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COMPARATIVE ANALYSIS OF POPULATION CHARACTERISTICS OF THE BROWN PLANTHOPPER, *NILAPARVATA LUGENS* STÅL, BETWEEN WET AND DRY RICE CROPPING SEASONS IN WEST JAVA, INDONESIA

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SUMMARY

Population dynamics of the brown planthopper (BPH), *Nilaparvata lugens* Stål, were investigated in paddy fields in the coastal lowland of West Java, Indonesia, where rice is cultivated twice a year, in the wet and dry cropping seasons. Distinct differences in the basic features of population dynamics were detected between the two rice cropping seasons: (1) In the wet season, BPH populations multiplied rapidly in the period from initial to peak generation, reaching quite often the destructive level despite the low density of initial immigrants. However, in the dry season, the population growth rate and the peak population density were much lower than those in the wet season. The abundance of natural enemies such as arthropod predators played a major role in determining such a difference in seasonal population development. (2) The density at the peak generation or the occurrence of outbreaks in each field was predictable in the wet season with fairly high accuracy on the basis of the density at the initial or previous seasonal generations. In the dry season, however, the rate of population growth and the peak population density widely varied among the fields depending on the water status in each field. (3) Density-dependent processes to regulate the population density were detected in both cropping seasons. In the wet season, the regulatory processes were only detected in such high densities as cause the considerable deterioration of host plants, which suggested that the processes were largely attributable to intra-specific competition. In the dry season, however, the regulatory processes operated at a much lower density in the earlier stages of the crops. The results of an analysis of adult longevity or residence period suggested that the density-dependent dispersal of macropterous adults played an important role in stabilizing the population fluctuation among the fields in the early dry season.

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KEYWORDS: *Nilaparvata lugens*, population dynamics, natural enemy, rice, cropping season.

INTRODUCTION

The brown planthopper (BPH), *Nilaparvata lugens* Stål, is a major pest of rice widely distributed in Asia. The pest causes serious crop loss by both direct sap-sucking and transmitting virus diseases. In Indonesia, this pest caused destructive infestation to rice fields extending to 300,000–800,000 ha annually in the late 1970s (Soenardi, 1977; Mochida, 1977; Dyck and Thomas, 1979), and seriously discouraged those involved in the nation-wide endeavor toward self-sufficiency in food through the national rice intensification program (e.g. Sogawa, 1990). The threats have taken place succeedingly in the 1980s; serious BPH outbreaks occurred in North Sumatra in 1982–1983, in Central and West Java in 1986–1987, and in East Java and Lampung in 1987–1988 (Subroto et al., 1992)

BPH became a major pest accompanied by the introduction of high yielding rice varieties and modern cultivation technologies during the green revolution period. Predominance of high yielding varieties, areal expansion of irrigation systems and double cropping, and increased use of nitrogen fertilizers and insecticides have caused an enormous increase in BPH populations (e.g. Dyck, et al., 1979; Kenmore et al., 1984).

In the irrigated coastal lowland of West Java, where rice is cultivated twice a year, in wet and dry cropping season, by intensive modern rice technologies, BPH threatens rice fields every year. This study was conducted to determine the basic features of the BPH population dynamics in paddy fields to prepare an ecological basis to establish the effective control system of this pest. Since the BPH populations in different cropping seasons were subjected to different environmental conditions such as weather, natural enemies etc., the factors contributing to the pattern of population changes are described separately for the two rice cropping seasons. The two aspects of population changes, i.e., seasonal generation to generation population development and field to field population fluctuations, have been analyzed.

MATERIALS AND METHODS

The Insect

Taxonomically, BPH belongs to Delphacidae of the suborder Homoptera. The female deposits eggs in masses each consisting of several to several tens of eggs, in the tissue of rice plants mainly in the leaf sheath. The potential fecundity of this pest is very high, the total number of oocytes per female being about 2000 (Suenaga, 1963). Kuno (1968), and Kuno and Hokyo (1970a) reported that the fecundity was 800–900 eggs per female under a confined condition using potted rice plants, and about 400 eggs per female in the field. The nymphs pass through five instars till their emergence

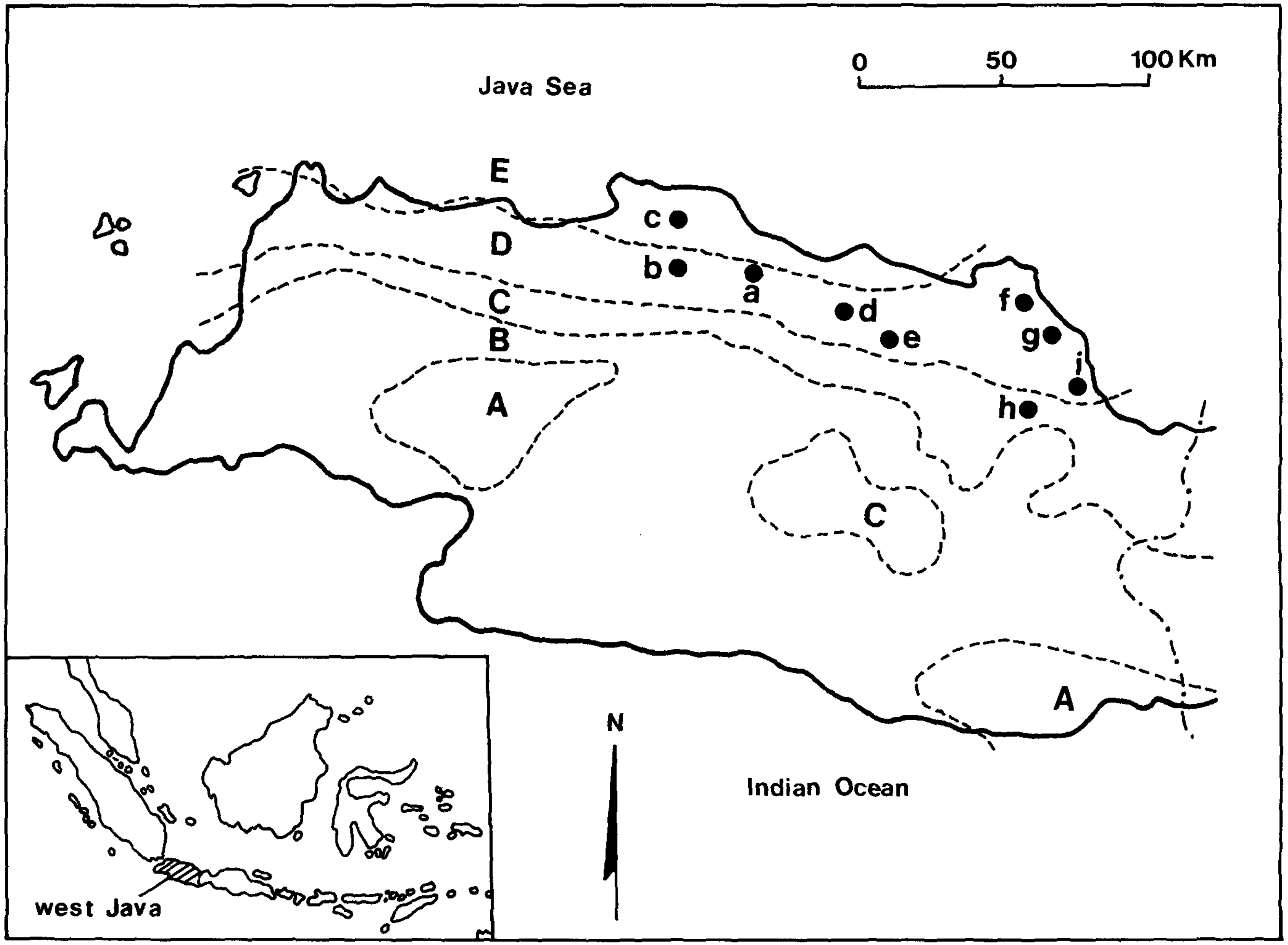

Fig. 1. Locations of nine study sites (a–i) in the 1984/1985 wet season, and the climatic zone in West Java (A–E). A, B, C, D and E show the area with >9, 8–9, 6–7, 4–5 and <3 wet months (>200 mm rainfall per month) in a year, respectively.

as adults. The average period required for the completion of egg and nymphal stages is 7.9 days and 12.0 days, respectively, at the temperature between 27–28°C (Mochida and Okada, 1979). In both sexes, adults have two wing-forms, i.e., macropterous and brachypterous forms which are distinguishable by the length of the wing. The wing-forms are determined depending on the crowding and host stage during the nymphal stage (Kisimoto, 1965). Host plants of the BPH are substantially restricted to rice, while a few alternate hosts have been noted in the literature (e.g. Hinckley, 1963; Dyck et al, 1979).

