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THE SPATIAL DISTRIBUTION PATTERN OF THE BROWN PLANTHOPPER *NILAPARVATA LUGENS* STÅL (HOMOPTERA: DELPHACIDAE) IN WEST JAVA, INDONESIA

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Introduction

The brown planthopper (BPH), *Nilaparvata lugens* Stål has recently become one of the most destructive insect pests of rice in Indonesia as in many other countries of South-East Asia (e.g., Dyck and Thomas, 1979). Both nymphs and adults of BPH suck sap from the phloem of growing rice plant, causing severe damage called 'hopper-burn'. In addition, they transmit 'grassy stunt' virus disease which further reduces the yield considerably.

To establish an efficient strategy to control BPH, basic population characteristics of this species in the region concerned must first be understood on the basis of analysis of field population data. In particular, analysis of distribution pattern is an essential first step not only for better understanding of its population dynamics (e.g. Iwao, 1970) but also for deriving efficient sampling plans for estimating population density from time to time (e.g. Kuno, 1977).

Most of the intensive studies on the spatial distribution pattern of BPH have been conducted in Japan and much information has been accumulated on its characteristics (Suenaga and Nasu, 1954; Kuno, 1968; Kuno, 1977). In Indonesia, however, almost no information has been reported on the spatial pattern of this species except for Ôtake and Hokyo's (1976) analysis of its adult spatial distribution pattern. In this study, we present detailed information on the spatial distribution pattern of this species for both nymphs and adults.

Materials and Methods

The Insect

In the tropics the life cycle of BPH is completed in about one month. Adult females become mature and copulate a few days after emergence. Then, they begin and continue to lay eggs in masses each consisting of 1 to 62 eggs (Mochida and Okada, 1979) in the tissue of rice plant mainly in the leaf sheath. Although the potential fecundity of this species is very high being about 2000 per female (Suenaga, 1963), the number of eggs actually laid by a female is usually not more than 500 (Kuno and Hokyo, 1970). The average developmental time of egg is 10.4 days at 25°C constant, and 7.9 days at temperature between 27–28°C (Mochida and Okada, 1979). The nymph has five instars. The average period required for the completion of nymphal stage is 14.3 days at 25°C constant, and 12.0 days at temperature between 27–28°C (Mochida and Okada, 1979). Both male and female adults show wing polymorphism, i. e. macropterous and brachypterous forms. Wing form determination occurs during nymphal development, depending on the density of the nymph. The macropterous form predominates at higher densities, and the brachypterous form at lower densities (Kisimoto, 1956).

Experimental Fields and Census Methods

The data analyzed in this study were collected from December 1984 to August 1985 on nine experimental plots distributed in an open paddy field in the northern coastal area of West Java (Fig. 1) by the research team of the Indonesia-Japan Joint Program on Food Crop Protection Project. There are two different seasons in this region: the wet and dry season. The wet season (December to March) has an average amount of rainfall of more than 200 mm per month, while the dry season (April to September) has less than 200 mm of average rainfall. Corresponding to these seasons farmers set out rice seedlings twice a year, in December and May respectively.

The size of each experimental plot was 20 × 30 m, except in Jatisari, where it was 20 × 50 m. A susceptible rice variety, Pelita I_1, was grown in the plots at a spacing of 25 × 25 cm. No insecticide was used throughout the study, but other cultural practices were done in accordance with farmers' practices.

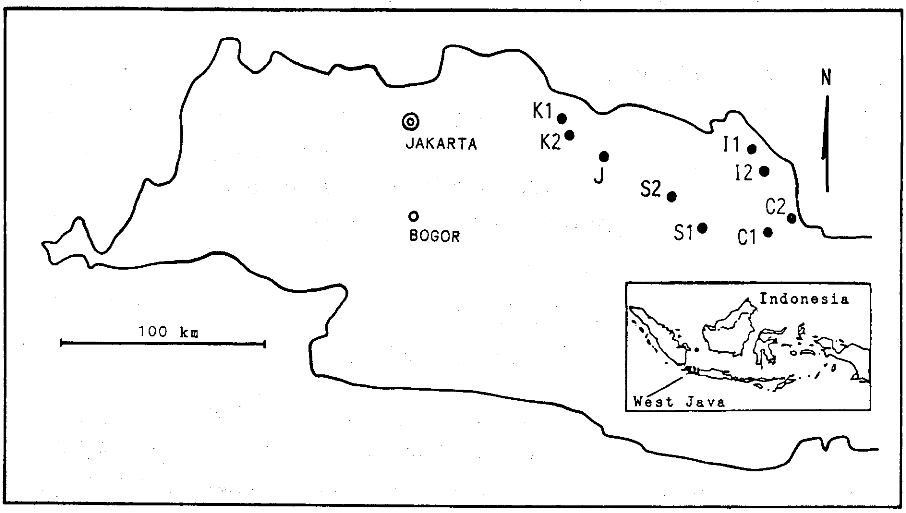

Fig. 1. Locations of the experimental fields. C1 = Cirebon 1, C2 = Cirebon 2, I1 = Indramayu 1, I2 = Indramayu 2, J = Jatisari, K1 = Karawang 1, K2 = Karawang 2, S1 = Subang 1, S2 = Subang 2.

