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POPULATION DYNAMICS AND GROWTH PATTERN OF THE BROWN PLANTHOPPER, *Nilaparvata lugens* (Stål) AND ITS NATURAL ENEMIES IN SUSCEPTIBLE AND RESISTANT TROPICAL RICE VARIETIES IN CENTRAL THAILAND

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ABSTRACT

The brown planthopper (BPH), *Nilaparvata lugens* (Stål), is an important rice insect pest in tropical Asia. This study examined the population dynamics of BPH and its natural enemies in Central Thailand over two cropping seasons in 2015 in rice fields planted with susceptible and resistant varieties to BPH. Our results showed three implications in the behavior of populations of BPH and its natural enemies under non-outbreak conditions: 1. No consistent differences were found in the growth pattern of BPH between rice fields planted with resistant and susceptible rice varieties. 2. Typical seasonal growth pattern of BPH tropical populations, characterized by early density peaks and high initial density was only found in fields planted with susceptible rice in Nakhon Nayok Province in the wet season. 3. The natural enemies *Pardosa pseudoannulata* (Bösenberg & Strand), the wolf spider (WS) and *Cyrtorhynus lividipennis* (Reuter), the mirid bug (MB) responded differently to changes in the density of BPH among rice fields and crop seasons. This study suggests that pest low-density conditions and the crop seasons have an effect on the population dynamics of BPH and its natural enemies and therefore, on the pest natural control by predators and the level of pest suppression in fields planted with BPH-resistant varieties.

Key words: community, insect predators, pest, population density, rice cultivars,

INTRODUCTION

The brown planthopper (BPH), *Nilaparvata lugens* (Stål) is one of the most important rice insect pests in temperate, tropical and sub-tropical regions of Asia (Bottrell and Schoenly 2012, Cook and Perfect 1989, Kuno and Dyck 1985). The development of BPH is incomplete, with life stages from egg to nymph and to dimorphic adults; brachypterous (short-winged) and macropterous (long-winged) (Denno and Roderick 1990). Population growth characteristics of BPH are different in temperate and tropical regions. In temperate areas, the pest growth is abrupt and stable in time. Thus, it is possible to predict potential outbreaks by monitoring density of BPH long-winged adults that migrate into rice fields (Cheng and Holt 1990, Kisimoto 1981). Immigration of BPH in the tropics, is continuous over the crop period and is believed to be basically controlled by natural enemies (Cook and Perfect 1989, Kenmore et al. 1984). Outbreaks of BPH in tropical rice fields have been mainly attributed to the misuses of pesticides that disturbs the natural control of the pest by killing predators and parasitoids (Heinrichs and Mochida 1984), including those related with the spraying of higher concentrations of harmful pesticides than the legally allowed by the authorities and the use of pesticide cocktails (Arunmit et al. 2012). Abiotic factors such as temperature and rainfall also influence fluctuations of BPH populations (Win et al. 2011) and in-field factors such as rice varietal use and planting methods have been also associated with BPH outbreaks (Cook and Perfect 1989, Magunmder et al. 2013, Tetarwal et al. 2014, Wada and Salleh 1992, Win et al. 2011, Zhu et al. 2004).

Breeding resistant rice varieties to BPH and to other insect pests has been one of the most effective and environmentally friendly approaches for insect pest management in rice crops (Alagar et al. 2007, Brar et al. 2009, Jena et al. 2006). Resistant rice can cause reductions in the pest density by about 100-fold, saving rice farmers the need to use pesticides and its economic cost (Aquino and Heinrichs 1979, Brar et al. 2009, Kenmore et al. 1984). Among the benefits of BPH-resistant rice varieties, lower nymph development, less fecundity of the pest and reduced population build-up have been demonstrated (Alagar et al. 2007, Cohen et al. 1997, Saxena and Pathak 1979). The main mechanisms of resistance are known to come from the manipulation of BPH resistance genes that involve changing the plant phloem chemistry and the loss of important feeding components for the insect pest that affect its behavior and physiology and in some cases producing insecticidal Bt-toxins (Bottrell and Schoenly 2012, Cook and Denno 1994, Fisk 1980, Sogawa 1982, Sogawa 2015, Lundgren et al. 2009). Twenty-one genes for BPH-resistance have been identified from genetic resources such as wild species of *Oryza* and landrace cultivars (Jena and Kim 2010).

Parallel to the benefits for crop pest management, concerns about the advantages of host pest-resistance and its possible risks have been also claimed, especially possible adverse effects of pest-resistant cultivars on the community of natural enemies and the emergence of new BPH biotypes, which are BPH populations that have adapted to a particular resistant rice variety (Bottrell et al. 1998, Jena and Kim 2010, Lundgren et al. 2009, Poppy 2000, Poppy and Sutherland 2004, Wolfenbarger and Phifer 2000). In order to visualize the benefits of pest-resistant rice plants as an alternative for crop protection, risk assessment of potential changes on ecosystem services like the natural pest control provided by natural enemies, needs to be evaluated especially in rice cropping systems, where pest resistant rice is used as the only pest management strategy (Lundgren et al. 2009). Until now, this kind of assessment has been mainly focused on the toxicity of insecticidal chemicals produced by the pest-resistant rice host (Jumin et al. 2000, Li et al. 2007, Lee et al. 2014). However, the pest and its natural enemies interact with the resistant host-plant in ways that are not assessed under the toxicological approach, and an assessment under a community-based approach, is also required (Lundgren et al. 2009).

A community-based assessment of pest-resistant crops is necessary to be conducted under field conditions and involves monitoring the density of the pest population and the populations of natural enemies in fields planted with the pest-resistant and fields planted with non-resistant plants. Although this type of studies are difficult to conduct since they require numerous field sites and years of study, they have relevance for the assessment of some ecological impact of pest-resistant crops (Lundgren et al. 2009, Bernal et al. 2002).

Thailand is an important world rice exporter and outbreaks of BPH seriously affected rice production in the central plain and lower northern regions of the country from 2009 to 2012 (Chaiyawat 2011, Heong and Hardy 2009, Luecha 2010, Rattanakarn et al. 2012, Soitong et al. 2011, Sriratanasak et al. 2011, Thongdeethae 2009, Wattanesk 2010). Previous research on BPH in Central Thailand has been mainly focused on studying the mechanisms for the development of BPH-resistance to pesticides and to BPH-resistant rice cultivars (Arunmit et al. 2012, Chaiwong et al. 2010, Pongprasert and Weerapat 1979, Punyawattoe et al. 2013, Sriratanasak et al. 1996). Meanwhile, studies about the population dynamics of BPH in Central Thailand have been conducted only in resistant rice varieties (den Braber and Meenakanit 1992).

Therefore, this study examined under a community-based approach, the population dynamics and growth pattern of BPH and its natural enemies in two important provinces of rice production in Central Thailand over two cropping seasons in farmers' fields, non-sprayed with insecticide and planted with different BPH-resistant and susceptible rice varieties. This study aimed to contribute to the clarification of the knowledge about the population dynamics of BPH and its natural enemies in tropical rice agroecosystems and to provide insights about the potential ecological impact of BPH-resistant rice varieties for farmers and its implications for the local management of BPH.

MATERIALS AND METHODS

Area of study and climate

Population surveys of BPH and its natural enemies were conducted at rice fields in Chai Nat and Nakhon Nayok Provinces in the Central Thailand (Fig. 1) during the dry and wet seasons in 2015.

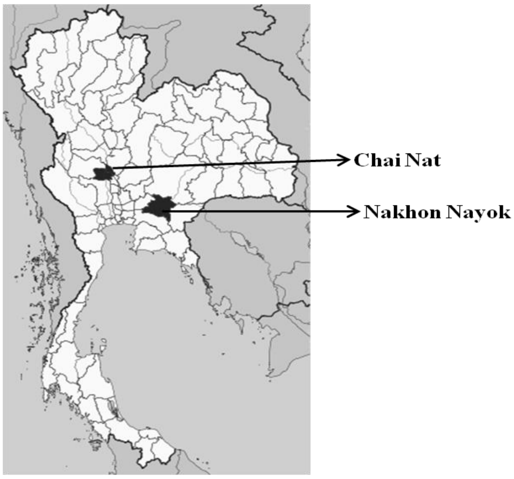

Fig. 1. Location of Chai Nat and Nakhon Nayok Provinces in Central Thailand - the survey area for rice fields sampling.

