European Arachnology 2000 (S. Toft & N. Scharff eds.), pp. 57-64.
 ISBN 87 7934 001 6
(Proceedings of the 19th European Colloquium of Arachnology, Århus 17-22 July 2000)

Early season natural biological control of insect pests in rice by spiders - and some factors in the management of the cropping system that may affect this control

LENE SIGSGAARD
International Rice Research Institute (IRRI), EPPD, MCPO 3127, 1271 Makati City, Philippines
Present address: *Royal Veterinary and Agricultural University, Dept. of Ecology, the Zoology Section, Thorvaldsensvej 40, DK-1871 Frederiksberg C, Denmark* (les@kvl.dk)

Abstract
There are relatively few insect pest problems in unsprayed, irrigated rice. Spiders are numerous early season predators and are thought to play an important role in the suppression of insect pests such as plant- and leafhoppers. Pest resurgence after insecticide spraying has been clearly linked to the negative impact of insecticides on spiders and other natural enemies. In particular, recent studies show that spiders depend on detritivores for food during fallow periods. The relatively low prey quality of pest species suggests that alternative prey serve as important food supplements. Future changes in the irrigated rice cropping system, such as direct seeding, chemical rather than manual weed control, mechanization and larger field sizes, will have significant impacts on spiders and other beneficials, thus disrupting natural biological control in rice.

Key words: *Nilaparvata lugens*, *Nephotettix virescens*, *Pardosa pseudoannulata*, *Atypena formosana*, spider, rice, natural biological control

INTRODUCTION

Small fields characterize traditional rice farming in Asia. Rice is the dominant staple food in the developing world. More than 90% of the world's rice is produced and consumed in Asia. Water is a prominent factor in the irrigated rice system making it different from other agricultural productions. The biodiversity of irrigated rice is higher than in many natural ecosystems (Schoenly et al. 1998).

Several insects feed on rice. Until the 1960s stemborers were considered the most important rice pests, in particular *Chilo suppressalis*, *Scirpophaga incertulas* and *S. innotata* (Lepidoptera: Pyralidae). With the widespread introduction during the green revolution in the sixties and seventies of fertilizers, of improved varieties and of pesticides to rice crops, leaf- and planthoppers became important pests, most notably the leafhoppers *Nilaparvata lugens* Stål, the brown planthopper (BPH), and *Sogatella furcifera* (Horvath) (Homoptera: Delphacidae), and the green planthopper (GLH) *Nephotettix virescens* (Distant) (Homoptera: Cicadellidae). Other herbivores in rice that can be insect pests include the rice gall midge (*Orselia oryzae* (Wood-Mason) (Diptera: Cecidomyiidae)), the rice leaffolder complex of which three have attained pest status: *Cnaphalocrocis medinalis* (Guenee), *Marasmia patnalis* Bradley and *M. exigua* (Butler) (Lepidoptera: Pyralidae), rice bugs, in particular the genus *Leptocorisa*

(Hemiptera: Coreidae), pentatomid bugs, rice hispa (*Dicladispa armigera* (Oliver) (Coleoptera: Hispidae), rice thrips (Thysanoptera: Thripidae), rice caseworm (*Nymphula depunctalis* (Guenee) (Lepidoptera: Pyralidae) and whorl maggot flies (several species of the genus *Hydrellia* (Diptera: Ephydridae)) (see for example Pathak & Kahn 1994).

However, unsprayed, irrigated rice fields have relatively few insect pest problems. This is largely attributed to natural biological control, which keep planthoppers, most notably BPH, and other potential pests in check (Kenmore et al. 1984; Way & Heong 1994).

SPIDERS IN RICE

Three guilds of spiders are found in rice: orb-weaving spiders, hunting spiders and space-web spiders. Orb-weavers include the families Araneidae, Tetragnathidae and Theridosomatidae. The most common orb-weaver genera are *Tetragnatha*, *Araneus* and *Argiope*. Lycosids dominate the guild of hunters, while the guild of space-web spiders contain three families Theridiidae, Linyphiidae and Agelenidae (Barrion and Litsinger 1995).

