Entomology 9: 101-108.

van Lenteren, J.C.; Bakker, K. 1976. Functional responses in invertebrates. Netherlands Journal of Zoology 26(4):567-572.

van Vreden, G.; Ahmadzabidi, A.L. 1986. Pests of rice and their natural enemies in Peninsular Malaysia. Pudoc, Wageningen.

Velusamy, R.; Chelliah, S. 1985. Field screening for resistance to leaffolder (LF). International Rice Research Newsletter 10(1):9.

Velusamy, R.; Subramaniam, T.R. 1974. Bionomics of the rice leaf roller, *Cnaphalocrocis medinalis* Guenee (Pyralidae: Lepidoptera). Indian Journal of Entomology 36:185-189.

Venugopal, M.S.; Litsinger, J.A. 1984. Effect of carbofuran on rice growth. Protection Ecology 7:313-317.

Vet, L.E.M.; Dicke, M. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. Annual Review of Entomology 37:141-172.

Vo Mai 1992. Brown planthopper problem in Vietnam and research needs. Paper presented at the International Rice Research Conference, IRRI, Los Baños, Philippines, 21-25 April 1992.

Vo Mai; Thu Cuc, N.; Hung, N.Q.; Chau, N.M.; Chien, H.V.; Escalada, M.M.; Heong, K.L. 1993. Farmers' perceptions of rice pest problems and management tactics used in Vietnam. International Rice Research Notes 18(2):31.

Vyas, A.M.; Shah, A.H.; Patel, C.B. 1981. Biology of the rice leaf roller *Cnaphalocrocis medinalis* Gn. (Pyralidae: Lepidoptera). GAU Research Journal 6(2):75-79.

Waage, J.K. 1992. Biological control in the year 2000. In: A.A.S.A. Kadiz; H.S. Barlow (Eds.), Pest management and the environment in 2000, pp.329-340.

Waage, J.K. 1994. Biodiversity, business and biotechnology: shaping the future of biological control. Vijfde voordracht gehouden ter herdenking van prof.dr. J. de Wilde, hoogleraar in de entomologie aan de Landbouwunversiteit te Wageningen (1954-1982), op vrijdag 18 november 1994.

Wada, T. 1979. Influence of the temperature and the growing stages of the rice plant on the number of larval instars in the rice leafroller, *Cnaphalocrocis medinalis* Guenée. Japanese Journal of Applied Entomology and Zoology 23:178-182.

Wada, T. 1989. Ecology of rice leaffolder. Ph.D. thesis, Nagoya University, Japan.

Wada, T.; Kobayashi, M. 1980. Effects of temperature on development of the rice leaf roller, *Cnaphalocrocis medinalis* Guenée (Lepidoptera: Pyralidae). Applied Entomology and Zoology 15:207-214.

Wada, T.; Kobayashi, M. 1982. Mating status depending on the growing stage of the rice plant in the population of *Cnaphalocrocis medinalis* (Guenée). Applied Entomology and Zoology 17:278-281.

Wada, T.; Kobayashi, M. 1985. Distribution pattern and sampling techniques of the rice leaf roller, *Cnaphalocrocis medinalis*, in a paddy field. Japanese Journal of Applied Entomolology and Zoology 29:230-235 (In Japanese, English abstract).

Wada, T.; Kobayashi, M. 1991. Life history of the rice leaffolder, *Cnaphalocrocis medinalis* in Japan - Invasion, population explosion and dispersal. Proceedings of International Seminar on Migration and Dispersal of Agricultural Insects, Tsukuba, Japan, September 1991. pp.61-70.

Wada, T.; Nik, M. N. 1991. Ecology of the rice leaffolder, *Cnaphalocrocis medinalis*, with special reference to its migration strategy. Internal Report, MARDI. pp.41-48.

Wada, T.; Shimazu, M. 1978. Seasonal population trends of the rice leaf roller, *Cnaphalocrocis medinalis* Guenee (Lepidoptera: Pyralidae) in the paddy fields at Chiguko in 1977. Proceedings of the Association for Plant Protection, Kyushu 24:77-80.

Wada, T.; Kobayashi, M.; Shimazu, M. 1980. Seasonal changes of the proportions of mated females in the field population of the rice leaffolder, *Cnaphalocrocis medinalis* Guenée (Lepidoptera: Pyralidae). Applied Entomology and Zoology 15:81-89.