Climate of the central region of Thailand shows characteristics of Köppen's tropical savanna climate with clear dry and wet seasons. There is prevalence of the dry conditions from November until April of the next year and the rainy season occurs from May to October (Ginigaddara and Ranamukhaarachchi 2009). In 2015, the Central Thailand was warmer than an average year (average of 29 years; 1981-2010) (Thai Metereological Department 2015). Annual mean temperature in the Central Thailand was 28°C, 0.8 °C above average (Fig. 2). The central region of Thailand was also drier in 2015; the annual 2015 rainfall was 1202 mm, 73 mm less than the average value (1275 mm) during the same period as shown above (Fig. 2).

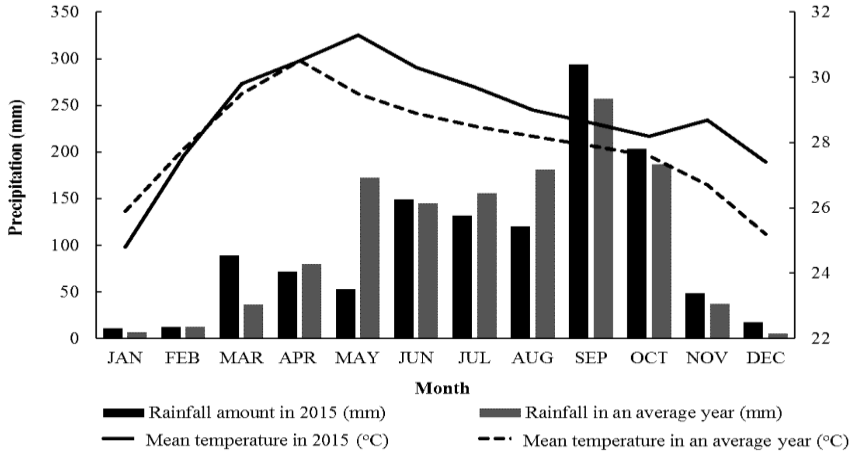

Fig. 2. Monthly average temperature and rainfall in Central Thailand in 2015 and in an average year. Source: TMD 2016.

Rice cultivation in central Thailand

The central region of Thailand is the most intensively rice cultivated alluvial area in the country. During the rainy season, rice production in Central Thailand represents about 20 percent of the whole rice cultivated area in the country (AEO 2011, IRRI 2016). The system of production is highly mechanized, irrigation is common and the direct-seeded method of cropping is the most common among farmers. Several high yielding rice varieties adapted for the irrigated environment with insect pest resistance have been released in the region, being Chai Nat 1, RD 47 and Pisanulok 2 among some of them (Kupkanchanakul 2000). Details of varietal use, planting methods and transplanting/seeding dates at the sampled fields in this study are shown in Table 1.

Chai Nat and Nakhon Nayok Provinces are considered as two of the most intensive rice producing provinces in the country (AEO 2011). In Chai Nat the current planted rice area ranges from 120,000 to 150,000 ha. In Nakhon Nayok about 60,000 ha of rice fields have been planted during the last six years (AEO 2011). Fallow periods are longer in Nakhon Nayok than in Chai Nat and the main rain-fed rice variety grown in Nakhon Nayok is Thai Jasmine Rice 105 (Table 1).

Fig. 3 shows the details about rice cropping calendar in the two provinces of the study. Rice growing at Chai Nat Province is mainly irrigated, following the cropping system "rice-rice-rice" or “rice-rice” with no alternating crops. Rice is grown once or twice in the dry season and once in the wet season (AEO 2011). In Chai Nat, the first rice crop in the dry season starts from November up to mid March of the next year, the second dry season crop from mid-March to mid-June and the wet season crop from mid-June up to October. When the cropping system “rice-rice” is taken, the wet season crop will happen as described before but the schedule for the dry season crop will mostly depend on the availability of irrigation resources for each rice farmer. At the studied fields in Chai Nat, the wet season crop planting was practiced in June and harvested in September, while the dry season crop planting was from December to late February and harvesting from early March to April (Table 1).

Rice growing in Nakhon Nayok Province is rain-fed or irrigated. In Nakhon Nayok the cropping pattern generally follows the "rice-rice" system with no alternating crop. There are two main rice growing seasons, one in the dry season from November to the end of February and a wet season crop from May until the end of October. At the studied fields in Nakhon Nayok planting during the wet season was practiced from June until the end of August; harvest was done from September until late October.

Table 1. Crop season, varietal use, planting method, duration of the crop and planting/seeding date of the sampled rice fields at Chai Nat and Nakhon Nayok Provinces in Central Thailand

Field No.	Province	Season	Resistance to BPH	Variety	Planting method	Crop duration (DAT/S)*	Planting/seeding date
1	Chainat	Dry	Resistant	Pisanulok 2	Transplanting	72	19/01/2015
2	Chainat	Dry	Resistant	RD41	Transplanting	66	12/01/2015
3	Chainat	Dry	Resistant	RD41	Transplanting	60	16/02/2015
4	Chainat	Dry	Resistant	RD57	Direct seeding	50	26/02/2015
5	Chainat	Dry	Resistant	RD49	Direct seeding	69	26/12/2015
6	Chainat	Dry	Resistant	Pisanulok 2	Direct seeding	58	06/01/2015
7	Chainat	Dry	Resistant	Pisanulok 2	Direct seeding	58	06/01/2015
8	Chainat	Dry	Resistant	RD57	Direct seeding	66	10/02/2015
9	Chainat	Dry	Susceptible	RD31	Transplanting	66	25/01/2015
10	Chainat	Dry	Susceptible	Chainat 1	Transplanting	69	16/01/2015
11	Chainat	Dry	Susceptible	RD31	Transplanting	52	18/01/2015
12	Chainat	Dry	Susceptible	Pathumtani1	Transplanting	67	18/01/2015
13	Chainat	Dry	Susceptible	Pathumtani1	Direct seeding	63	19/02/2015
14	Chainat	Dry	Susceptible	Pathumtani1	Direct seeding	63	19/02/2015
15	Chainat	Dry	Susceptible	Pathumtani1	Direct seeding	81	27/12/2015
16	Chainat	Dry	Susceptible	Pathumtani1	Direct seeding	62	20/02/2015
17	Chainat	Dry	Susceptible	Pathumtani1	Direct seeding	63	19/02/2015
18	Chainat	Wet	Resistant	RD41	Transplanting	75	19/06/2015
19	Chainat	Wet	Resistant	RD41	Direct seeding	69	25/06/2015
20	Chainat	Wet	Resistant	RD41	Direct seeding	74	20/06/2015
21	Chainat	Wet	Resistant	RD47	Direct seeding	75	20/06/2015
22	Chainat	Wet	Resistant	RD49	Transplanting	71	23/06/2015
23	Chainat	Wet	Susceptible	RD31	Direct seeding	77	17/06/2015
24	Chainat	Wet	Susceptible	RD31	Direct seeding	77	17/06/2015
25	Chainat	Wet	Susceptible	RD31	Direct seeding	80	14/06/2015
26	Chainat	Wet	Susceptible	RD31	Direct seeding	77	17/06/2015
27	Chainat	Wet	Susceptible	RD31	Direct seeding	72	23/06/2015
28	Nakhon Nayok	Wet	Susceptible	Thai jasmine rice 105	Direct seeding	87	22/07/2015
29	Nakhon Nayok	Wet	Susceptible	Thai jasmine rice 105	Direct seeding	82	22/07/2015
30	Nakhon Nayok	Wet	Susceptible	Thai jasmine rice 105	Transplanting	87	22/07/2015
31	Nakhon Nayok	Wet	Susceptible	Thai jasmine rice 105	Direct seeding	87	22/07/2015
32	Nakhon Nayok	Wet	Susceptible	Thai jasmine rice 105	Direct seeding	93	04/08/2015
33	Nakhon Nayok	Wet	Susceptible	Thai jasmine rice 105	Direct seeding	93	04/08/2015
34	Nakhon Nayok	Wet	Resistant	RD47	Direct seeding	90	28/06/2015
35	Nakhon Nayok	Wet	Resistant	RD47	Direct seeding	77	20/06/2015
36	Nakhon Nayok	Wet	Resistant	RD47	Direct seeding	88	23/06/2015
37	Nakhon Nayok	Wet	Resistant	RD47	Direct seeding	85	26/06/2015
38	Nakhon Nayok	Wet	Resistant	RD47	Direct seeding	93	26/06/2015