Natural biological control in irrigated rice at the early crop stages can mainly be attributed to spiders. Orb-weaving spiders are the most abundant spiders assessed across the cropping season, with *Tetragnatha* spp. being the single most common genus in South East Asian countries, except the Philippines where *Pardosa pseudoannulata* is the more common species. Heong et al. (1992) found a relative abundance of *P. pseudoannulata* of 25 to 54% of all spiders at five rice sites in the Philippines across the season. Lowest abundance of *A. formosana* was found at the two sites at higher elevations of 800 and 1500 m (7 and 9%), highest at the lower elevations (23, 35 and 40%). Three species of tetragnathids, *Tetragnatha virescens* Okuma, *T. maxillosa* Thorell, and *T. javana* (Thorell) together comprised 10 to 39% of the spiders in these sites. However, orb-weavers usually become abundant when insect damage has already occurred (Barrion and Litsinger 1984).

In the first 35 days after transplanting the dominant predators in irrigated rice are the lycosid *Pardosa pseudoannulata* (Bösenberg & Strand) and the linyphiid *Atypena formosana* (Oi) (Sigsgaard et al. 1999, the Philippines; Sahu et al. 1996, Northern Bihar, India). Both spiders are considered important predators of BPH and *Nephotettix virescens* (Distant) (Hemiptera: Cicadellidae), the green leafhopper (GLH). *P. pseudoannulata* is perhaps the single most important predator of BPH, and can effectively regulate the pest population of leafhoppers and planthoppers (Kiritani et al. 1972; Gavarra & Raros 1975; Kiritani & Kakiya 1975; Kenmore 1980; Kenmore et al. 1984; Shepard et al. 1987; Ooi & Shepard 1994). Both spiders occur throughout the year. *P. pseudoannulata* is most common among the tillers at the base of the plants. It preys on a wide array of insect pests, including leafhoppers and planthoppers, whorl maggot flies, leaffolders, caseworm and stem borers (Barrion & Litsinger 1984; Shepard et al. 1987, Rubia et al. 1990). Field densities of both spiders co-vary with hopper densities (Reddy & Heong 1991). References to the importance of the smaller and less conspicuous *A. formosana* have been few until recently (Shepard et al. 1987; Inthavong et al. 1996; Barrion 1999; Sigsgaard & Villareal 1999). *A. formosana* adults and immatures prefer to live among the rice stem or at the base of rice hills. They have been observed to hunt for nymphs of planthoppers and leafhoppers, Collembola, and small dipterans, such as whorl maggot flies (Barrion and Litsinger 1984, Shepard et al. 1987, Sigsgaard and Villareal 1999a).

Later in the cropping season predatory bugs become the most numerous predators. The most abundant of these are *Microvelia douglasi atrolineata* Bergoth (Veliidae), *Mesovelia vittigera* (Horvath) (Mesoveliidae), and *Cyrtorhinus lividipennis* Reuter (Miridae) (Heong et al. 1991).

PEST MANAGEMENT IN RICE

Until the green revolution BPH was considered a minor pest, but during the seventies it became a major pest in rice. This demonstrated the effects of 'turning off' the biological control of this pest, which is normally controlled at low levels by the many spiders and other natural enemies (Matteson 2000). Kenmore et al. (1984) showed that BPH populations increased drastically when spider and veliid predators were removed. When insecticide use was intensified, insecticide resistant strains of insect pests emerged. Rice varieties resistant to some pests including BPH were developed, but planting over large areas created pests, most notably BPH, which could overcome the plant resistance (Heinrichs & Mochida, 1984). Subsequently new pest management strategies, Integrated Pest Management (IPM) were developed that emphasized host plant resistance, biological control and minimal use of insecticides (Waage 1999).