Waibel, H.; Meenakanit, P. 1988. Economics of integrated pest control in Southeast Asia. In: P.S. Teng; K.L. Heong (Eds.), Pesticide Management and Integrated Pest Management in Southeast Asia. pp.103-112. Consortium for International Crop Protection, Maryland, U.S.A.

Waldbauer, G.P.; Marciano, A.P. 1979. Rice leaffolder: mass rearing and a proposal for screening for varietal resistance in the greenhouse. IRRI Research Paper Series 27.

Waldbauer, G.P.; Marciano, A.P.; Pathak, P.K. 1980. Life-span and fecundity of adult rice leaf folders, *Cnaphalocrocis medinalis* (Guenée) (Lepidoptera: Pyralidae), on sugar sources, including honeydew from the brown planthopper, *Nilaparvata lugens* (Stål). Bulletin of Entomological Research 70:65-71.

Way, M.J.; Heong, K.L. 1994. The role of biodiversity in the dynamics and management of insect pests of tropical irrigated rice - a review. Bulletin of Entomological Research 84:567-587.

White, T.C.R. 1978. The importance of a relative shortage of food in animal ecology. Oecologia 33:71-86.

Wiedenmann, R.N.; O'Neil, R.J. 1991. Laboratory measurement of the functional response of *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae) Environmental Entomology 20(2):610-614.

Wilhoit, L.R.; Stinner, R.E.; Axtell, R.C. 1991. CARMOD: A simulation model for *Carcinops pumilio* (Coleoptera: Histeridae) population dynamics and predation on immature stages of house flies (Diptera: Muscidae). Environmental Entomology 20:1079-1088.

Win, Y. 1989. Biology of the coccinellid *Micraspis hirashimai* (Sasaji) (Coleoptera: Coccinellidae) and its predation on some rice insect pests. M.Sc. thesis, Central Luzon State University, Nueva Ecija, Philippines.

Wu, J.C.; Zhang, X.X. 1984. Effects of temperature on the growth and the development of experimental populations of the rice leaf roller, *Cnaphalocrocis medinalis* Guenée. Journal of Nanjing Agricultural College 1984(4):19-28.

Wu, J.C.; Zhang, X.X. 1985. The spatial distribution pattern of the rice leaf roller *Cnaphalocrocis medinalis* Guenee and its application. Journal of Nanjing Agricultural University 12(4):28-35.

Wu, H.L.; Liang, G.W.; Pang, X.F. 1986. Evaluation of the effectiveness of various treatments to rice leaf roller suppression. Journal of South China Agricutural University 7(1):7-16.

Yadava, C.P.; Santaram, G.; Israel, P.; Kalode, M.B. 1972. Life-history of rice leaf-roller, *Cnaphalocrocis medinalis* Guenee (Lepidoptera: Pyralidae) and its reaction to some rice varieties and grasses. Indian Journal of Agricultural Science 42:520-523.

Yasumatsu, K.; Wongsiri, T.; Navavichit, S. and Tirawat, C. 1975. Approaches toward an integrated control of rice pests: Part 1: Survey of natural enemies of important rice pests in Thailand. Plant Protection Service Technical Bulletin No. 24.

Yasumatsu, K.; Wongsiri, T.; Tirawat, C.; Navavichit, S.; Lewvanich, A.; Yasumatsu, Y. 1981. Contributions to the development of integrated rice pest control in Thailand. Report Japan International Cooperation Agency.

Yoshida, S. 1981. Fundamentals of rice crop science. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

You, M.S.; Wu, Z.F.; Zhou, L.F. 1993. A simulation model of action threshold for the rice leaffolder (RLF) in Fujian, China. In: Research on rice leaffolder management in China. Proceedings of the International Workshop on Economic Threshold Level for Rice Leaffolder in China, March 1-2, 1992, Beijing, pp.75-82.

Yuen, P.M. 1982. Bio-ecological studies on the leaf feeding pyralids of rice plants, with emphasis on *Cnaphalocrocis medinalis* (Guenée). M.Sc.-thesis, University of Malaya.

Zhang, G.F.; Liu, Q.X.; Shen, X.C. 1993. Economic thresholds for rice leaffolder, *Cnaphalocrocis medinalis* (Guenee) in the rice areas along the Yellow River, Henan Province. In: Research on rice leaffolder management in China. Proceedings of the International Workshop on Economic Threshold Level for Rice Leaffolder in China, March 1-2, 1992, Beijing, pp.51-58.