*Duration in days of the crop season after transplanting or seeding in the rice field until harvest; Days after transplanting/seeding (DAT/S)

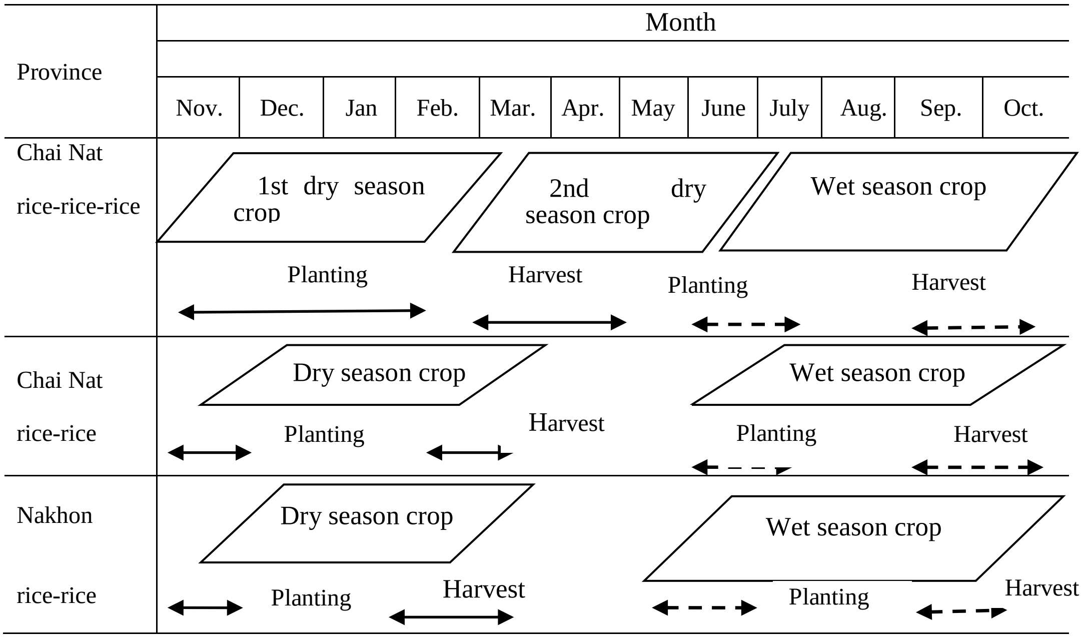

Fig. 3. Rice cropping calendar at Chai Nat and Nakhon Nayok.

Rice samples

Sampling was carried out in a total of 38 paddy fields during the late dry season (March-May) and wet season (July-September) of 2015. During the dry season, eight fields from resistant rice varieties and nine fields from susceptible rice varieties to BPH were sampled in Chai Nat Province (Table 1) every seven days. In the wet season, five fields from resistant rice varieties and five fields from susceptible varieties to BPH were sampled in Chai Nat every fourteen days. In Nakhon Nayok, five fields from resistant rice varieties and six fields from susceptible varieties to BPH were sampled during the wet season every seven days (Table 1). It was not possible to collect data during the dry season of 2015 in Nakhon Nayok due to limited irrigation resources available for rice farmers in the region and thus, significantly reduced amount of available rice fields to conduct sampling.

Densities of BPH including adults and nymphs and its major natural enemies, were assessed by carrying out sampling in the rice fields from about 13 to 20 days after transplanting/seeding (DAT/S) until harvest (70-90 DAT/S). Susceptible rice fields during the dry season in Chai Nat were sampled earlier after transplanting than in other fields since the presence of BPH was detected at 13 DAT/S. Visual counting from two transects of 10 rice hills in a diagonal way per rice field was conducted on each sampling date. A hill was considered to be the sampling unit. Sweep netting was also carried out in order to collect samples of long-winged BPH macropterous (migrants) adults following the same sampling protocol as mentioned above. Immigration was assessed counting the densities of winged adults present in the rice field up to 45 DAT/S.

Data collected were used to calculate mean densities of BPH (per hill) as well as densities of the major species of BPH natural enemies in Central Thailand (Chaiwong et al. 2010); *Cyrtorhynus lividipennis*, the mirid bug (hereinafter, MB) and *Pardosa pseudoannulatta*, the wolf spider (hereinafter, WS) (Chaiwong et al. 2010). It is important to mention that this study was conducted under two special conditions:

1. Outbreaks of BPH were not reported in Central Thailand in 2014 and 2015 (Rice Department 2015) and sampling occurred under non-outbreak conditions of BPH.

2. Farmers did not spray any pesticides at the sampled rice fields in the two provinces of the study, mainly due to the lack of economical resources that in a normal situation allow them to invest in chemical control and protect the rice harvest (Chaiwong et al. 2012). At present, rice farmers over Thailand face increasing balance due (Pingali 1993, Slayton and Timmer 2008, Sricharoen 2015) and decisions of rice crop management by farmers depend on the profits they get from the crop. If the price of rice is low, farmers try to reduce costs and they stop insecticide spraying (Matteson 2000, Pingali 1993, Sricharoen 2015).

Data Analysis

Statistical analysis was performed using the software STATISTICA10 (StatSoft, Inc.). The analysis of variance (ANOVA) was performed to evaluate the effects of three factors, i.e. province, crop season and rice variety. Although three factors are involved, overall ANOVA with three factors was not possible to perform because data for one crop season are missing (Nakhon Nayok, dry season). Thus, we performed ANOVA with two factors (province/season and rice variety). Density peaks of BPH and its growth pattern at each province and season were also compared between BPH-resistant and susceptible rice fields (hereinafter, resistant and susceptible fields) performing Mann-Whitney U-tests. Pearson's correlation analysis was conducted to evaluate the relationship between the mean density of BPH and each of its natural enemies at each study site and season.

RESULTS

Incidence of BPH and its natural enemies, MB and WS in resistant and susceptible rice fields

The analysis of variance with two factors (province/season and rice variety) in the studied rice fields at two Provinces was performed for the density of each one of the life stages of BPH and both natural enemies. As significant or nearly significant interactions between factors were found in most of densities of BPH at different growth stages and natural enemies, data for the average densities of BPH and its natural enemies are shown in Table 2. The average density of BPH and its natural enemies at each season and province were compared at BPH-resistant and susceptible fields as it follows. At fields in Chai Nat during the dry season, the mean density of BPH-long-winged adults and MB were significantly higher at fields with susceptible rice varieties. Densities of BPH nymphs, short-winged adults, and WS were not significantly different between rice varieties (Table 2).

In fields at Chai Nat during the wet season, the mean incidence of BPH nymphs, short-winged adults and long-winged adults as well as the densities of both natural enemies were not significantly different between resistant and susceptible varieties (Table 2). At fields in Nakhon Nayok, the mean density of short-winged adults was significantly higher at susceptible fields. Densities of nymphs, long-winged adults and both natural enemies were not significantly different between resistant and susceptible fields. Although WS did not show significantly different incidence in resistant and susceptible fields, its mean density over the crop season tended to be higher than densities of MB at both study sites and both crop seasons (Table 2).

Correlations between mean densities of BPH and its natural enemies, throughout the crop season in resistant and susceptible fields.