An increasing amount of research evidence from tropical irrigated rice areas shows that there is little or no crop loss in insecticide untreated fields (Kenmore 1991; Litsinger 1991; Way & Heong 1994). This includes defoliators and stem borers that were recorded as important pests even before the green revolution. This inconsistency may be explained by: a) earlier estimates of yield loss were based more on damage than on actual yield, b) moderate resistance against insect pests in many modern varieties, c) the ability of some modern varieties to compensate for damage, because they produce more tillers (Rubia et al. 1989), and d) better control of insect pests by natural enemies with less use of insecticides (Way & Heong 1994).

Findings that moderately BPH-resistant and BPH-susceptible rices grown by a large number of farmers have had low and stable BPH populations for several years suggest that the pest control strategy in rice should be revised to put higher priority on natural biological control (Heong & Schoenly 1998).

Apart from the fact that insecticide use is rarely necessary, it also poses a risk to farmer health and the environment (Heong et al. 1995). Continued insecticide use stresses the need to bridge the gap between research and farmers. FAO (Food and Agriculture Organization of the United Nations) has supported Farmers' Field Schools in many countries and provided farmers with a practical understanding of integrated pest and nutrient management (Matteson 2000). The expectation is that the farmers who receive training will pass their new knowledge on to other farmers. Another approach was developed by Heong et al. (1998). Here farmers were motivated to 'test' a simple rule of thumb (no spray necessary in the first 40 days after sowing) by the use of communication media, including the radio. The practice of no early spray is now adopted by many farmers in southern Vietnam, and recommended by the National Agricultural Research and Extension Agencies in Malaysia, the Philippines, and Thailand (K.L. Heong, pers. comm.).

SPIDERS AND THEIR ROLE IN THE IRRIGATED RICE AGROECOSYSTEM

Detritivores and organic material

The population build-up of natural enemies is dependent on the availability of suitable host/prey. The abundant detritivores early in the season may be one key to the success of the current rice agroecosystem (Settle et al. 1996). Being polyphagous predators, spiders can prey on alternative prey such as Collembola during fallow periods, hereby maintaining high population levels. (I here use the term alternative prey to describe all suitable prey other than the target species). The levels of these alternative prey in turn depend on decaying organic material available in the field. Field and laboratory data from research at the International Rice Research Institute in the Philippines (IRRI) and elsewhere indicate that spiders survive and build up their populations on alternative prey, such as Collembola and dipterans, before the crop is established and in the first weeks after crop establishment (Guo et al. 1995; Settle et al. 1996).

Settle et al. (1996) were able to increase the number of detritus feeders, such as collembola, and of plankton feeders by adding organic material to the rice field in the treated plots. Most interestingly the number of spiders increased in the same plots. Plankton feeders in that study included mosquito larvae and chironomid midge larvae, of which many species also feed on detritus (Settle et al. 1996). In a study at IRRI, the addition of rice straw bundles in the rice field after harvest increased the number of *A. formosana* and *P. pseudoannulata* as well as plant- and leafhoppers (Shepard et al. 1989). Though the study by Shepard et al. (1989) did not report effects on Collembola density, high Collembola density can be observed in recently cut straw, so probably the beneficial effect was also due to an increase in Collembola. In upland, rice weed residues placed within the rice fields can significantly increase spider densities (Afun et al. 1999). Apart from providing refuges for predators and increasing the density of alternative prey, organic material will also influence plant nutrition, which in turn can influence herbivores feeding on the crop. One can speculate that this in turn could indirectly affect predators.

Dietary value of insect pests and alternative prey

Spiders may not be as polyphagous as earlier thought (Toft 1999). The dietary value of alternative prey would determine its role in maintaining a high population of spiders early in the cropping season. The dietary value of alternative prey in terms of immature survival and development and adult fecundity can be high, as found in a recent study at IRRI (Sigsgaard et al., 2001a). In contrast BPH and GLH are of low quality to *A. formosana*. Similar results were obtained for *P. pseudoannulata* with fecundity as a fitness parameter, but BPH was of intermediate to high quality for this predator (Sigsgaard et al. 2001b). Earlier, Toft (see for example Toft 1995, 1996, 1999), found aphids to be a generally poor quality prey for linyphiid and lycosid spiders. These findings extend this to other Homopterans, like the BPH and GLH. Results suggest that spiders would perform less well in an agroecosystem with little alternative prey.