Study Area and Census Methods

The coastal lowland of West Java containing 460,000 ha of rice fields is an advanced area that has adopted modern rice technologies under a large-scale irrigation system. There are two different rice cropping seasons in this region; the wet (December to April) and dry (May to September) cropping seasons. This study was implemented in the four rice cropping seasons from 1984/1985 wet to 1986 dry season at nine (1984/85 and 1985), seven (1985/86) or six (1986) selected field plots distributed over this region (Fig. 1). While rice cultivation started soon after harvesting of the wet season crop, a fallow period was clearly interposed after the dry season crop through the water management of the irrigation systems. It lasted for approximately two months from October to November (Fig. 2). The rice fields were almost completely dried up in the fallow period, when BPH could not survive. It was therefore presumed that re-invasion of the BPH occurred every wet cropping season from southern, mountainous areas, where rice was continuously cultivated throughout the

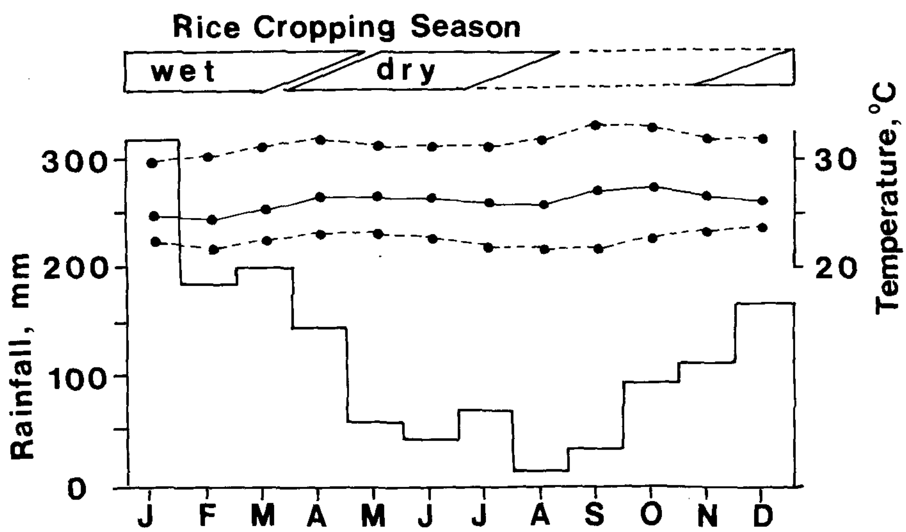

Fig. 2. Meteorological data observed at site a (Jatisari Pest Forecasting Center) for 11 years, 1980–1990, and rice cropping seasons in the coastal lowland of West Java. Histogram shows the mean monthly precipitation. Solid and broken lines show the mean, and maximum and minimum monthly temperature, respectively.

year.

The size of a study plot was either $20 \times 50\ m^2$ (at an experimental field of Jatisari Pest Forecasting Center), or $20 \times 30\ m^2$ (at the others in farmers' paddy fields), where a susceptible variety, Pelita I/1, was hill-planted with a spacing of 25 cm. Cultural practices adopted were the standard procedures generally employed in this region, except that no pesticides were applied in the study. Routine censuses to estimate population incidences were conducted at weekly intervals throughout the rice growing season. Fifty (Jatisari field) or 30 (the others) units were sampled in each census by a systematic procedure with a random start. The standard sampling unit was a hill of rice plant, but was a quadrat comprising four adjacent hills in the earlier period of the season (until 7 weeks after transplanting). All insects inhabiting rice plants and water surface were collected with an IRRI-type car-battery suction machine (Cariño et al., 1979) after covering the hill with a transparent plastic cage. The insects thus sampled were carefully identified and counted under a microscope. Reproductive organs of adult females sampled were dissected to estimate the daily survival rate and the mean longevity at each generation.

Results

Pattern of Seasonal Population Development

Seasonal trends of the BPH population in individual census plots are presented for both the wet and dry seasons in Figs. 3 and 4 , respectively, as the total number of adults and 4–5th instar nymphs. During the first 4–5 weeks after transplantation, macropterous adults that apparently had immigrated from the outside were dominant, though some brachypterous adults probably originating from the eggs laid in the nursery bed were also observed (Table 4). After the small peak of these initial immigrants, three distinct peaks are usually observed each at a 3 to 4-week interval, which corresponds to the period of approximately one BPH generation in the tropics (Mochida and Okada, 1979). This suggests that the population peaks imply generation peaks. Macropterous adults may easily disperse from one field to another, and hence they may cause generation overlapping in BPH population trends. However, BPH populations in Indonesia and other Southeast Asian countries are known in many cases to show rather discrete generation cycles (Hirao, 1989; Sawada and Kusumayadi, 1991; Sawada et al., 1992). This might be caused, at least partly, by the preference of macropterous immigrants to young rice plants.

The generation of BPH populations was identified in the order of succession as the initial, the 1st, the 2nd and the 3rd based on the time of each peak incidence observed. The duration of each generation was fairly constant around 3.5 weeks due to the almost constant temperature in this region (Fig. 2). The representative population density was estimated for each generation by a graphical method (Southwood, 1978), the area under the line of population incidence during the period

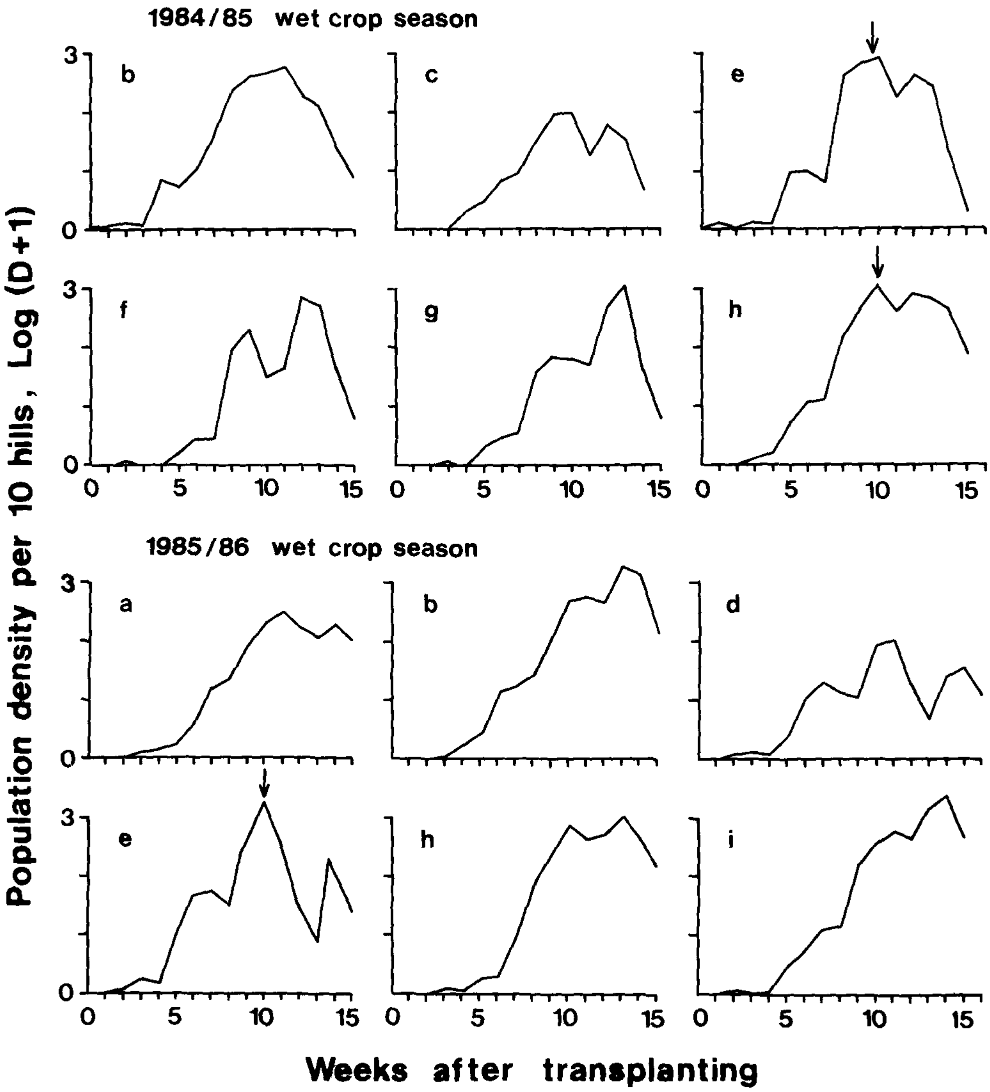

Fig. 3. Examples of the seasonal trend of the BPH population development in the wet cropping seasons. Values are shown as the sum for adults and 4–5th instar nymphs in the fields. Arrows show the occurrence of BPH outbreaks.

in each generation being divided by the generation period. The mean values of thus obtained densities at each generation for 6–9 census plots in each cropping season are presented in Table 1.