Table 3 shows the correlation between the crop season mean densities of BPH and its natural enemies, MB and WS. Densities of BPH long-winged adults were positively correlated with densities of MB and WS in both resistant and susceptible fields at Chai Nat during the dry season. Densities of BPH nymphs and short-winged adults were not significantly correlated with the occurrence of both species of natural enemies at both resistant and susceptible fields at Chai Nat during the dry season. Furthermore, densities of BPH were not correlated with densities of MB and WS neither in resistant nor in susceptible fields at Chai Nat during the wet season. In resistant rice in Nakhon Nayok during the wet season, densities of BPH nymphs were positively correlated with densities of MB and densities of BPH short-winged adults were negatively correlated with densities of WS (Table 3). Densities of long-winged adults were not correlated with the occurrence of both species of natural enemies. In susceptible fields, densities of BPH nymphs, short-winged adults and long-winged adults were not correlated with densities of both, MB and WS (Table 3).

Table 2. Mean density of BPH and each of its natural enemies in fields planted with resistant and susceptible rice varieties

Site and Season	Variety	Mean density throughout the crop season ((individuals/hill)±SE**)				
		BPH			Natural enemies	
		Nymphs	Short-winged adults*	Long-winged adults*	*C. lividipennis** (MB)	*P. pseudoannulata* (WS)
Chai Nat / Dry Season	Resistant	0.17±0.07	0.04±0.01	0.07±0.02 **A**	0.12±0.04 **A**	0.43±0.22
	Susceptible	0.50±0.24	0.05±0.02	0.25±0.06 **B**	0.43±0.13 **B**	0.47±0.16
Chai Nat / Wet Season	Resistant	0.34±0.08	0.08±0.02	0.30±0.03	0.30±0.14	0.62±0.28
	Susceptible	0.44±0.09	0.07±0.02	0.38±0.11	0.30±0.13	0.51±0.23
Nakhon Nayok / Wet Season	Resistant	0.37±0.06	0.05±0.01 **A**	0.32±0.07	0.21±0.09	0.44±0.19
	Susceptible	0.79±0.24	0.36±0.11 **B**	0.48±0.07	0.23±0.09	0.42±0.17

*Means in a column with different letters are significantly different according Fisher's LSD test ($p < 0.05$).

**Data are reported as the mean ± standard error

Table 3. Correlation matrix between mean densities of BPH and mean densities of its natural enemies in fields planted with resistant and susceptible rice varieties

Site	**Rice Variery**		*C. lividipennis* (MB)	*P. pseudoannulatta* (WS)
Chai Nat / Dry Season	Resistant	BPH - Nymphs	-0.37	-0.23
		BPH - Brachypterous	-0.19	-0.08
		BPH - Macropterous	*0.99	*0.93
	Susceptible	BPH - Nymphs	0.61	0.56
		BPH - Brachypterous	0.11	0.11
		BPH - Macropterous	*0.78	*0.79
Chai Nat / Wet Season	Resistant	BPH - Nymphs	0.36	0.05
		BPH - Brachypterous	0.10	-0.17
		BPH - Macropterous	-0.12	-0.09
	Susceptible	BPH - Nymphs	-0.73	0.46
		BPH - Brachypterous	-0.74	0.48
		BPH - Macropterous	0.78	-0.54
Nakhon Nayok / Wet Season	Resistant	BPH - Nymphs	*0.99	-0.82
		BPH - Brachypterous	0.85	*-0.96
		BPH - Macropterous	0.28	-0.07
	Susceptible	BPH - Nymphs	0.38	-0.42
		BPH - Brachypterous	-0.21	0.33
		BPH - Macropterous	0.49	0.28

*Pearson's correlation analysis significant at $p < 0.05$

Growth pattern of BPH and its natural enemies throughout the crop season in resistant and susceptible fields.

Chai Nat-Dry season: Total BPH population in resistant fields at Chai Nat during the dry season showed lower initial densities followed by higher densities late in the crop season (Fig. 4A). However, the magnitude of total BPH density was low during all the crop period, reaching a peak density of only 0.5 BPH per rice hill at 62 DAT/S. Meanwhile, in susceptible fields, total BPH incidence was higher, with two density peaks of 1 and 1.4 BPH per rice hill at 41 and 70 DAT/S, respectively (Fig. 5A). However, the mean density of total BPH between resistant and susceptible fields was not significant. Contrary to densities in resistant fields, total BPH densities in susceptible fields continued to increase until the end of the crop period (Fig. 5A).

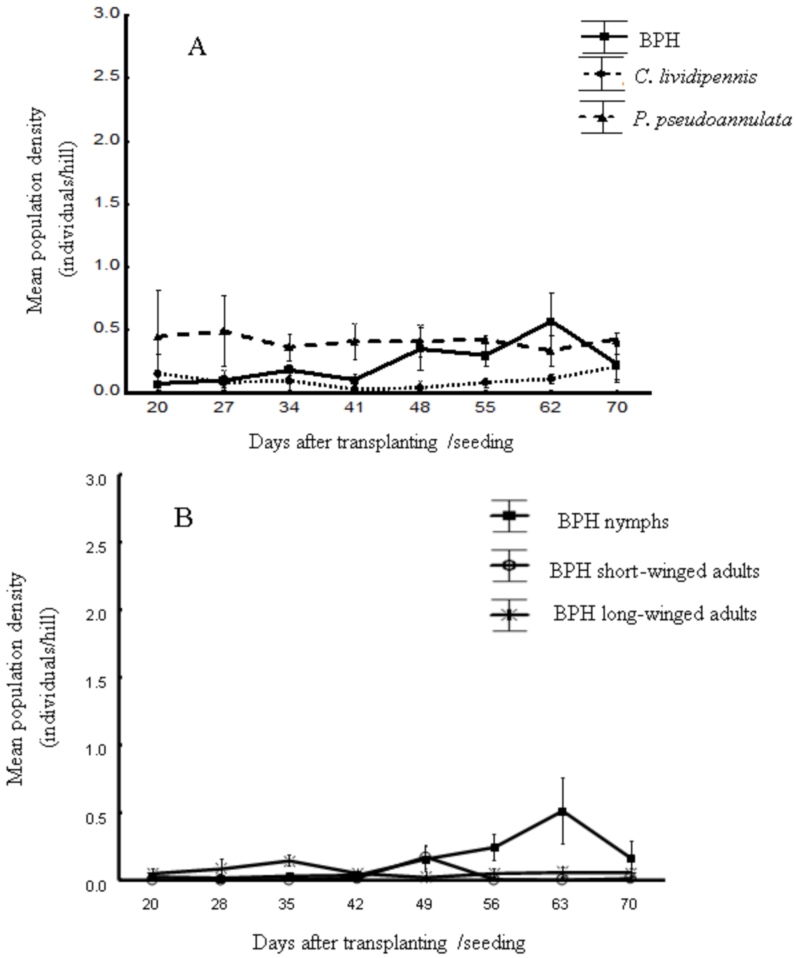

Fig. 4. Population growth pattern throughout the rice crop season of *N. lugens* (BPH) and its natural enemies in resistant rice fields at Chai Nat during the dry season. A. Growth pattern of total BPH (nymphs + short winged adults + long-winged adults) and its natural enemies, *C. lividipennis* and *P. pseudoannulata* B. Growth pattern of BPH life stages.

Long-winged adults showed a very low incidence during all the crop period in resistant fields (Fig. 4B) but in susceptible fields, there was an initial peak density of long-winged adults at 27 DAT/S of about 0.75 individuals per hill (Fig. 5B). The magnitude of the peak density of BPH-long-winged adults was significantly higher in BPH-susceptible fields (*p= 0.048*) as well as the magnitude of the first peak density of nymphs (*p= 0.0087*) than those in resistant fields. BPH nymphs showed a similar growth pattern to the one of total BPH, in both resistant and susceptible fields (Figs. 4 and 5).