Intraguild predation has been documented by Heong et al. (1990), in cage experiments with *P. pseudoannulata* preying upon BPH and the mirid bug *C. lividipennis*, and by Fagan et al. (1998), with *P. pseudoannulata* preying upon hoppers and mesoveliid bugs. Predator prey-switching, intraguild predation and cannibalism are thought to help predator survival when prey is scarce (Way & Heong 1994).

Bunds and surrounding habitats

Between the irrigated rice fields there are usually bunds, which may be narrow and low and reconstructed often with low and poor vegetation, or which may be wider and higher and with more permanent vegetation. Some bunds are used for growing vegetables or fruits. The bunds surrounding the rice fields provide refugia for predators during fallow periods as well as during farm operations. Bunds may be particularly important as a source of colonization by ground dispersing predators, such as large *P. pseudoannulata* spiderlings and adults, and may be less important for linyphiids as *A. formosana*, which colonizes the rice field by ballooning. Preliminary results from a study of the directional movement of predators between the rice field and the bund show that *P. pseudoannulata* is an early colonizer of newly established rice, with the highest relative abundance of *P. pseudoannulata* in the bund, stressing the importance of this habitat (Sigsgaard et al. 1999). The same study showed that three or four weeks after transplanting of rice the directional movement changed and the early planted field may have become a source of *P. pseudoannulata* to later planted fields. Even within the soil cracks of the fallow rice field some spiders like *P. pseudoannulata* are commonly found (Arida and Heong 1994). The management of bunds can also affect spiders. Grazing of bunds reduced the density of web-building spiders as well as of two hunting spider families, Lycosidae and Oxyopidae, probably due to loss of webbing sites for the web-building spiders and hunting grounds for the hunting spiders (Barrion 1999). Rice fields are usually intermingled with other crops and habitats such as coconut or banana, and houses, gardens, fallow fields and forests, creating a varied landscape mosaic. Rice is often grown in rotation with vegetables such as onions, or with legumes.

Surrounding habitats may also serve as a source of spiders for the rice field. Barrion (1999) found, that the most abundant species in some non-rice habitats (irrigation canal, set-aside rice field, edge of bund, a common road-side habitat (the grass *Saccharum spontaneum* L.), coconut, banana, and coconut-banana mixed) were *Theridion* sp. (family Theridiidae), *P. pseudoannulata* and *A. formosana*. Two key spider species in rice, *A. formosana* and *P. pseudoannulata* are thus utilizing non-rice habitats. Of these habitats the bunds held the highest densities of *A. formosana* followed by the uncropped rice field, while *P. pseudoannulata* was almost equally abundant in all habitats except relatively low densities in the roadside habitat and banana plantation.

THE RICE CROPPING SYSTEM IS FACING NEW CHANGES

Resource conserving strategies such as the use of compost and the integration of fish and duck production with irrigated rice, practices that contribute to the control of weeds and insect pests (Zhang 1992), are now being actively promoted in some countries such as Malaysia (Ibrahim 1999). These practices decreased substantially with the introduction of pesticides and other partially or fully incompatible technologies.

Today, the irrigated rice cropping system is facing changes, which may have equally strong effects on the characteristics of the system as the green revolution had, and may in turn affect the natural biological control of insect pests in rice. With the rapid growth of cities there is less available water and labour for rice farming. It is foreseen that production will change towards more direct seeding and less transplanting, and towards other potentially water and labour saving methods, such as mechanization, larger fields and more synchronous cropping (IRRI 2000). In peninsular Malaysia direct seeding has now become the predominant method of crop establishment (Normiyah & Chang 1997). Larger fields and more synchronous planting may delay colonization by predators, also reducing the benefit gained from the abundant early season alternative prey. A delay in colonization by predators in large monocultures of rice has been shown by Settle et al. (1996) in Indonesia. Continuous flooding has been found to be associated with higher spider numbers (Lam et al. 1997), suggesting a possible lower density of spiders with less available water. The growth of areas under directly-seeded rice, as well as the increasing cost of hand weeding, causes the use of herbicides to rise. Genetically modified rice may also affect the cropping system in ways not yet fully anticipated. For example, we do not know the consequences of creating a field with no lepidopterans, as may be the case in rice genetically modified to contain the *Bacillus thuringiensis* toxin.