The results show that the BPH populations in this region are characterized by the low density of initial immigrants and the high rate of subsequent population growth. In the wet season, BPH populations multiplied with as great an increasing rate as about 1,500–2,500 times (60.3 × 25.0 or 91.5 × 27.4 in Table 1) towards the 2nd, or the peak generation, which would lead to the population outbreaks causing destructive damage in rice yield, despite the low density of the initial immigrants. Interestingly,

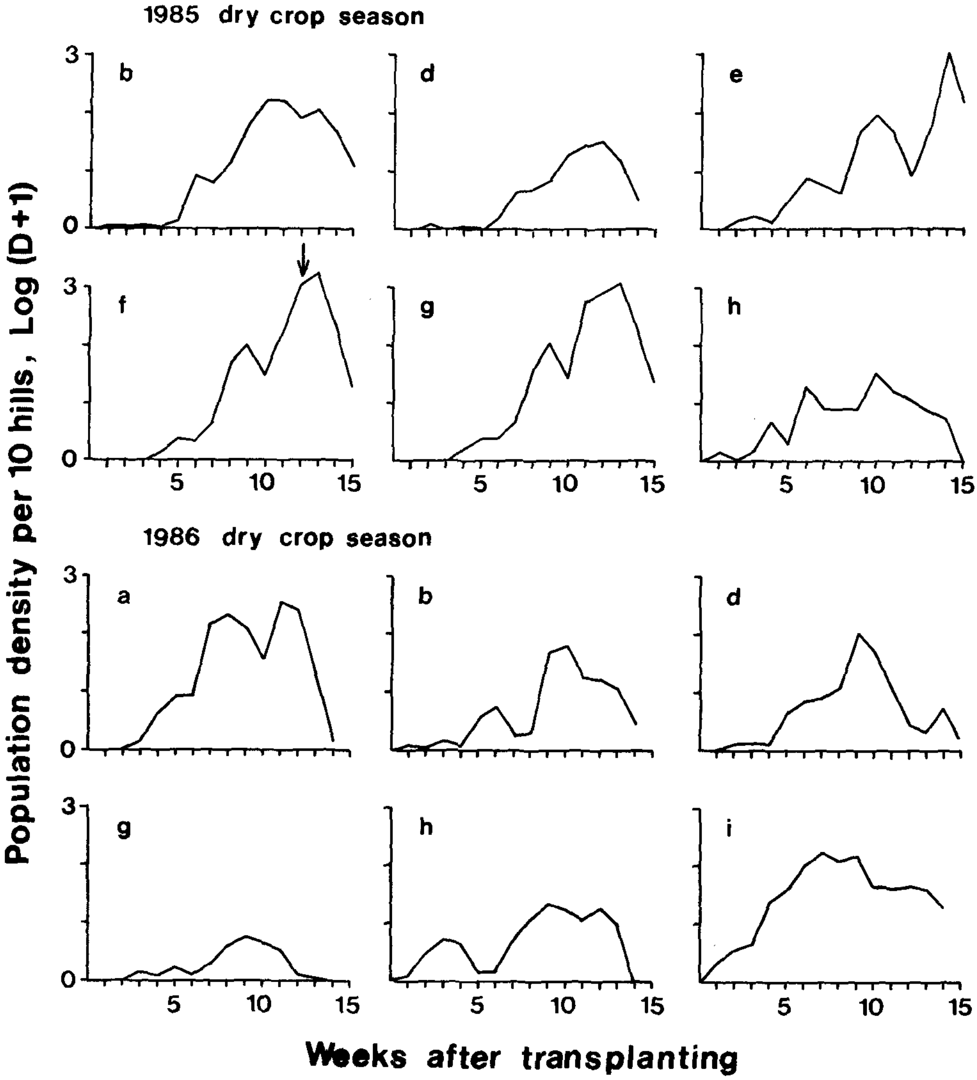

Fig. 4. Examples of the seasonal trend of the BPH population development in the dry cropping seasons. Values are shown as the sum for adults and 4–5th instar nymphs in the field. Arrows show the occurrence of BPH outbreaks.

the pattern of BPH population development is rather similar to that observed in temperate regions like Japan (Kuno and Hokyo, 1970a), but is quite different from those reported by earlier studies in the tropics such as the Philippines, in which BPH populations were characterized by high initial density followed by slow population growth thereafter (Kuno and Dyck,1985).

The overall population growth rate and the peak density in the dry season were much lower, i.e., about one tenth as low as those in the wet season (Table 1). It is a common feature for both cropping seasons that the rate of population growth is highest at the initial generation and gradually decreases thereafter.

Table 1. Population density in each seasonal generation and population growth rate between the two successive generations in four cropping seasons.

cropping season		population density				population growth rate		
		P_0	P_1	P_2	P_3	r_1	r_2	r_3
wet season	1984/85	0.010	0.91	24.9	22.0	91.5	27.4	0.88
	1985/86	0.020	1.23	30.7	30.8	60.3	25.0	1.00
		(0.127)	(0.235)	(0.196)	(0.356)	(0.079)	(0.108)	(0.296)
dry season	1985	0.015	0.41	4.1	4.0	27.8	10.1	0.96
	1986	0.041	0.49	3.7	0.90	12.0	7.5	0.24
		(0.425)	(0.220)	(0.182)	(1.339)	(0.364)	(0.176)	(0.820)

1) P_0, P_1, P_2, P_3: Population density at initial, 1st, 2nd and 3rd generation, respectively.
2) r_1, r_2, r_3: Population growth rate from initial to 1st, 1st to 2nd, and 2nd to 3rd generation, respectively.
3) Values are shown as the geometric mean among the study sites in each cropping season. Variances in logarithms are shown in parentheses, for the wet (1984/85 and 1985/86) and the dry (1985 and 1986) cropping seasons.

Population Changes among the Fields

Predictability of the peak population density. BPH is well known for its status as a typical outbreak-type pest, which is characterized by great fluctuations in population size from year to year and from field to field (Kisimoto, 1981). In the 1984/1985 wet season, for instance, the density at the peak (2nd) generation ranged from 5 to 140 insects per hill (sum of adults and 4–5th instar nymphs) at 9 study sites, among which outbreaks occurred at three sites, i.e. sites e, h and i.

Field-to-field variations in the population density at each generation and the population growth rate between the two successive generations are shown in the logarithm in Fig. 5, for the two cropping seasons, the 1984/1985 wet and 1985 dry seasons. Since the log population density at a given (*i* th) generation is shown as the sum of both the log density at the preceding generation and the log rate of subşequent reproduction (i.e. $\log P_i = \log P_{i-1} + \log r_i$), the relative importance of either P_{i-1} or r_i upon the variation of P_i can be evaluated from Fig. 5 by graphical comparison.

In the wet season, it is evident that the population densities of the initial, 1st and 2nd generations (P_0, P_1 and P_2) fluctuate with patterns that are rather similar to each other. This indicates the existence of high correlation in population fluctuation between successive generations. In fact, the values of coefficient of determination, r^2 (r: correlation coefficient) are 0.67 between P_0 and P_1, and 0.56 between P_1 and P_2 (Fig. 6), indicating that P_0 and P_1 could account for approximately 70% or 60% of the variations in P_1 and P_2, respectively. These data suggest that the population density at the peak generation, P_2, or the occurrence of BPH outbreaks is predictable with a fairly high accuracy on the basis of the population densities in the initial or the previous seasonal generation. Such a high correlation can be produced by the steady population growth rate among the fields, as shown by the low values of the variance of population growth rates, r_1 and r_2 (Table 1).