Zhang, J.P.; Chen, C.M. 1991. The yield component and compensation reactions of rice on the damage of rice leafroller. Acta Phytophylacica Sinica 18:1-4.

Zhang, R.; Gu, D.; Wen, G. 1989. Economic injury levels and economic thresholds for the rice leaf-roller, *Cnaphalocrocis medinalis* guenee. Supplement To The Acta Scientiarum Naturalium Universitatis Sunyatseni 8(1):90-97 (In Chinese, English abstract).

Zhang, R.J.; Heong, K.L.; Domingo, I.T. 1995. Possible effect of global warming on rice leaffolder. European journal of Plant Pathology. Abstracts XIII International Plant Protection Congress, the Hague, the Netherlands, 2-7 July 1995.

Zhang, X. X. 1991. Migration of rice leaf roller, *Cnaphalocrocis medinalis* Guenee, in China. Proceedings of International Seminar on Migration and Dispersal of Agricultural Insects, Tsukuba, Japan, September 1991. pp.51-60.

Zhang, X.X, Geng, J.G., Gu, H.N.; Wang, X. 1988. Forecasting model for the population life system of rice leafroller, *Cnaphalocrocis medinalis* Guenée [in Chinese, English summary]. Acta Ecologica Sinica 8:18-26.

Curriculum vitae

Jacobus (Joop) de Kraker was born on 15 February 1965 in Terneuzen, in the South-west of the Netherlands. In 1983 he graduated there from the secondary school Zeldenrust College. The same year he moved to Wageningen to start his study Crop Protection at the Agricultural University (WAU). During his graduate studies he did three research projects at the WAU departments of Entomology, Theoretical Production Ecology, and Phytopathology respectively, and spent a 6-month practical period in Mexico. There he was involved in field studies of the coffee berry borer at the Centro de Investigaciones Ecologicas del Sureste, in Tapachula, Chiapas. He obtained his 'Ir' degree, equivalent to MSc, in 1989 (*cum laude*). After graduation he was hired as a consultant by the World Meteorological Organization to conduct roving seminars on simulation modelling of primary production in Botswana and Lesotho. From 1990 to 1994 he was based on behalf of WAU at the International Rice Research Institute, Los Baños, Philippines, to conduct the studies on natural control of rice leaffolder described in this thesis. Since April 1995 he works at the WAU department of Theoretical Production Ecology for the NATURA - European Community training programme for agricultural universities in southern regions (NECTAR). His responsibilities concern the development of post-graduate training modules in 'Sustainable Crop Protection'.

Appendix. Presence of taxa of rice leaffolder natural enemies in arthropod samples from eight rice crops, Laguna, Philippines: (+) = present, (−) = absent, (*) = numerically most common in samples. Locations: VI=Victoria, PI=Pila, IR=IRRI farm; seasons: DS=dry season, WS=wet season; sampling methods: su=suction sampler, sw=sweepnet; prey/host stages: A=adult, E=egg, L=larva, P=pupa. See **Chapter 1** for details.

Natural enemy taxon		Location Year Season Sampling method	VI 91 Ds su	VI 91 Ds sw	PI 91 Ds su	PI 91 Ds sw	PI 92 Ds su	PI 92 Ds sw	PI 93 Ds su	PI 91 Ws su	PI 91 Ws sw	PI 93 Ws su	IR 92 Ws su	IR 92 Ws sw	IR 93 Ws su
Predators		Prey stage													
Araneae:															
* Lycosidae		L/A	+	+	+	+	+	+	+	+	+	+	+	+	+
Oxyopidae		L/A	−	+	−	+	+	+	+	+	+	+	−	−	+
Araneidae		A	−	+	−	+	−	+	+	+	+	+	+	+	+
* Tetragnathidae		A	+	+	+	+	+	+	+	+	+	+	+	+	+
Salticidae		A	+	−	+	+	+	+	+	+	+	+	+	+	−
Coleoptera:															
* *Ophionea* spp.	(Carabidae)	E/L	+	+	+	+	+	+	+	+	+	+	+	+	+
* *Micraspis* spp.	(Coccinellidae)	E/L	+	+	+	+	+	+	+	+	+	+	+	+	+
Harmonia octomaculata	(Coccinellidae)	E/L	+	+	+	+	−	+	+	+	−	−	−	−	−
undet. Coccinellidae	(Coccinellidae)	E/L	−	−	−	−	+	+	+	+	+	−	−	−	−
Paederus fuscipes	(Staphylinidae)	E/L	+	−	+	−	+	−	−	+	−	+	−	−	+
undet. Staphylinidae	(Staphylinidae)	E/L	+	−	+	+	+	+	+	+	+	−	+	−	+
Orthoptera:															
* *Anaxipha longipennis*	(Gryllidae)	E/L	+	+	+	+	+	+	+	+	+	+	+	+	+
* *Metioche vittaticollis*	(Gryllidae)	E/L	+	+	+	+	+	+	+	+	+	+	+	+	+
* *Conocephalus longipennis*	(Tettigoniidae)	E/L/A	+	+	+	+	+	+	+	+	+	+	+	+	+
Hemiptera:															
* *Cyrtorhinus lividipennis*	(Miridae)	E	+	+	+	+	+	+	+	+	+	+	+	+	+
* *Microvelia d. atrolineata*	(Veliidae)	L	+	−	+	+	+	−	+	+	−	+	+	−	+
* *Mesovelia vittigera*	(Mesovelia)	L	−	−	+	−	+	−	+	+	+	+	+	−	+
Limnogonus fossarum	(Gerridae)	L	−	−	−	−	−	−	−	−	−	+	+	−	+
* *Polytoxus fuscovittatis*	(Reduviidae)	L	+	−	−	+	+	+	+	+	+	+	+	+	+
undet. Reduviidae	(Reduviidae)	L	−	−	−	−	−	−	+	−	−	+	−	−	+