Understanding of the biology of insect pests, their natural enemies and the factors in the management of the cropping system, which may affect this control, can be an important tool in maintaining the desirable traits of the current irrigated rice ecosystem, as the rice cropping system changes.

ACKNOWLEDGEMENTS

Thanks to K.L. Heong, K.G. Schoenly, A. Barrion, S. Toft and M. Cohen for valuable discussions. Thanks to K.L. Heong, S. Toft and two anonymous referees for commenting on an earlier draft of this paper.

REFERENCES

Afun, J.V.K., Johnson, D.E., & Russell-Smith, A. 1999. The effects of weed residue management on pests, pest damage, predators and crop yield in upland rice in Cote d'Ivoire. *Biological Agriculture & Horticulture* 17 (1), 47-58.

Arida, G.S. & Heong, K.L. 1994. Sampling spiders during the rice fallow period. *International Rice Research Notes* 19 (1), 20.

Barrion, A. & Litsinger, J. 1984. The spider fauna of Philippine rice agroecosystems. II. Wetland. *Philippine Entomologist* 6, 11-37.

Barrion, A. & Litsinger, J. 1995. *Riceland spiders of South and Southeast Asia*. CAB International/International Rice Research Institute. University Press, Cambridge.

Barrion, A. 1999. Ecology of spiders in selected non-rice habitats and irrigated rice fields in two southern Tagalog provinces in the Philippines. Ph.D. Thesis. University of the Philippines at Los Banos.

Fagan, W.F., Hakim, A.L., Ariawan, H. & Yuliyantiningsih, S. 1998. Interactions between biological control efforts and insecticide applications in tropical rice agroecosystems: the potential role of intraguild predation. *Biological Control* 13 (2), 121-126.

Gavarra M. & Raros R.S., 1975. Studies on the biology of the predatory wolf spider, *Lycosa pseudoannulata* Boesenberg & Strand. *Philippine Entomologist*, 2 (6), 427-444.

Guo, Y.J., Wang, N.Y., Jiang, J.W., Chen, J.W. & Tang, J. 1995. Ecological significance of neutral insects as a nutrient bridge for predators in irrigated rice arthropod communities. *Chinese Journal of Biological Control* 11, 5-9.

Heinrichs, E.A. & Mochida, O. 1984. From secondary to major pest status: the case of the insecticide induced rice brown planthopper, *Nilaparvata lugens*, resurgence. *Protection Ecology* 7, 201-218.

Heong, K., Bleih, S. & Rubia, E. 1990. Prey preference of the wolf spider, *Pardosa pseudoannulata* (Boesenberg et Strand). *Researches on Population Ecology* 32, 179-186.

Heong, K.L., Aquino, G.B. & Barrion, A.T. 1991. Arthropod Community Structures of Rice Ecosystems in the Philippines. *Bulletin of Entomological Research* 81 (4), 407-416.

Heong, K., Aquino, G. & Barrion, A. 1992. Population dynamics of plant- and leafhoppers and their natural enemies in rice ecosystems in the Philippines. *Crop Protection* 4, 371-379.

Heong, K.L., Escalada, M.M. & Lazaro, A.A. 1995. Misuse of pesticides among rice farmers in Leyte, Philippines. In: *Impact of pesticides and farmer health and the rice environment* (P.L. Pingali & P.A. Roger eds.), pp. 97-108. IRRI, Los Banos, Laguna.