In the dry season, however, a rather low correlation was observed between

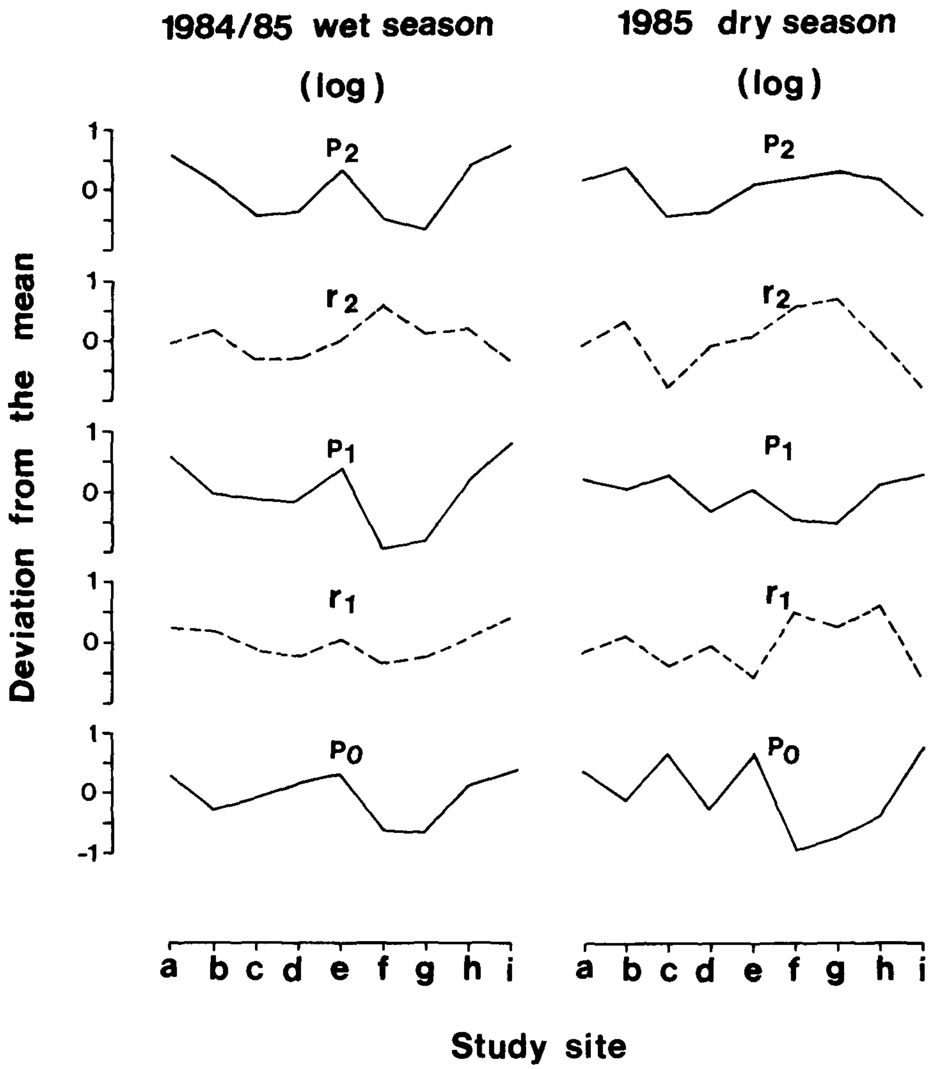

Fig. 5. Field-to-field fluctuations of the population density in each generation (solid line) and the population growth rate between the two successive generations (broken line), in the 1984/1985 wet (left) and 1985 dry (right) cropping seasons. Values are shown in logarithms.

population densities at successive generations, the value of r^2 being 0.21 between P_0 and P_1, and 0.32 between P_1 and P_2, respectively (Fig. 6). P_2 fluctuates in close correlation with r_2, instead of P_0 and P_1 (Fig. 5, right). Accordingly, it is important for the prediction of the peak population density in the dry season to identify the factors influencing the variation of r_2, population growth rate in the middle stage of the cropping season.

Detection of density-dependent processes. The regulation or stabilization of population densities will be realized as the outcome of density-dependence in the reproduction process. A simple and straightforward method for detecting the existence of density-

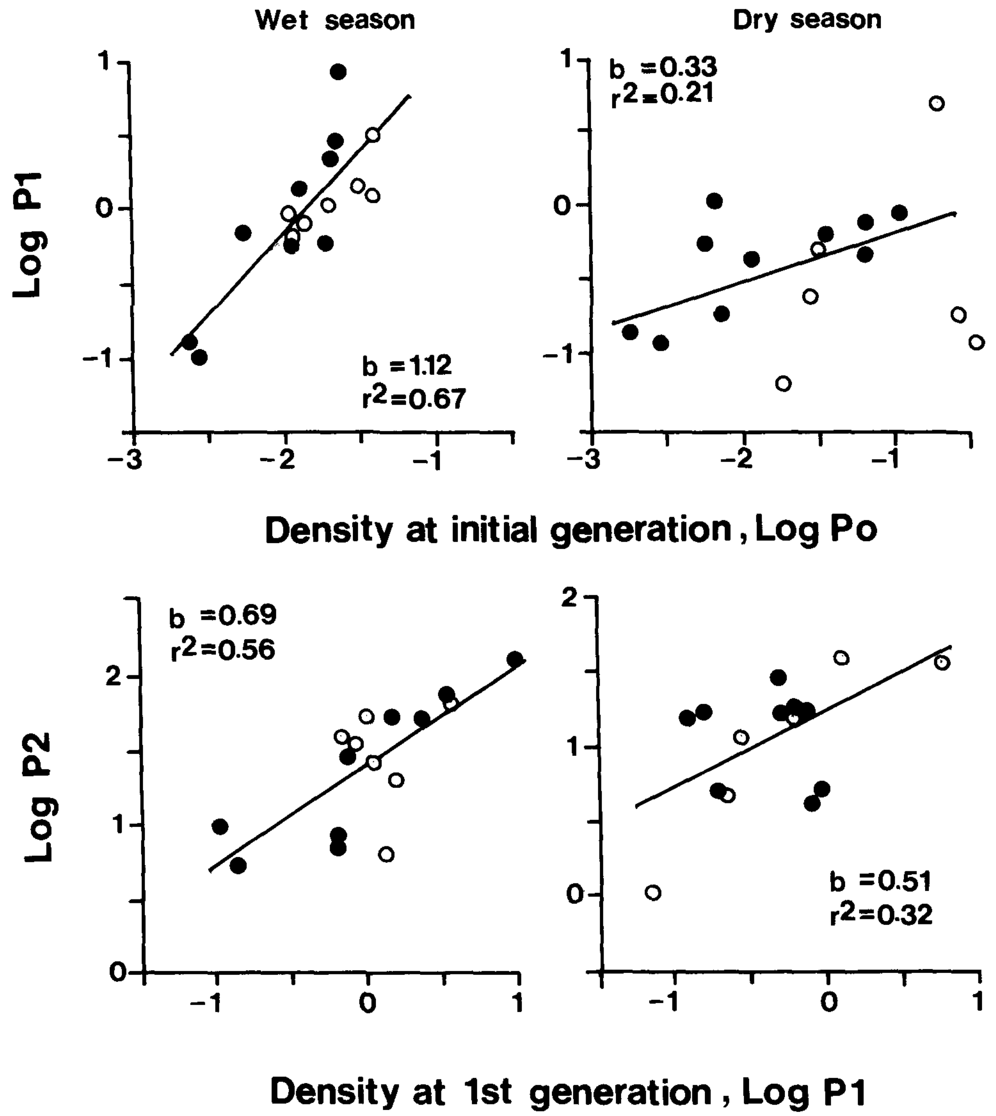

Fig. 6. Relations between the population density at the two successive generations in logarithms, in the wet (left) and dry (right) cropping seasons. Solid and open circles show the 1984/1985 wet (left) and 1985 dry (right) seasons, and the 1985/1986 wet (left) and 1986 dry (right) seasons, respectively.

dependent processes is to compare the extent of population fluctuation with the progress in seasonal generations; the decrease of variation in the population fluctuation from a given generation to the next may indicate the occurrence of population stabilization through a density-dependent process in the relevant period (Kuno, 1968). The values of variance in log-transformed population densities were used here as a measure estimating the degree of variations in population fluctuation. In this criterion, it is suggested from Table 1 that density-dependent processes operate in the following three cases; the reproduction from the 1st to 2nd generation in the wet

Table 2. Values of the slope b in the regression equation between log population densities in two successive generations for detecting the density-dependent processes. Confidence intervals for P=0.95 are shown.

	P_1/P_0	P_2/P_1	P_3/P_2
Wet season	1.116±0.446	0.686±0.345	0.654±0.677
Dry season	0.330±0.383	0.514±0.449	1.924±1.145

Wet season: 1984/85 and 1985/86 cropping season.
Dry season: 1985 and 1986 cropping season.
P_0, P_1, P_2, P_3: See the footnote of Table 1.

season, and from the initial to 1st and 1st to 2nd generation in the dry season. Thus the data suggest that some density-dependent processes in the dry season operate in an earlier stage and lower density level than in the wet season.

Following Morris (1963), the values of slope b in the regression of log population density at a given generation on that at the preceding one were estimated for the statistical examination of the above results. As shown in Table 2, the b-values are less than unity in all the three cases, which gives numerical confirmation to the above conclusion. Since the sampling error in population estimation in each generation is sufficiently small in relation to the extent of population fluctuation among the field (Kusmayadi et al., 1990), the conclusion may be regarded as reliable and statistically valid (Kuno, 1971).

Characteristics of Adult Populations

Parasitism. Both nymphs and adults of the BPH were parasitized by Dryinid wasps, *Pseudogonatopus* spp., a Strepsiptera, *Elenchus* spp., and a nematode. The parasites usually leave the host's body in the adult stage, and the parasitism results in sterilization of either sex of the host attacked. The percentage of parasitism was estimated by dissecting the adult insect. As shown in Table 3, the total percentage parasitized by the three parasites is low in the initial generation, but shows a gradual increase with the progress in generation. The percentage parasitism by the nematode

Table 3. Proportion of parasitized adults (%) in each generation.

Wing form	Generation	nematode	Dryinid	Strepsiptera	total
Macropterous	Initial	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	1st	2.5 (7.8)	0.5 (2.8)	1.5 (7.9)	4.5 (8.9)
	2nd	2.1 (12.2)	0.1 (0.8)	0.3 (0.9)	2.6 (12.6)
	3rd	0.7 (4.7)	0.0 (0.0)	0.3 (1.0)	1.0 (5.7)
Brachypterous	Initial	1.3 (6.5)	0.0 (0.0)	0.0 (0.0)	1.3 (6.5)
	1st	6.5 (33.3)	0.0 (0.0)	0.5 (1.6)	6.9 (33.3)
	2nd	5.2 (25.5)	0.1 (0.5)	1.0 (2.7)	6.4 (26.5)
	3rd	2.6 (15.1)	0.8 (3.8)	4.4 (13.9)	7.8 (21.5)

Values are shown as the mean of seven study sites, with the maximum values among the sites in parentheses.

Table 4. Proportion of macropterous adults (%) in each generation.