In both the seasons census was started a week after transplanting, and continued at weekly intervals until harvest. During each census 50 sampling units in Jatisari and 30 in the others were extracted by a systematic procedure with a random start. The standard sampling unit adopted for the present study was a hill of rice plants. But in the earlier period of the season (until 7 weeks after transplanting) in which each rice hill was fairly tiny and BPH density was generally low, the census was made by sampling a quadrat comprising four adjacent hills as the unit. In the present distribution analyses, these data based on four-hill unit were pooled together with those based on the standard one-hill unit without discrimination, since no consistent difference in distribution characteristics could be found between both the data series.

A FARMCOP suction machine powered by a 12 volt car battery (Cariño et al., 1979) was used for collecting insects from the hill. Sampled insects were examined in laboratory under binocular microscope. Only adults and 3rd-5th instar nymphs (hereafter simply referred to as 'nymphs') were counted due to difficulty in identifying younger nymphs. In the adults, macropters and brachypters of both sexes were separately counted.

ANALYTICAL PROCEDURE AND RESULTS

In this study, statistical analysis of the pattern of spatial distribution was made according to the following procedure, based on the frequency distribution of the number of individuals per sampling unit: (1) Description of general pattern by fitting some mathematical models to the observed frequency distribution. (2) Description of quantitative feature of individual distributions by statistical measurement of the degree of aggregation. (3) Overall characterization of the distribution pattern and analysis of its variations among different developmental stages, wing forms, locations, or seasons by using some standard techniques.

Fitness to the Poisson Distribution

To determine whether the distribution of each developmental stage departs from randomness, the count of BPH per sampling unit was examined in terms of the variance-mean ratio. The random (Poisson) distribution is characterized by the equality of mean to variance. The statistic $I=\frac{(n-1)s^2}{m}$, which is known to follow approximately the chi-square distribution with n-1 degrees of freedom, was used to test the fitness of the observed distribution to the random distribution. A summary of the goodness-of-fit test to the random distribution is shown in Fig. 2. In most cases the values of variance-mean ratio for each developmental stage exceeded the critical value of $P=0.05$ for the random distribution. When mean density was still very low (during the earlier stage of the rice), however, the ratios did not seem to depart from the randomness.