Heong, K.L., Escalada, M.M., Huanh, N.H. & Mai, V. 1998. Use of communication media in changing rice farmers' pest management in the Mekong Delta, Vietnam. *Crop Protection* 17 (5), 413-425.

Heong, K.L. & Schoenly, K.G. 1998. Impact of insecticides on herbivore-natural enemy communities in tropical rice ecosystems. In: *Ecotoxicology: pesticides and beneficial organisms*, (P.T. Haskell & P.McEwen eds.), pp. 381-403. Kluwer, Dordrecht, Netherlands.

Ibrahim, R. 1999. Malaysia. *Far East Agriculture* May/June 1999, 16-17.

Inthavong, S., Inthavong, K., Sengsaulivong, V., Schiller, J.M., Rapusas, H.R., Barrion, A. T. & Heong, K.L. 1996. Arthropod biodiversity in Lao irrigated rice ecosystem. In: *Proceedings of the Rice Integrated Pest Management (IPM) Conference: Integrating science and people in Rice Pest Management*, 18-21 November 1996, Kuala Lumpur, Malaysia (A. A. Hamid et al., eds.), pp. 69-85. Malaysian Agricultural Research and Development Institute, Kuala Lumpur, Malaysia.

IRRI, 2000. *IRRI Annual Report 1999-2000. The Rewards of Rice Research*. International Rice Research Institute, Los Banos, Philippines.

Kenmore, P.E. 1980. Ecology and outbreaks of a tropical insect pest of the green revolution, the rice brown planthopper, *Nilaparvata lugens* (Stål), PhD dissertation. University of California, Berkeley, USA.

Kenmore, P.E., Carino, F., Perez, C., Dyck, V. & Gutierrez, A. 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, 1-37.

Kenmore, P.E., 1991. *Indonesia's integrated pest management – a model for Asia*. Food and Agriculture Organisation, Manila, Philippines.

Kiritani, K. & Kakiya N. (1975) An analysis of the predator-prey system in the paddy field. *Research in Population Ecology* 17 (1), 29-38.

Kiritani, K., Kawahara, S., Sasaba, T. & Nakasuji, F. (1972) Quantitative evaluation of predation by spiders on the green leafhopper *Nephotettix cincticeps* Uhler, by sight-count method. *Research in Population Ecology* 13, 187-200.

Lam, P.V., Huong, T.H. & Lan, T.T. 1997. A study on spider fauna of rice fields. *Nong Nghiep Cong Ngiep Thuc Pham* 3, 107-109.

Litsinger, J.A. 1991. Crop loss assessment in rice. In: *Rice insects: management strategies* (E. A. Heinrichs & T.A. Miller eds.), pp. 1-65. Springer Verlag, New York.

Matteson, P.C. 2000. Insect pest management in tropical Asian irrigated rice. *Annual Review of Entomology* 45, 549–574.

Normiyah, R. & Chang, P.M. 1997. Pest management practices of rice farmers in the Muda and Kemubu irrigation schemes in peninsular Malaysia. In: *Pest management of rice farmers in Asia*, (K.L. Heong & M.M. Escalada eds.), pp. 115-127. IRRI, Los Banos, Philippines.

Ooi, P.A.C. & Shepard, B.M. 1994. Predators and parasitoids of rice insect pests. In: *Biology and management of rice insects*, (E.A. Heinrichs ed.), pp. 585-612. Wiley Eastern Limited [For] IRRI, New Delhi.

Pathak, M.D. & Kahn, Z.R. 1994. *Insect pests of rice.* International Rice Research Institute, Manila, Philippines.

Reddy, P.S. & Heong, K.L. 1991. Co-variation between insects in a ricefield and important spider species. *International Rice Research Notes* 16 (5), 24.

Rubia, E.G., Shepard, B.M., Yamba, E.B., Ingram, K.T., Arida, G.S., Penning de Vries, F. 1989. Stem borer damage and grain yield of flooded rice. *Journal of Plant Protection in the Tropics* 6, 205-211.