Sex	Cropping season	Generation			
		initial	1st	2nd	3rd
female	wet season 1984/85	60.7	6.5	29.8	68.0
	1985/86	61.0	8.5	33.1	55.2
	dry season 1985	85.9	25.0	18.0	50.0
	1986	64.7	34.0	20.7	50.1
male	wet season 1984/85	83.8	26.3	43.6	82.6
	1985/86	90.0	20.1	46.5	76.4
	dry season 1985	89.2	49.2	25.2	65.2
	1986	92.7	50.8	35.8	67.0

Values are shown as the mean for all the study sites in each cropping season.

is the highest among the three parasites.

Proportions of different wing-forms. BPH has two wing-forms in the adult stage, macropterous form which can fly with wings and the brachypterous one which cannot fly. The former is regarded as the migratory type to find a new habitat, whereas the later, as the sedentary type to breed under suitable habitat conditions.

The proportion of macropterous adults at each generation was presented as the average among the study sites, for the four cropping seasons (Table 4). The majority of the adults in the initial generation were macropterous individuals that may have immigrated from the outside, but some brachypterous adults that may have originated from the eggs oviposited in the nursery bed were also observed. The percentage of the brachypterous form in the initial generation was higher in the wet season than in the dry season. After the initial generation a considerable difference in the seasonal prevalences of adult wing-form is observed between the two cropping seasons. In the wet season, most of the 1st generation females were of brachypterous form, and thereafter the proportion of macropterous females gradually increased with the progress of generation. These distinct seasonal changes in the proportion of adult wing-form may reflect the gradual deterioration of the habitat conditions, such as seasonal maturing of the host plant and increase of the population density (Kisimoto, 1965), and may account for gradual decrease of the reproduction rate with proceeding generations as shown in Table 1.

In the dry season, however, such a distinct pattern can not be detected, the proportions of different wing-forms showing more irregular variations among the generations, and also among the fields. The proportion of macropterous female in the 1st generation is apparently higher than in the 2nd generation in general (Table 4), and widely varies with the field, i.e. from 10% to 90% among the nine study sites in the 1985 dry season (Fig. 7). Since the rice cultivation continuously succeeds from the wet to the dry cropping season (see, Fig. 2), macropterous migrants produced in the late stage of the wet crops may frequently invade the early stage paddy field of the dry crops. Thus the number of macropterous adults invading in each field in the early dry

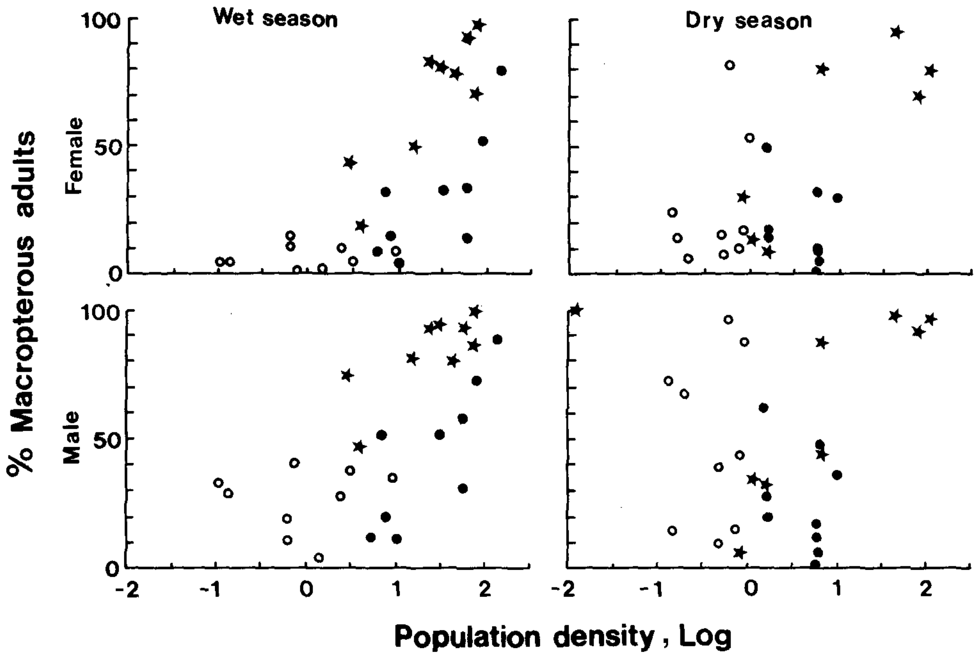

Fig. 7. Relations of the percentage of macropterous adults (%) to the population density in corresponding generations in each field, in the 1984/1985 wet (left) and 1985 dry (right) seasons. Each symbol shows 1st (○), 2nd (●), and 3rd (★) generation.

season may be strongly influenced by the proximity of the field to the source of immigrants in spatially heterogeneous rice cropping system in this region. The proportion of macropterous male were consistently higher than those of females in both the cropping seasons.

In the wet season, a distinct tendency for the proportion of macropterous females to increase with increasing population densities is observed in both the 2nd and 3rd generations (Fig. 7), the range of variation being 5% to 80% in the 2nd generation and 20% to 100% in the 3rd generation. Such a density-dependent variation in the proportion of macropterous females may be one of the probable mechanisms for population stabilization detected in the late stage of the wet season (Table 2), since most of the macropterous females that emerge in the field become emigrants and do not participate in the reproduction at that place. In the dry season, however, such density-dependence in the proportions of wing-forms could not be detected in the 2nd generation, which may indicate that the population densities at that time were much lower than the level above which the density-dependent increase of macropterous adults may occur.

Longevity or residence period. Adult longevity is closely related to the actual fecundity in the field, since the female adults begin to lay eggs several days after their emergence and the oviposition continues through a long period thereafter. The adult longevity (or residence period) was estimated by applying Hokyo and Kiritani's (1967) dissecting method on the basis of percentage incidence of the pre-mature females during the period of a given generation. Here, the daily survival rate, K, and mean longevity, L, in a given generation are estimated from the following formulae.

$$\hat{K}=\left\{\left(1-\frac{\hat{F}_{\alpha}}{\hat{F}}\right)\right\}^{\frac{1}{\alpha}}=\hat{P}^{\frac{1}{\alpha}},\quad \hat{L}=\frac{1}{1-\hat{K}} \qquad (1)$$

where F = the sum total of the numbers of females, $F\alpha$ = that of the females with inmature ovaries, P = the proportion of females with mature ovaries and α = mean length of the period for ovarial maturation in days.

The mean longevity of unparasitized brachypterous females was estimated for each field and each generation, by using the value 2.5 (days) for α which was determined experimentally by rearing adults on potted rice plants. Table 5 presents the thus obtained estimates of longevity as the mean for all the study sites in each cropping season. The estimates of mean longevity ranged from 3.4 to 11.8 days, showing the highest values at the initial generation and declining with the progress in the generation. Early in the cropping season, the brachypterous longevity in the wet season tends to be much longer than that in the dry season. Since brachypterous females are very inactive in their movement unlike the macropterous adults, such a difference in longevity between the two cropping seasons may be ascribed to the action of biological mortality factors such as predators.

In Fig. 8, the proportions of females with mature ovary, which are comparable to the daily survival rate, K, and the mean longevity, L, as shown in formula (1), are plotted for macropters and brachypters, on the population density in each field in the different seasonal generation. The figure indicates that the proportion of mature females in macropterous adults has a definite tendency to decline with the progress in seasonal generation and also with the increase in population density. The proportion of mature adults, for instance, decrease from nearly 100% to 50%, as the population density increases from 0.01 to 0.1 per hill in the initial generation in the dry season crop and also with the increase from 0.1 to 1.0 per hill in the 1st generation in both the wet and dry season crops (Fig. 8). Since the macropterous adults can easily disperse from one field to another, such a change in the proportion of mature adults suggests that the residence period and hence the dispersal activity of macropterous adults

Table 5. Longevity of brachypterous adults (days) in each generation estimated by Hokyo and Kiritani's (1967) dissecting method.

Cropping season	Generation			
	initial	1st	2nd	3rd
wet season 1984/85	11.8	11.0	9.3	5.5
1985/86	9.9	9.2	5.9	4.7
dry season 1985	8.6	6.2	5.4	5.4
1986	—	5.2	5.3	3.4

See the footnote of Table 4.