Short-winged adults showed very low occurrence during the crop period at both, resistant and susceptible fields (Figs. 4B and 5B) and no significant difference for peak densities between rice varieties was found. The incidence of the natural enemies, MB and WS in resistant fields was low during all the crop period and its growth pattern was not similar to the one of BPH population. Nevertheless, MB showed a slight increasing density after 48 DAT/S until the end of the crop season when BPH-nymphs were also increasing until 63 DAT/S (Fig. 4A and 4B). In susceptible fields, MB showed a similar growth pattern to that of the total BPH (Fig. 5A). Densities of MB continued to increase until the end of the crop period as total BPH and BPH nymph densities did. WS showed a synchronized growth pattern with the one of BPH-long-winged adults, and both, WS and BPH-long-winged adults showed density peaks at 27 DAT/S and 62 DAT/S and decreased in density at the end of the crop period (Figs. 5A and 5B).

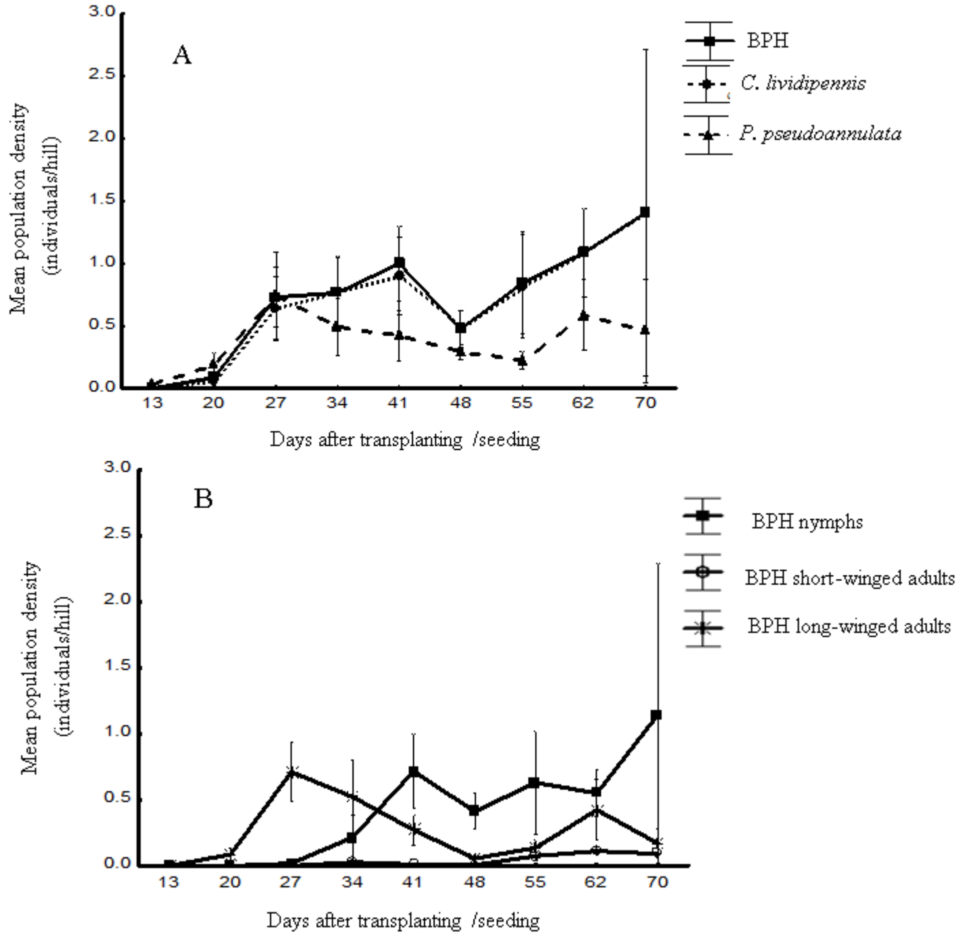

Fig. 5. Population growth pattern throughout the rice crop season of *N. lugens* (BPH) and its natural enemies in susceptible rice fields at Chai Nat during the dry season. A. Growth pattern of total BPH (nymphs + short winged adults + long-winged adults) and its natural enemies, *C. lividipennis* and *P. pseudoannulata*, B. Growth pattern of BPH life stage.

Chai Nat- Wet season: Growth pattern of total BPH was not notably different between resistant and susceptible fields in Chai Nat during the wet season (Figs. 6A and 7A) and significant differences were not found for the peak density of nymphs, BPH-long winged adults and BPH-short winged adults. In both cases, densities were lower early in the crop period and higher after 48 DAT/S, reaching a maximum density of about 1 individual per rice hill at 62 DAT/S. However, the magnitude of BPH density in both types of fields was small during the crop season (Figs. 6A and 7A). Peaks of BPH long-winged adults in Chai Nat occurred early (Figs. 4B and 5B) and close to the mid-crop period (Figs. 6B and 7B) during the dry and wet season, respectively in both resistant and in susceptible fields at 48 DAT. In both resistant and susceptible fields, short-winged adults only increased by the end of the crop season in both cases, after 48 DAT/S (Figs. 6B and 7B). MB and WS responded positively to increases in the density of BPH early in the crop period but after 48 DAT/S their growth patterns were not synchronized with that of BPH in resistant fields (Fig. 6A). In susceptible fields, WS showed a similar growth pattern to that of total BPH during all the crop period (Fig. 7A).

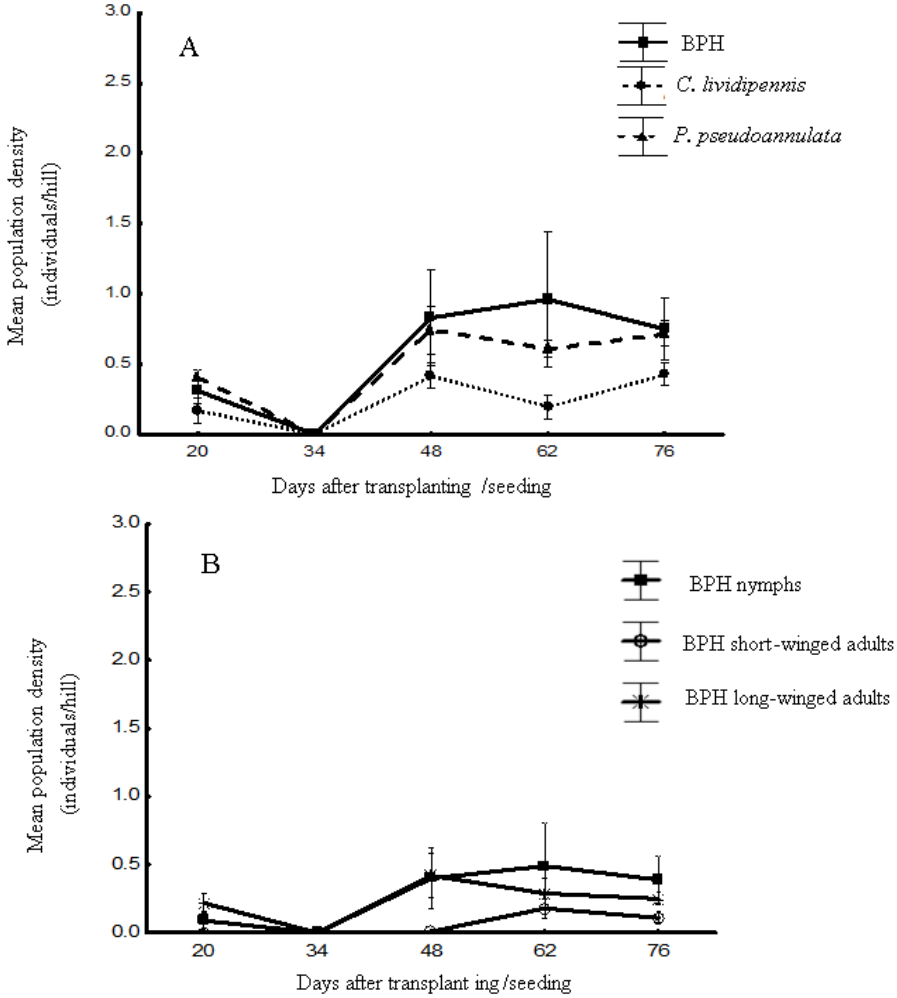

Fig. 6. Population growth pattern throughout the rice crop season of *N. lugens* (BPH) and its natural enemies in resistant rice fields at Chai Nat during the wet season. A. Growth pattern of total BPH (nymphs + short winged adults + long-winged adults) and its natural enemies, *C. lividipennis* and *P. pseudoannulata* B. Growth pattern of BPH life stage