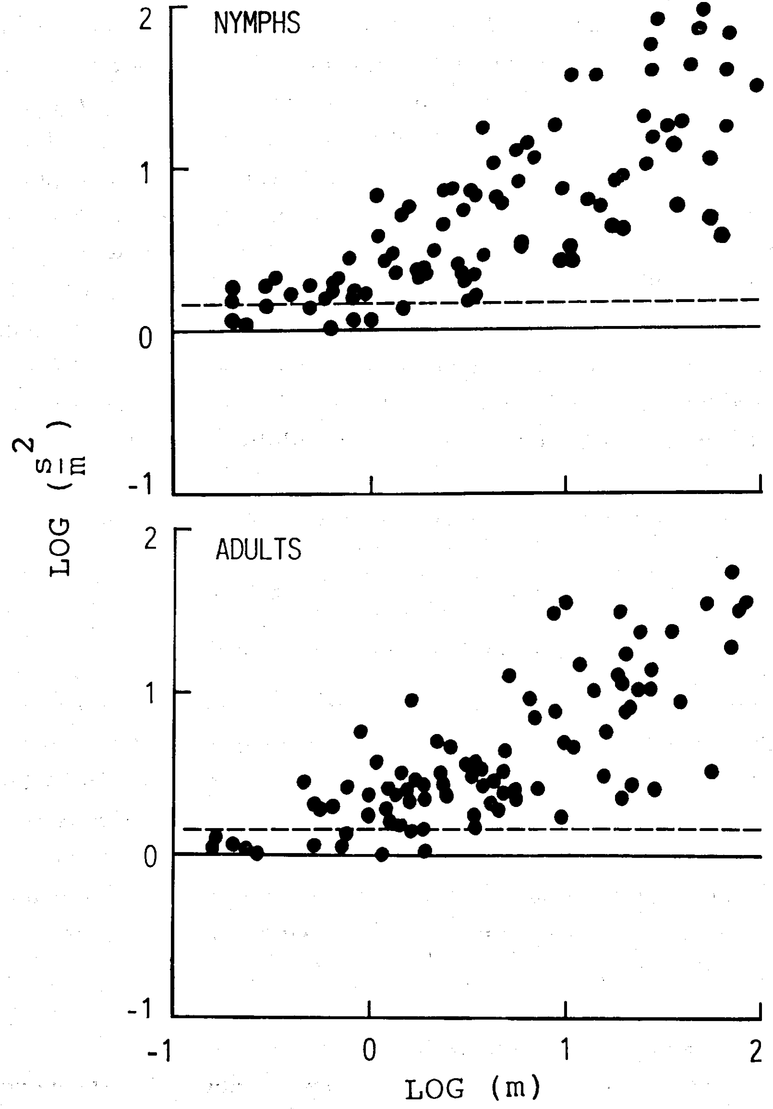

Fig. 2. Relation of the variance-mean ratio to the mean. Broken line is the critical value at $P=0.05$ for the random distribution.

Fitness to the Negative Binomial Distribution

The negative binomial model is known to be most widely applicable for describing the spatial distribution of insects. The variance in the negative binomial distribution is equal to $m+m^2/k$ or $m+m^2C_A$ where m is the mean and k or its reciprocal C_A is a parameter related to the degree of aggregation or contagiousness (Kuno, 1968). Namely, a series of observed distributions will follow this model if the variances increase quadratically with the means.

The fitness of observed distributions to the negative binomial model was tested according to the method proposed by Anscombe (1950). The goodness of fit of the counts for each developmental stage and wing form was examined using Anscombe's statistic:

$$T=\frac{1}{n}\sum_{i=1}^{n}(x_i-m)^3-s^2\left(\frac{2s^2}{m}-1\right)$$

and its standard error :

$$\mathrm{SE.T}=\sqrt{\frac{1}{n}\cdot\frac{2}{C_A}\left(\frac{1}{C_A}+1\right)p^3(1+p)^2\left\{2(3+5p)+\frac{3}{C_A}(1+p)\right\}}$$

where $n=$ sample size; $x_i=$ the number of individuals in the ith sample unit; $p=mC_A$. A summary of the goodness of fit to the negative binomial model for all the observed data is presented in Table 1. The results indicate that only two of the 329 samples tested showed significant departure from the model, showing that the distribution pattern of both nymphal and adult stages of BPH can be described fairly well by the negative binomial distribution.

Temporal Changes in Spatial Distribution Pattern

The temporal changes in spatial distribution pattern within each crop season were measured in terms of the C_A-index. Kuno (1968) defined that C_A-index equals to the squared coefficient of variation minus its expected value for the Poisson distribution:

$$CA=\left(\frac{s^2}{m^2}\right)-\frac{1}{m}$$

Thus, C_A should be zero for a random distribution ($s^2=m$); greater than zero for an aggregated distribution ($s^2>m$); and less than zero for a uniform distribution ($s^2<m$). The unbiased estimates of C_A for each developmental stage were calculated using the following equation:

$$C_A=\frac{s^2-m}{m^2-s^2/n}$$

Fig. 3 shows an example of the changes in spatial distribution pattern for nymphs and adults at Karawang 1 during the wet season. Temporal changes in the number of

Table 1. Summary of the goodness of fit test to the negative binomial distribution for nymphs and adults.

Season and BPH stage	Total number of samples tested	Average of T/SE.T values	Range of T/SE.T values	Number of samples showing departure from negative binomial distribution ($P=0.05$)
Wet season				
Nymphs	95	−0.31	−1.33∼3.02	1
Adults	95	−0.44	−2.25∼1.45	1
Dry season				
Nymphs	70	−0.39	−1.12∼0.80	0
Adults	69	−0.37	−0.98∼0.86	0

BPH for nymphs as well as for adults are also illustrated in the same figure. Population of each developmental stage generally showed exponential increase starting from the middle age of rice, reaching the peak several weeks later, and gradually declining toward the end of the crop season. Although population densities varied remarkably with time, the values of C_A-index for each developmental stage seemed to be independent of seasonal changes in mean density. Table 2 shows the relation between mean density and C_A-value for both nymphs and adults in terms of the correlation coefficient (r). The relative independency of C_A from mean density is apparently recognized by the lower values of r observed in most experimental plots in both the seasons.

Overall Feature of Distribution Pattern throughout the Crop Period

To interpret the general feature of BPH distribution throughout the period of each rice crop season, the overall distribution pattern of this insect was analyzed.