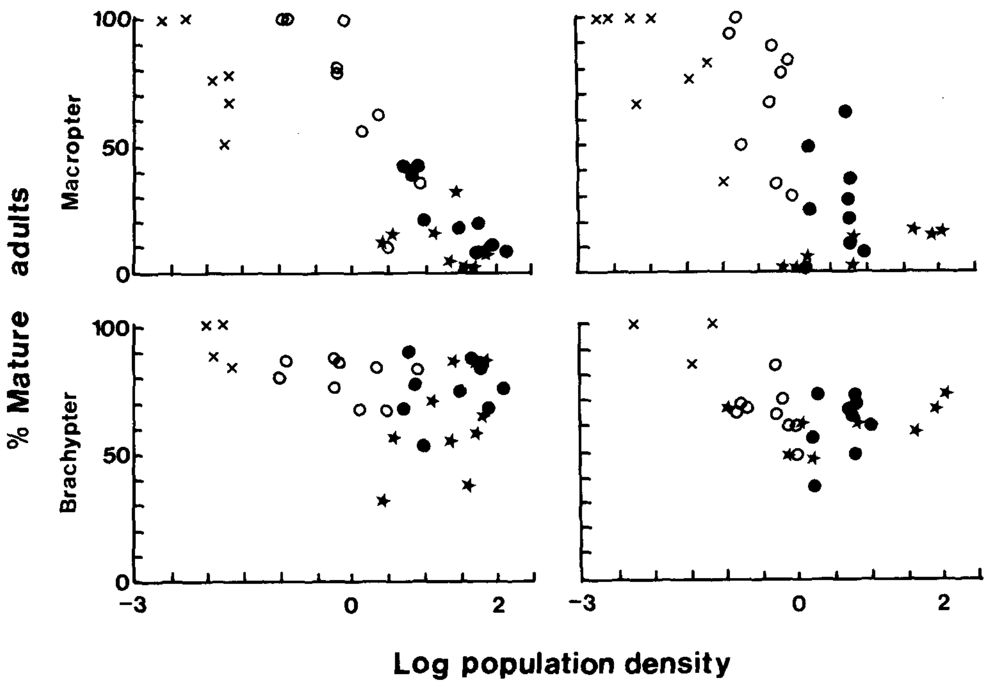

Fig. 8. Relations of the proportion of mature adults (%) to the population density in corresponding generations in each field, in the 1984/1985 wet (left) and 1985 dry (right) seasons. Each symbol shows initial (×), 1st (○), 2nd (●), and 3rd (★) generation.

sensitively respond to both the population density and the suitability of the host plants. In the late stage of both cropping seasons, most of macropterous adults may emigrate from the field. The proportion of mature females in brachypterous adults, however, did not show such a characteristic change as observed in macropterous

Table 6. Population density of major predators in each generation.

Predator	Cropping season	Generation			
		initial	1st	2nd	3rd
spiders	wet season 1984/85	0.194	0.684	2.69	5.76
	1985/86	0.413	1.143	3.24	4.48
	dry season 1985	0.922	1.876	4.67	3.78
	1986	0.923	2.018	5.15	7.98
Microvelia	wet season 1984/85	0.048	0.766	3.39	2.10
	1985/86	0.304	1.488	4.02	3.20
	dry season 1985	0.455	1.991	2.40	0.67
	1986	0.553	2.234	2.34	2.21
Cyrtorhinus	wet season 1984/85	0.005	0.082	1.37	6.90
	1985/86	0.003	0.044	0.89	3.13
	dry season 1985	0.015	0.056	0.27	0.45
	1986	0.009	0.124	1.11	3.47

See the footnote of Table 4.

adults.

Abundance and Role of Predatory Natural Enemies

Among the predators of the planthopper, several species of spiders such as *Lycosa pseudoannulata* and *Oxyopes javanus*, a veliid, *Microvelia douglasi* which attacks young nymphs, and a mirid, *Cyrtorhinus lividipennis* which attacks eggs and young nymphs were predominant in abundance. In addition, a coccinellid beetle, *Micraspis lineata,* rove beetles, *Paederus fuscifes* and *P. tamulus,* a ground beetle, *Ophionea ishii*, a water bug, *Mesovelia vittigera* and some others were also continuously observed in each study plot, though the population density of these enemies was much lower than that of the first three predators. The representative population densities of these major predators in the study sites were respectively estimated as the mean values of their incidence numbers in each period of the BPH generations, and these are shown in Table 6.

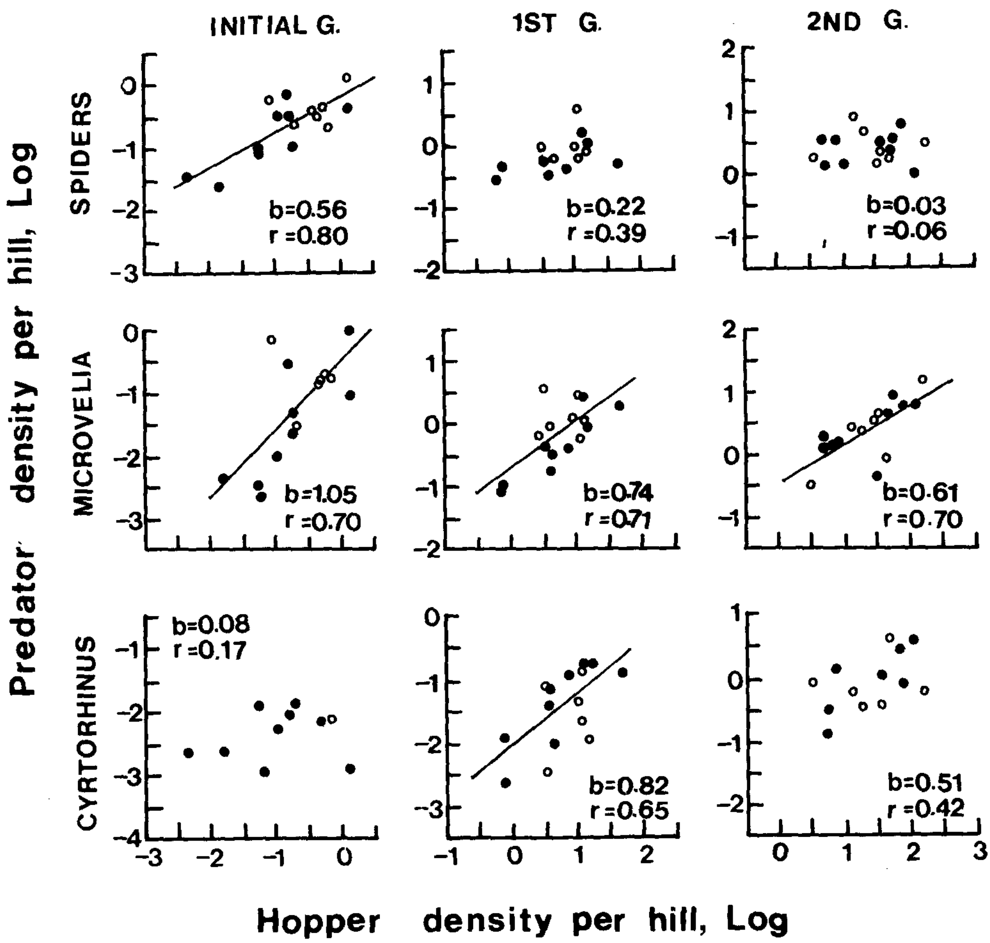

Fig. 9. Numerical correlations between the planthopper and each of major predators in each seasonal generation, in the 1984/1985 (●) and 1985/1986 (○) wet seasons. Lines show significance of correlation coefficients, r, at $P<0.05$.

Early in the cropping season, population levels of spiders and the other predators were much higher in the dry season; in fact, at the initial generation, they are several times higher than those in the wet season. Most paddy fields in this region are completely dried up for two or three months in the fallow period after the harvest of the dry season crop (Fig. 2). Accordingly, marked decrease in the abundance of natural enemies may be inevitable during this fallow period, and this may result in the low density of their population colonized in the early wet season paddies.

Figs. 9 and 10 show the relationships between the density of each species of major predators and the total population density of leaf- and plant-hoppers in the relevant BPH generations for the wet and dry cropping seasons. In the wet season, the spider population shows a significant correlation with the prey density at the initial generation. This high correlation suggests that the success in the early colonization of spiders in the paddy fields is dependent on the prey abundance there. However, such