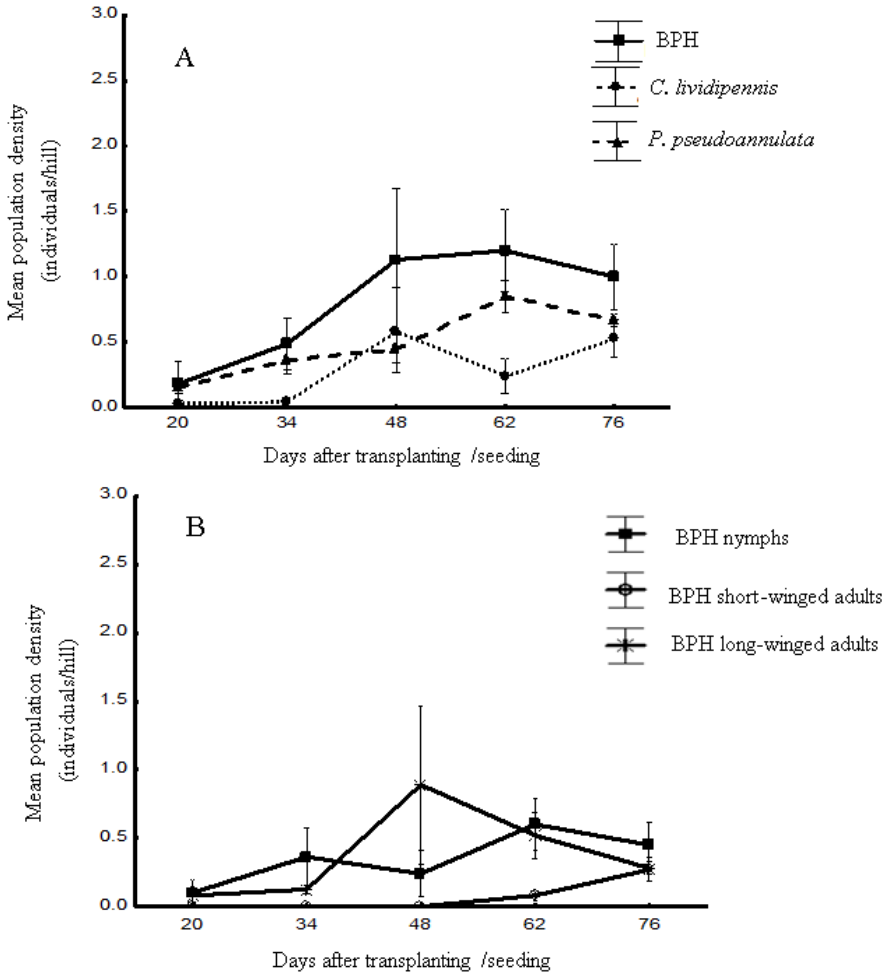

Fig. 7. Population growth pattern throughout the rice crop season of *N. lugens* (BPH) and its natural enemies in susceptible rice fields at Chai Nat during the wet season. A. Growth pattern of total BPH (nymphs + short winged adults + long-winged adults) and its natural enemies, *C. lividipennis* and *P. pseudoannulata* B. Growth pattern of BPH life stage

Nakhon Nayok-Wet season

Growth pattern of BPH in rice fields at Nakhon Nayok during the wet season was significantly different between susceptible and resistant fields (Figs. 8 and 9). The first nymph peak density was significantly higher in extent and occurred later in the crop season in BPH-resistant fields than in susceptible fields (*p= 0.035; p= 0.012*, extent and time occurrence, respectively). Total BPH population in resistant fields (Fig. 8A) showed higher incidence late in the crop season than at the beginning of the crop period with two density peaks of 2.5 and 2.8 individuals per hill at 62 and 76 DAT/S, respectively. Long-winged adults showed a peak density at 55 DAT/S. Short-winged adults and nymphs increased in density after 55 DAT/S, showing their maximum densities at 62, 76 and 83 DAT /S (Fig. 8B).

On the other hand, total BPH population in susceptible fields showed higher incidence early in the crop season with a density peak of 1.8 BPH per hill at 41 DAT/S. This density peak was followed by smaller densities later in the crop season (Fig. 9A). Nymph growth pattern showed a similar trend to total BPH, initial higher density and smaller occurrence at the end of the crop period (Fig. 9B). Long-winged adults peaked earlier (34 DAT/S) in susceptible than in resistant fields (55 DAT/S) with this time occurrence in the crop period, being significantly different between resistant and susceptible fields (*p= 0.012*). Short-winged adults showed very small incidence over the crop season (Fig. 9B). Generally, densities of BPH in Nakhon Nayok (Figs. 8 and 9) were higher than those in Chai Nat during both the dry (Figs. 4 and 5) and the wet seasons (Figs. 6 and 7).

In resistant fields at Nakhon Nayok, the natural enemies, MB and WS showed very low incidence throughout the crop season with densities being not higher than 0.5 individuals per hill (Fig. 8A). Growth pattern of MB and WS did not show a similar trend to the growth pattern of total BPH neither, to any of the life stages of BPH (Figs. 8A and 8B).

In susceptible fields at Nakhon Nayok, growth pattern of MB (Fig. 9A) was similar to that of long-winged adults and nymphs (Fig. 9B) and it responded more notably to the increases in BPH density early in the crop period than at the end of it. WS (Fig.9A) instead, responded more notably to increases in BPH density after 62 DAT/S, close the end of the crop season (Figs. 9A and 9B).

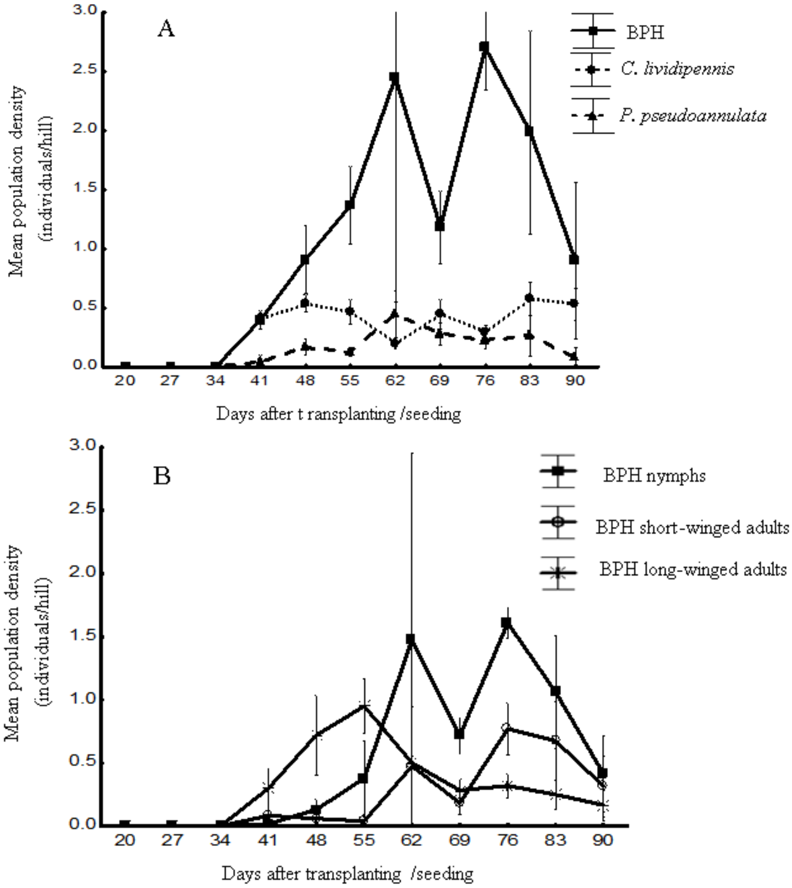

Fig. 8. Population growth pattern throughout the rice crop season of *N. lugens* (BPH) and its natural enemies in resistant rice fields at Nakhon Nayok during the wet season. A. Growth pattern of total

BPH (nymphs + short winged adults + long-winged adults) and its natural enemies, *C. lividipennis* and *P. pseudoannulata* B. Growth pattern of each BPH life stage.