Hymenoptera:															
Formicidae		E/L	+	+	+	+	+	+	+	+	+	+	+	+	+
Odonata:															
Libellullidae		A	−	+	−	+	−	+	−	+	+	−	−	+	+
Coenagrionidae		A	+	+	+	+	+	+	+	+	+	+	+	+	+
Total no. of predator taxa / sampling method			16	14	16	18	18	18	20	21	18	19	17	14	20
Total no. of predator taxa - methods combined			19		20		21			21			18		
Parasitoids		Host stage													
Hymenoptera:															
Goniozus spp.	(Bethylidae)	L	+	+	+	+	+	+	+	+	+	+	+	+	−
Bracon chinensis	(Braconidae)	L	−	−	−	−	−	−	+	−	−	−	−	−	+
Cardochiles philippinensis	(Braconidae)	L	+	+	+	+	−	+	−	+	+	−	+	+	+
* *Cotesia* spp.	(Braconidae)	L	+	+	+	+	+	+	+	+	+	+	+	+	+
Macrocentrus philippinensis	(Braconidae)	L	+	−	+	−	+	+	+	+	+	+	+	+	+
* *Opius* spp.	(Braconidae)	L	+	+	+	+	+	+	+	+	+	+	+	+	+
Brachymeria spp.	(Chalcididae)	L/P	+	+	+	+	+	+	+	+	+	+	−	−	−
Elasmus spp.	(Elasmidae)	L	+	+	+	+	+	+	+	+	+	+	+	+	−
Copidosomopsis nacoleiae	(Encyrtidae)	E/L	−	−	−	−	−	−	+	−	−	+	−	−	+
* *Tetrastichus* spp.	(Eulophidae)	L/P	+	+	+	+	+	+	+	+	+	+	+	+	+
Itoplectis narangae	(Ichneumonidae)	L/P	+	+	+	+	+	+	+	+	+	+	−	+	−
Temelucha philippinensis	(Ichneumonidae)	L	+	+	+	+	−	+	+	+	+	+	−	+	+
Temelucha stangli	(Ichneumonidae)	L	+	+	−	+	+	+	+	+	+	−	−	−	−
Trichomma cnaphalocrocis	(Ichneumonidae)	L/P	−	−	−	−	−	−	+	−	−	+	−	−	+
Xanthopimpla flavolineata	(Ichneumonidae)	L/P	+	+	+	+	−	+	+	−	−	−	−	+	−
Trichomalopsis spp.	(Pteromalidae)	L/P	+	−	−	+	−	−	+	−	−	+	−	−	−
Trichogrammatidae		E	+	+	+	+	−	−	+	−	−	+	−	−	+
Total no. of parasitoid taxa / sampling method			14	12	12	13	9	12	16	11	11	13	7	10	10
Total no. of parasitoid taxa - methods combined			14		14		12			11			10		
Total no. of natural enemy taxa / sampling method			30	26	28	31	27	30	36	32	29	32	24	24	30
Total no. of natural enemy taxa - methods combined			33		34		33			32			28		