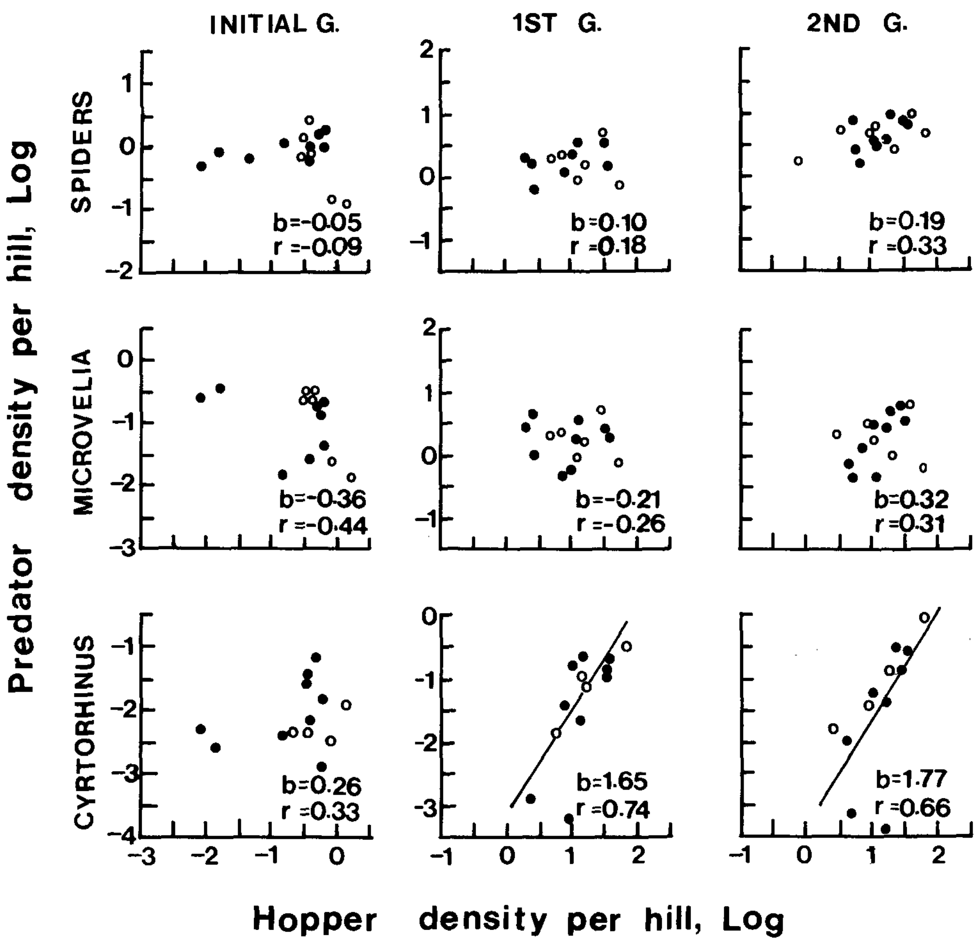

Fig. 10. Numerical correlations between the planthopper and each of major predators in each seasonal generation, in the 1985 (○) and 1986 (●) dry seasons. Lines: Refer to the footnote of Fig. 9.

a correlation becomes less conspicuous with the progress of seasonal generations, indicating that the total spider population growth takes a saturation type curve that lacks numerical response above a certain prey population density. In contrast to spiders, *Microvelia* and *Cyrtorhinus* show a rather high response to the prey density, even in the late wet season when the planthopper population reaches the peak in density (Fig. 9). In the dry season, such a significant correlation was observed only in the case of *Cyrtorhinus* (Fig. 10).

The effects of the major predators on the BPH population growth rate were examined for each generation of BPH in the wet and dry seasons (Figs. 11 and 12). In the wet season (Fig. 11), some negative correlations between the predator density and the prey population growth rate are observed in the later cropping season. This

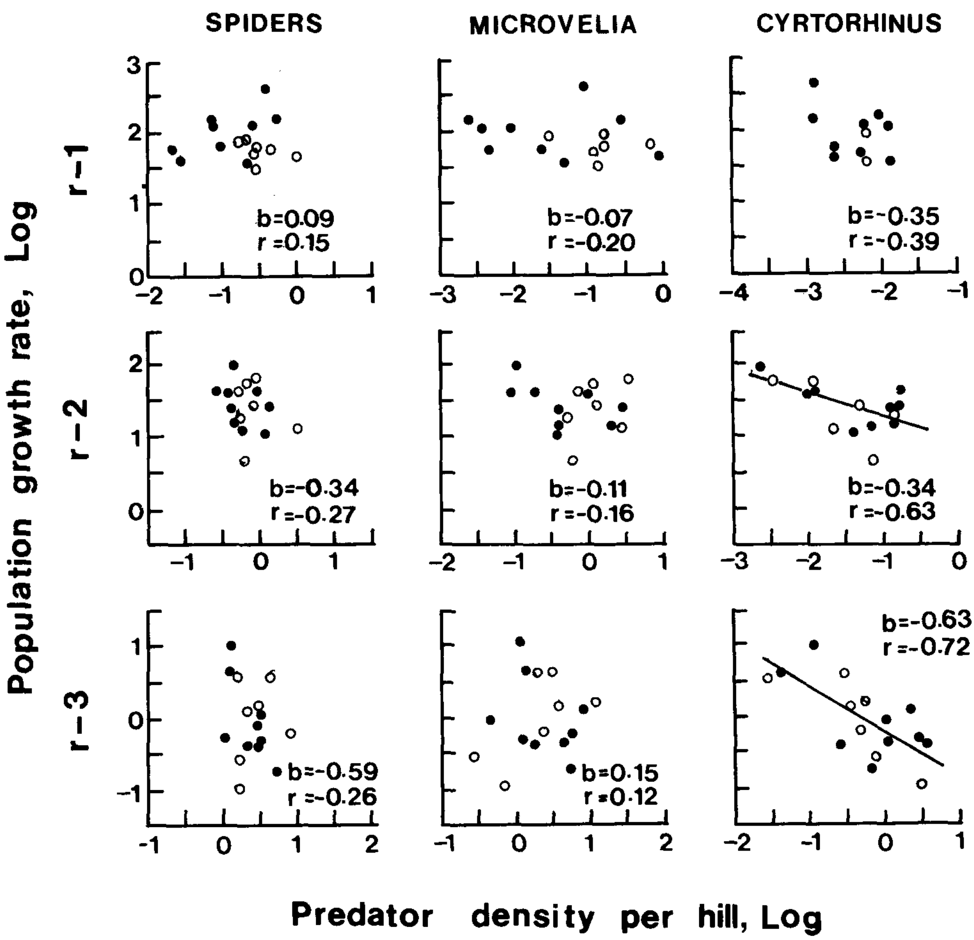

Fig. 11. BPH population growth rates and predator densities in the wet season. The population growth rates of BPH from a given generation to the next are plotted to the population density of major predators in that generation, in the 1984/1985 (●) and 1985/1986 (○) wet cropping seasons. Lines and r1, r2, r3: Refer to the footnotes of Fig. 9 and Table 1, respectively.

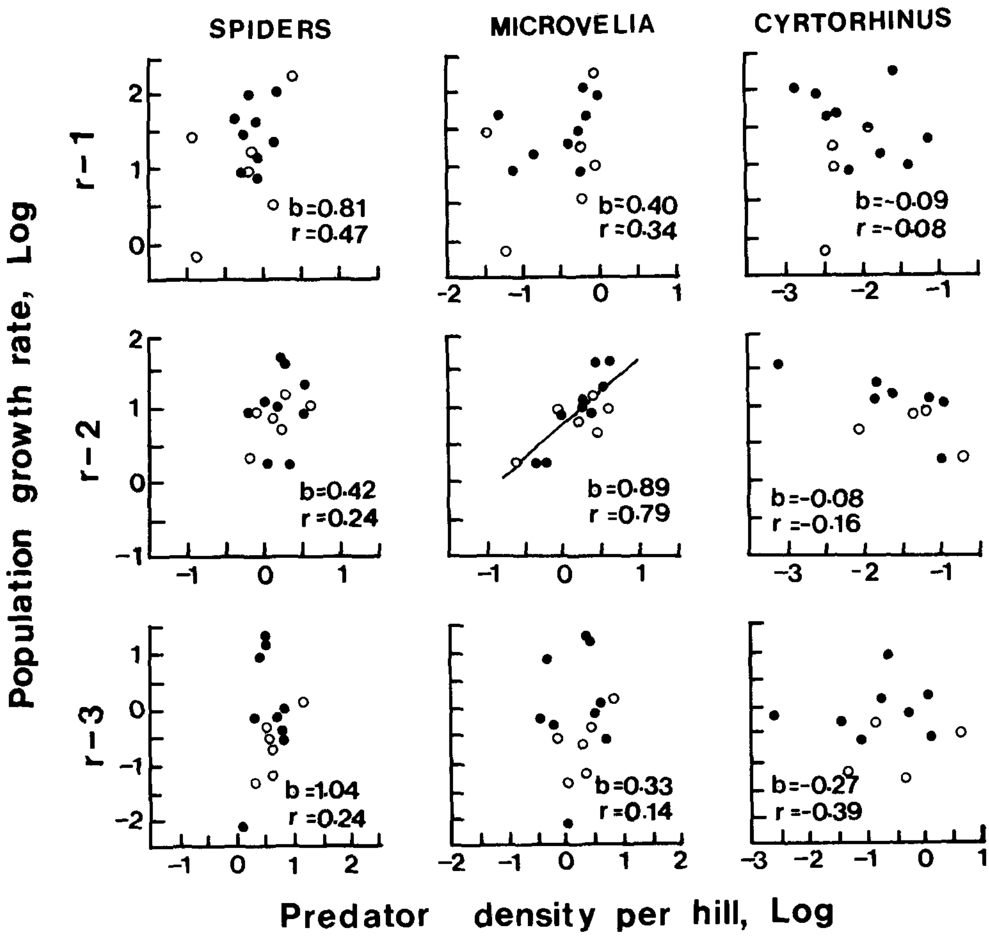

Fig. 12. BPH population growth rates and predator densities in the dry season. The population growth rates of BPH from a given generation to the next are plotted to the population density of major predators in that generation, in the 1985 (●) and 1986 (○) dry cropping seasons. Lines and r1, r2, r3: Refer to the footnotes of Fig. 9 and Table 1, respectively.

indicates that the local BPH population growth rate in the later period is influenced to some extent by the predators though the effects seems to be generally weak. In the dry season, however, no such negative correlations as observed in the wet season were prevailed. Moreover, a highly positive correlation was detected between the density of *Microvelia* and the BPH population growth rate from 1st to 2nd generation, r_2 (Fig. 12). Since *Microvelia* inhabits the water surface, its abundance is probably affected by the state of water supply to the field through the local irrigation system. Thus the positive correlation suggests that the BPH population growth rate might surmount the predation pressure under the condition of sufficient water supply in the dry season. More intensive life table studies (Sawada and Subroto, 1991) indicated that the realized daily fecundity per female of the BPH widely varied reflecting the difference in water supply among paddy fields. These lines of evidence strongly suggest that the irrigation factor in the dry season is primarily important in determining the among field variation of population density at the peak generation, because the peak population density is governed by the behaviour of r_2 (Fig. 5, right).