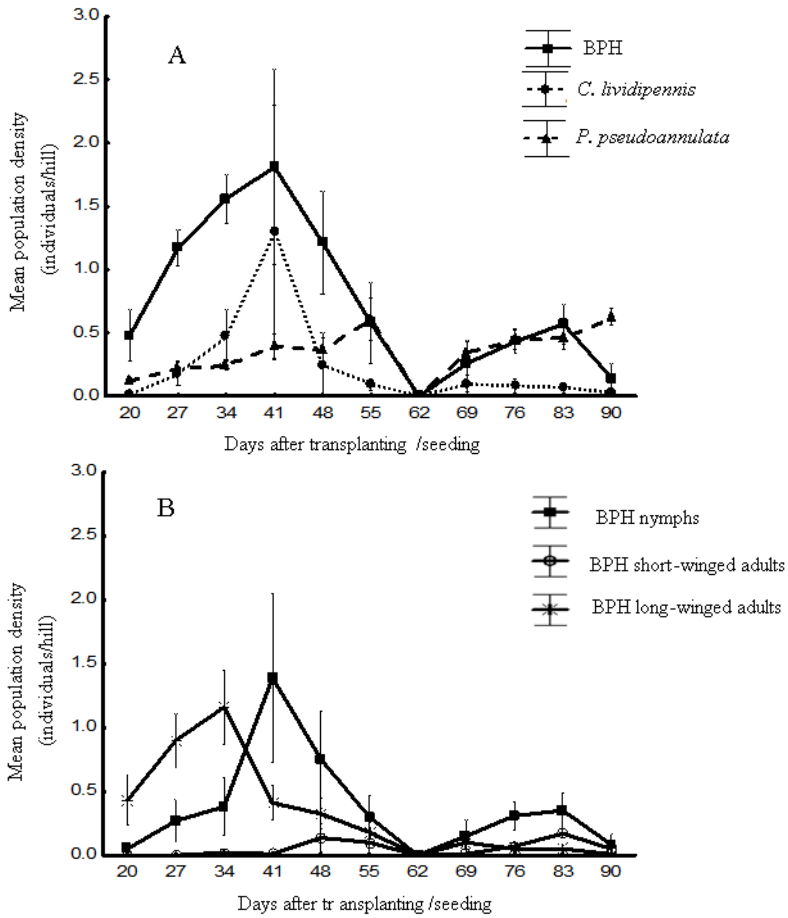

Fig. 9. Population growth pattern throughout the rice crop season of *N. lugens* (BPH) and its natural enemies in susceptible rice fields at Nakhon Nayok during the wet season. A. Growth pattern of total BPH (nymphs + short winged adults + long-winged adults) and its natural enemies, *C. lividipennis* and *P. pseudoannulata* B. Growth pattern of each BPH life stage

DISCUSSION

Significant implications in the population dynamics and growth pattern of BPH and its natural enemies in rice fields planted with BPH-resistant and BPH-susceptible fields were identified in this study:

1. **No consistent differences were found in the population dynamics and the growth pattern of BPH between resistant and susceptible rice fields.**

Resistance allows rice plants to affect pest fertility, development and feeding behavior (Baldwin and Preston 1999). Thus, lower densities of BPH are expected in resistant rice cultivars and less conspicuous density peaks when compared with susceptible rice plants (Alagar et al. 2007, Kartohardjono and Heinrichs 1984). However, the results of this research showed that densities of BPH were not smaller at all the BPH-resistant fields that were studied. Only the average and maximum density of BPH long-winged adults in resistant fields at Chai Nat during the dry season and the mean density of BPH short-winged adults in resistant fields at Nakhon Nayok during the wet season, were smaller than in BPH-susceptible fields (Table 2). Additionally, mean densities at all BPH life stages were not significantly different between susceptible and resistant fields in Chai Nat during the wet season (Table 2). Furthermore, we only found a different growth pattern between resistant and susceptible fields in Nakhon Nayok during the wet season (Figs. 8 and 9). Nevertheless, resistant fields in Nakhon Nayok during the wet season were planted with the rice variety RD47 and susceptible fields with Thai Jasmine rice. Transplanting dates were clearly different between resistant and susceptible fields (Table 1). We acknowledge that factors related with the difference in the planting dates between resistant and susceptible fields, may also explain our results.

Compared to pest-resistant rice, pest-susceptible rice varieties can be cultivated at a lower cost, due to a less water requirement of susceptible rice plants (Hussain et al. 2008, Third World Network 1990). In case farmers in Central Thailand would require in the future to plant only susceptible rice varieties, the evidence of this study cannot support the idea that the use of such rice varieties could be riskier for pest control than the use of pest-resistant rice varieties. Actually, under natural conditions, a healthy rice plant has a great capacity for damage compensation or insect pest resistance (Sogawa 2015, Way and Heong 1994). It has been demonstrated in tropical rice fields in the Philippines, yield loss did not occur even though susceptible rice had a density of about 30 BPH per plant (IRRI 1990). Actually, some studies have shown that in Thailand some susceptible rice varieties have the potential to develop tolerance to insect pests (Oupkaew et al. 2011, Rerkasem 2015). Other studies in India and Pakistan, revealed susceptible varieties are not as prone to diseases as high-resistant rice varieties are (Hussain et al. 2008, Third World Network 1990). Additionally, evidence demonstrating that improving the diversity of the rice agroecosystem with a mixture of resistant and susceptible varieties in insecticide-untreated fields has reduced the harmful effects by different species of hoppers (Cook and Perfect 1985, Kenmore 1991). This may also represent an alternative for pest management for farmers. However, future research that provides evidence about potential risks of this varietal mixture is necessary.

2. Typical seasonal growth pattern of BPH tropical populations was only found in fields planted with susceptible rice varieties in Nakhon Nayok during the wet season.

Although it has been found in several studies that tropical populations of BPH are characterized by low densities late in the crop season that happen after early and high initial pest densities (Hirao 1989, Kisimoto 1981, Kuno and Dyck 1985, Wada and Salleh 1992), in this study, only BPH populations in susceptible fields at Nakhon Nayok during the wet season followed the typical pattern of tropical populations of BPH (Fig.9). BPH populations in resistant and susceptible fields in Chai Nat during the dry (Figs. 4 and 5) and wet (Figs. 6 and 7) seasons and in resistant fields in Nakhon Nayok during the wet season (Fig. 8), showed the opposite pattern; lower initial pest densities followed by higher incidence of BPH later in the crop period.

BPH populations vary significantly in time and space (Denno et al. 1980, Denno and Grissell 1979, Kuno 1977, Strong et al. 1989) and diverse factors like host plant physiology, predation, population density and even planting dates influence the growth and size of the BPH population (Denno and Roderick 1990, Denno et al. 1991). For example, selective pressures related with the finding of mates and habitat conditions seem to affect wing form and dispersal in BPH populations (Denno et al. 1991). When the population density is low, individuals become dispersed in the rice field and potential mates for the reproduction get limited, causing male long-winged adults to be favored over short-winged ones in order to facilitate searching for females (Denno et al. 1991). Habitat stability and changes in the physiology of the rice plant can also favor long-winged individuals, so that the pest population is able to disperse searching for new rice fields or better plant hosts when conditions are not favorable (Denno et al. 1991, Dyck et al. 1979, Saxena et al. 1981).