Rubia, E., Almazan, L., & Heong, K. 1990. Predation of yellow stem borer (YSB) by wolf spider. *International Rice Research Newsletter* 15, 22.

Sahu, S., Singh, R. & Kumar, P. 1996. Host preference and feeding potential of spiders predaceous in insect pests of rice. *Journal of Entomological Research* 20 (2), 145-150.

Schoenly, K.G., Justo, H.D., Barrion, A.T., Harris, M. & Bottrell, D.G. 1998. Analysis of invertebrate biodiversity in a Philippine farmer's irrigated rice field. *Environmental Entomology* 27 (5): 1125-1136.

Settle, W.H., Ariawan, H., Astuti, E., Cahyana, W., Hakim, A.L., Hindayana, D., Lestari, A. S. & Pajarningsih 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology* 77 (7), 1975-1988.

Shepard, B.M., Barrion, A.T., & Litsinger, J.A. 1987. *Friends of the rice farmer. Helpful insects, spiders and pathogens*. International Rice Research Institute, Manila, Philippines.

Shepard, B.M., Rapusas, H.R., & Estano, D.B. 1989. Using rice straw bundles to conserve beneficial arthropod communities in the ricefield. *International Rice Research Notes* 14, 30-31.

Sigsgaard, L. & Villareal, S. 1999. Predation rates of *Atypena formosana* (Araneae: Linyphiidae) on brown planthopper, and green leafhopper. *International Rice Research Notes* 24 (3), 18.

Sigsgaard, L., Villareal, S., Gapud, V., & Rajotte, E. 1999. Directional movement of predators between the irrigated rice field and its surroundings. In *Biological control in the Tropics. Towards efficient biodiversity and bioresource management for effective biological control. Proceedings of the Symposium on Biological Control in the Tropics* (L.W. Hong, S.S. Sastroutomo, I.G. Caunter, J. Ali, L.K. Yeang, S. Vijaysegaran & Y.H. Sen eds.), pp. 43-47. The National Council for Biological Control (NCBC)/CAB International, South East Asian Regional Centre, Malaysia.

Sigsgaard, L., Toft, S. & Villareal, S. 2001a. Diet-dependent survival, development and fecundity of the spider *Atypena formosana* (Oi) (Araneae: Linyphiidae) – Implications for biological control in rice. *Biocontrol Science and Technology* 11, 233-244.

Sigsgaard, L., Toft, S. & Villareal, S. 2001b. Diet-dependent fecundity of the spiders *Atypena formosana* and *Pardosa pseudoannulata*, predators in irrigated rice. *Agricultural and Forest Entomology* 3, 285-295.

Toft, S. 1995. Value of the aphid *Rhopalosiphum padi* as food for cereal spiders. *Journal of Applied Ecology* 32, 552-560.

Toft, S. 1996. Indicators of prey quality for arthropod predators. In: *Arthropod natural enemies in arable land. II. Survival, reproduction and enhancement* (C.J.H. Booij & L.J.M.F. den Nijs eds.), pp. 107-116. Aarhus University Press, Aarhus.

Toft, S. 1999. Prey choice and spider fitness. *Journal of Arachnology* 27, 301-307.

Waage, J. 1999. Beyond the realm of conventional biological control: harnessing bioresources and developing biologically-based technologies for sustainable pest management. In: *Biological control in the Tropics. Towards efficient biodiversity and bioresource management for effective biological control. Proceedings of the Symposium on Biological Control in the Tropics* (L.W. Hong, S.S. Sastroutomo, I.G. Caunter, J. Ali, L.K. Yeang, S. Vijaysegaran & Y.H. Sen eds.), pp. 5-17. The National Council for Biological Control (NCBC)/CAB International, South East Asian Regional Centre, Malaysia.

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.

Zhang, Z.Q. 1992. The Use of Beneficial Birds for Biological Pest Control in China. *Biocontrol News and Information* 13 (1): 11-16.