Discussion

Factors Determining the BPH Population Densities in the two Rice Cropping Seasons

The number of initial immigrants of macropterous adults in paddy fields was generally much higher in the dry season than in the wet season. In the wet season which follows the two or three months of fallow period, macropterous immigrants probably invade into the field after a rather long distance migration from southern, mountainous areas where rice is continuously cultivated throughout the year. By contrast, in the dry season, they can invade there readily from the neighboring paddy fields which are at the late growing stage of the wet season crops, because there is no fallow period in transition from the wet to dry season crops. Thus the abundance of macropterous immigrants in the paddy field seems to be strongly influenced by the proximity to the source of immigrants in each cropping season (Cook and Perfect, 1989).

In the wet season, BPH populations multiplied rapidly and serious outbreaks occasionally occurred in the late cropping season, despite the fact that the initial immigrant density was much lower than in the dry season. These patterns of BPH population development are quite similar to those observed in temperate regions like Japan (Kisimoto, 1977; Kuno and Hokyo, 1970a). In the dry season, however, the levels of the overall population growth rate and the peak population density are much lower than those in the wet season. Such a difference results from the disparity in population growth rates at the early stage of the two cropping seasons (Table 1). The lower population growth rates in the early dry season may be explained at least partly by the higher predation pressure, because the population level of major predators is much higher, and also the estimated longevity of brachypterous adults whose mortality is largely attributable to the action of predators is much shorter than in the early wet season. Kuno and Hokyo (1970b) estimated the longevity of brachypterous adults at 8.1 days for the first generation of natural population in Japan by the same method used in this study. As shown in Table 5, the brachypterous longevity in the wet season is longer, but much shorter in the dry season than in the case observed in Japan. Besides the predators, the abundance of parasitic wasps which attack BPH eggs was 10–20 times as high as that in the early wet season (Sawada et al., unpublished). Since most paddy fields in this region are completely dried up for two or three months as the fallow fields after the harvest of the dry season crop, the population density of natural enemies may remarkably decrease during such the period in association with the decline of the relevant insect community in the region. Accordingly, the BPH population may realize a rapid increase in the early stage of paddy fields just after the fallow. Except for the population density of natural enemies, no distinct differences in the factors such as climate, irrigation and cultural practices, etc. were observed between the early stage of the two cropping seasons.

In addition to the difference in the average of the peak generation density, a marked difference in its variation among paddy fields was also detected between the two cropping seasons. In the wet season, a high correlation was observed between the population densities at the initial and the peak generation in each field, because the rate of population growth was quite stable among paddy fields over several generations. This means that the peak population density and the occurrence of BPH outbreaks are predictable with considerable certainty by estimating the initial population density. The role of predators was of secondary importance as the factor contributing to the among field fluctuation of the peak density of the BPH, because the predators density was low in general and relatively stable among paddy fields. These situations indicate that the field conditions in the wet season are highly suitable for the BPH population growth as a whole in this region.

However, in the dry season, the rate of overall population growth is not only lower on the average, but also much more variable among paddy fields than in the wet season. Thus the peak generation density fluctuated among the fields showing a high correlation with the overall population growth rate, in particular, the growth rate in the middle stage of the cropping season (Fig. 5). Several evidences suggested that the water status in each field was primarily important in determining such a fluctuation in the population growth rate and the peak density. In fact, the BPH outbreaks in the dry season occurred only at site f (Fig. 4), where the density of initial immigrants was the lowest among the nine study sites, while the paddy water was fully supplied there by the local irrigation system throughout the cropping season.

Detection of the Density Dependent Processes

Analyses of the density relationship between successive generations indicated that density-dependent processes regulating the population density exist in both cropping seasons. However, the level of population density around which the regulatory processes operate was quite different between the two cropping seasons, which indicates that the causal mechanisms leading to population regulation are also quite different between the two cropping seasons. In the wet season, the regulatory processes are only detectable at such a high density as to cause considerable deterioration of the host plant, which suggests that the processes are largely attributable to the intra-specific competition as shown in temperate regions (Kuno and Hokyo, 1970a). In fact, the proportion of macropterous females or emigrants widely varied depending on their population density in the fields.

However, in the dry season, regulatory processes were detected at much lower density levels, and only detectable in the early stage of the cropping season. An analysis of adult longevity or residence period showed that: (1) There is no density-dependence in daily survival rate or mean longevity in brachypterous adults, and this suggests that the action of predators has no density-dependence. (2) There exists a distinct tendency of density-dependence in the residence periods of macropterous females in the early dry season. This indicates that the dispersal of macropterous adults sensitively responds to the population density in the field. Since the flight activity of macropterous females occurs in the pre-mature stage (Ohkubo and Kisimoto, 1971), such a density-dependence should be realized within the short period after emergence. This may be the reason why the density-dependence in macropterous dispersal is less conspicuous in the initial generation of the wet season (Fig. 8) in which it takes a rather long period for macropterous immigrants to invade the new habitat in consequence of the long distance migration. In contrast, in the dry season macropterous adults can easily invade into the young paddy fields from the late wet season paddies, and may frequently disperse depending on the population density among the paddy fields of the early dry season crops. It thus may be concluded that such the dispersal of macropterous adults plays a major role in regulating the population density which shows the great fluctuation among the fields owing mainly to the proximity to the source of emigrants in the spatially and temporally heterogeneous rice cultivation system in transition from the wet to dry season crops. These features of the BPH population characterized by the distinct regulatory process operating at the low density level may exhibit their status as the indigenous population, and which makes a sharp contrast to the status of BPH population in temperate regions as the temporary fringe population which is recruited every year by the long-distance migration of macropterous adults from their original area.

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インドネシア西ジャワ北部平野の雨季作と乾季作での トビイロウンカの個体群特性の比較

沢田裕一・A. Kusumayadi・S. W. G. Subroto
E. Suwardiwijaya・Mustaghrin

インドネシア西ジャワ州北部平野の，のべ31ヶ所の水田でトビイロウンカ *Nilaparvata lugens* (Stål) の個体群動態を調査分析した．この地域の水田でのトビイロウンカの個体群発生は，初期水田への長翅成虫の侵入によって開始され，短翅成虫を主体とした増殖世代を経てピーク密度に達し，個体群の発生パターンに明瞭な季節性の存在することが示された．各調査地ごとに世代密度を推定し，世代間の季節的増殖パターンと場所間での世代密度の変動パターンを分析した結果，雨季作と乾季作で，以下の三点について顕著な相違が認められた．

1）ピーク世代の密度レベル：雨季作の個体群増加率とピーク世代密度は，日本など温帯地方の個体群に匹敵する高いレベルを示したが，乾季作では，雨季作に比べはるかに低いレベルに抑えられた．卵巣解剖法による短翅成虫の平均寿命やクモ類などの多食性捕食者の密度を推定・分析した結果，捕食者などの天敵生物の作用が両作期での個体群の密度増加率やピーク世代の密度レベルを決める基本的要因だと推察された．

2）ピーク世代密度の予測性：雨季作では，ピーク世代密度の変動は初期の個体群密度によりかなり正確に予測されること，他方，乾季作では初期密度によるピーク密度の予測は困難なことが示された．雨季作では，世代間の密度増加率が場所間で安定した変動を示すため，各世代の密度変動の間に高い相関が検出された．乾季作では，密度増加率の場所間での変動が大きいため，ピーク世代密度の変動は，初期の個体群密度よりも，その後の密度増加率に強く影響された．密度増加率の場所間での変動を決める要因として，灌漑や降雨による水田内での水利条件の重要性が指摘された．

3）密度調節過程の作用：雨季作では作期の後半の高い密度レベルで，乾季作では前半の低い密度レベルで調節過程の作用が検出された．雨季作では，寄主条件の悪化にともなう長翅型率の増大や幼虫生存率の低下などの種内競争が，密度調節の主要な要因だと考えられた．他方，長・短翅成虫の寿命や捕食者の作用を分析した結果，乾季作の初期水田で比較的低い密度レベルで作用する密度調節過程では，長翅成虫の移動率の増加やそれにともなう産卵数の低下が，主要な役割を果たしていると推論された．雨季作から乾季作にかけて作期は連続し，稲の発育ステージの異なる水田が混在するため，長翅成虫は比較的近距離の移動によって乾季作の初期水田に侵入する．従って，長翅成虫の移動分散特性とそれによる密度調節過程は，長距離移動をともなう日本など温帯地方での個体群とは異なる，定住個体群としての特徴を示していると考えられた．