Overall incidence of BPH long-winged adults was higher than BPH short-winged adults in the sampled fields in this study (Table 2). With the exception of resistant fields in Chai Nat during the dry season, where incidence of BPH long-winged adults was low over the crop period (Fig. 4B), occurrence of long-winged adults was frequent over the crop season, happening close or after the mid time of the crop period in fields at Chai Nat during the wet season (Figs. 6B and 7B) and in resistant fields at Nakhon Nayok during the wet season (Fig. 8B), or early in the crop season in susceptible fields at Nakhon Nayok (Fig. 9B). Susceptible fields in Chai Nat during the dry season showed the increase in the incidence of long-winged adults early and late in the crop period (Fig. 5B). Although long-winged adults are less fecund than short-winged adults (Cheng and Holt 1990, Kisimoto 1965) they still contribute to build-up the pest population. Immigration of long-winged adults to new rice fields normally explains the typical early high nymph densities of tropical BPH populations (Dyck et al. 1979) as it was observed in susceptible fields in Nakhon Nayok (Figs. 9A and 9B). However, occurrence of long-winged adults close or after the mid time of the crop season may also explain the non-typical higher nymph densities that were observed close to the end of the crop season in fields at Chai Nat during the dry (Figs. 4 and 5) and wet seasons (Figs. 6 and 7) and in resistant fields in Nakhon Nayok (Fig. 8). Actually, only in susceptible fields in Chai Nat during the dry season, BPH densities continued rising close to harvest time where the increase in the incidence of long-winged adults occurred both, early and late in the crop period.

Additionally, the smaller population densities observed in fields in Chai Nat during the dry (Figs. 4 and 5) and wet seasons (Figs. 6 and 7) could have been also caused by the less fertility of BPH long-winged adults. BPH populations can grow rapidly when aggregations of short-winged adults occur (Kisimoto 1965) but when conditions are not favorable, for example, a population low-density condition, a trade-off between fitness and wing form happens (Denno et al. 1991). Predominance of long-winged adults was considered typical of BPH populations at high-density conditions under the effects of crowding that stimulate macroptery (Denno et al. 1991). However, the results of this study support previous research that has shown that population low-density conditions also influence the triggering of macroptery (Denno et al. 1991, Kuno 1979).

On the other hand, although the use of insecticides has decreased dramatically in Central Thailand as a consequence of the termination of subsidies for rice production by the Government, some farmers still use them, especially when their purpose is seed production (non-published data from interviews to farmers in the study area). Sampled fields in this study were not treated with insecticides but the use of chemicals for BPH control in neighboring fields may have occurred. Rice areas in Chai Nat and Nakhon Nayok comprise a matrix of successional planted rice crops. Pests and fauna associated with the rice agroecosystem are connected among this assortment of continuous available rice due to asynchronous planting dates (Way and Heong 1994). It is also possible that the frequent and higher incidence of BPH long-winged adults over short-winged adults could have been the consequence of an “escape” from sprayed surrounding fields.

3. The natural enemies of BPH seem to respond differently to increasing densities of BPH in different crop seasons and different rice fields.

The effect of pest resistant crops on the behavior and performance of natural enemies has been widely discussed. Some researchers have suggested that high levels of resistance can be detrimental for natural enemies because resistant cultivars lower the pest to the densities, where food gets limited for natural enemies (Gould et al. 1991, Kenmore et al. 1984). Meanwhile, other studies have proposed that when crop resistance is combined with control by natural enemies, satisfactory pest suppression occurs (Carriere and Tabashnik 2001, Way and Heong 1994). This study showed results related to multiple scenarios concerning the behavior of natural enemies in resistant rice cultivars.

Firstly, in resistant fields in Chai Nat during the dry season both the pest and natural enemies seemed to be suppressed to some degree. Resistant fields had significantly less number of BPH long-winged adults and less number of MB individuals than in susceptible fields (Table 2 and Figs. 4A and 5A). In these fields, an adverse effect of resistant cultivars on natural enemies as reported in previous studies may have occurred (Gould et al. 1991, Kenmore et al. 1984). BPH could have been suppressed by plant resistance to a population density level, where it may have also caused less available food for natural enemies and thus, causing also lower densities of MB compared to the ones in susceptible fields. This may also explain why although there was a positive response of natural enemies to pest density in resistant and susceptible cultivars (Table 3), only in susceptible fields MB was higher in density and also showed a synchronized growth pattern to the one of BPH (Fig. 5A).

Secondly, in fields at Chai Nat during the wet season there were no consistent differences in the growth of BPH and both natural enemies between resistant and susceptible fields (Figs. 6 and 7) and there was no significant response of natural enemies to increasing densities of the pest in susceptible and resistant fields (Table 3). It is possible that other factors independent of the type of rice variety could have influenced the behavior of the pest and both natural enemies. In this case, density-related effects could have played an important role. When the pest is at a low density condition, BPH individuals get located at the bottom of the rice plant stem (Denno and Roderick 1990), making it more difficult for predators to find BPH. Under this unfavorable condition for the predators MB and WS could have changed their prey preference from BPH to other preys easier to find (Ferry et al. 2006, Mayntz et al. 2005). The lack of correlations between BPH density and both natural enemies in fields at Chai Nat during the wet season may be explained by a niche shift of BPH in the rice plant under low density conditions. In parallel, WS is a predator known for also having nocturnal habits (Maloney et al. 2003). Since sampling in this study occurred in the day-time, an underestimation of the spider response related to BPH is another limitation that cannot be discarded.

Lastly, the growth pattern of BPH in resistant fields at Nakhon Nayok during the wet season showed that BPH was not suppressed late in the crop period, when BPH densities increased and density peaks were clearer (3 BPH per hill) (Fig. 8A). Natural enemies instead, showed very low incidence over the crop period (Fig. 8A). Resistant fields at Nakhon Nayok showed a scenario, in which we observed less degree of BPH suppression and poor incidence of natural enemies, but in this case, not caused by a BPH low-density condition. Not only BPH but also natural enemies are connected to neighboring rice fields (Way and Heong 1994). It is possible that since BPH densities were very low early in the crop season (Fig. 8A), natural enemies could have migrated to other rice fields and their densities only started increasing after BPH also increased after 34 DAT/S. Poor control by natural enemies early in the crop season has been demonstrated to cause high BPH densities later in the crop period (Way and Heong 1994) as it happened in resistant fields in Nakhon Nakhon (Fig. 8A).

A significant amount of research has failed to report consistent differences in the population dynamics and performance of natural enemies between resistant and susceptible crops (Marvier et al. 2007, Rodrigo-Simón et al. 2006, Wolfenbarger et al. 2008). In this sense, the findings of this study support these previous research and report no consistent differences in the population dynamics and growth pattern of natural enemies between resistant and susceptible fields in Central Thailand and rather, suggest that diverse factors may influence the performance of natural enemies and their response to BPH in each rice field, location and crop season. Among these factors, BPH population density-related effects may play a significant role. Other two factors that may be important are the type of resistant variety (Way and Heong 1994) and specific climatic conditions at each cropping season (Döbel and Denno 1994). In a future study, the discrimination of different types of resistant varieties and a detailed effect of climate on the rice arthropod community may explain in a deeper way than our findings.

CONCLUSION

The extent of pest suppression on resistant crops has been thought to be location-specific (Gould et al. 1991, Way and Heong, 1994) and therefore, the relevance of assessing the dynamics of BPH populations on a specific region has been widely recalled when applying pest management strategies to a particular area (Kuno and Dyck 1985). Our study is one of the few comprehensive works that has assessed at a community-based level, the population dynamics of BPH and its natural enemies in different resistant and susceptible non-sprayed rice fields in Central Thailand under a non-outbreak condition, contributing with insights about the potential ecological impact of BPH-resistant rice varieties on BPH and its natural enemies and its implications for the local management of the pest. Our findings conclude that the low-density condition of the pest population and the crop season have a strong effect on the dynamics of BPH and its natural enemies and therefore, on the magnitude and effectiveness of natural control by predators and the level of pest suppression in fields planted with BPH-resistant varieties. Although we acknowledge the limitations of our study concerning the difficulty of conducting this type of research in farmers' fields, we do not expect the conclusions and findings of this study to be an absolute evaluation of the extent of pest suppression in BPH-resistant fields but instead, to clarify the knowledge about the dynamics of BPH and its natural enemies in tropical rice fields planted with BPH-resistant and BPH-susceptible varieties where the conditions vary in a way from experimental fields.

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