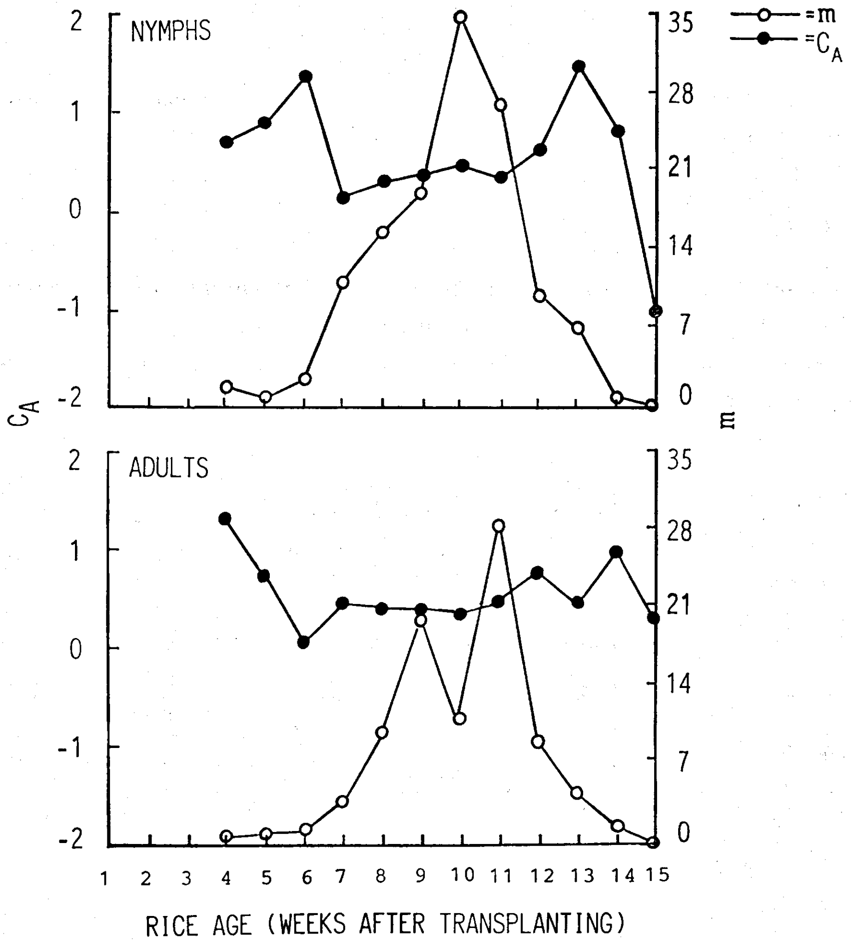

Fig. 3. Temporal changes in the degree of aggregation and number of BPH per hill at Karawang 1 during the wet season.

Table 2. Values of correlation coefficient between mean density and the C_A-index among successive samples for each developmental stage in each experimental field.

Season/Experimental field	Nymphs	Adults
Wet season		
C1	−0.535 (12)	−0.526 (10)
C2	−0.434 (11)	−0.652 (11)*
I1	−0.428 (10)	−0.515 (10)
I2	−0.593 (10)	−0.448 (11)
J	−0.421 (10)	−0.258 (11)
K1	−0.563 (11)	−0.257 (12)
K2	−0.352 (9)	0.711 (9)*
S1	0.034 (11)	−0.384 (11)
S2	0.131 (11)	−0.328 (10)
Dry season		
C1	−0.101 (6)	−0.405 (6)
C2	−0.464 (8)	−0.371 (6)
I1	−0.357 (10)	−0.485 (9)
I2	−0.366 (10)	−0.390 (11)
J	0.564 (9)	−0.064 (9)
K1	−0.010 (8)	−0.239 (7)
K2	0.097 (5)	−0.245 (6)
S2	0.598 (4)	0.556 (9)

Asterisks and numerals in parentheses indicate the significant correlation at $P=0.05$ and the number of samples examined, respectively.

Two approaches were adopted for this purpose, one utilizing Iwao (1968)'s $\overset{*}{m}$-m regression method and the other based on the weighted estimation of C_A-index ($=1/k$) by Bliss and Owen's (1958) method. The two methods are closely related in their mathematical background. In the first approach the spatial distribution pattern is examined using the linear relationship of Lloyd's (1967) mean crowding

$$\overset{*}{\mathrm{m}}=\frac{\sum_{i=1}^{n} x_i\,(x_i-1)}{\sum_{i=1}^{n} x_i}$$

to mean density (m), i.e., $\overset{*}{m}=\alpha+\beta m$, where α and β represent index of basic contagion and density-contagiousness coefficient, respectively. Fig. 4 shows an example of the $\overset{*}{m}$-m regression for nymphs and adults at Karawang 1 during the wet season. Tables 3 and 4 show values of the intercept α and the slope β of the $\overset{*}{m}$-m regression for each developmental stage at each experimental field. The relationship between $\overset{*}{m}$ and m for a given stage fitted well to a linear regression as judged by the r-values in the last column of the table. The fact that in most cases the confidence interval of α covers value of zero indicates that the basic component of the distribution in each developmental stage may be regarded as a single individual. The values of β in most locations were considerably greater than unity, indicating that individuals of this species at any

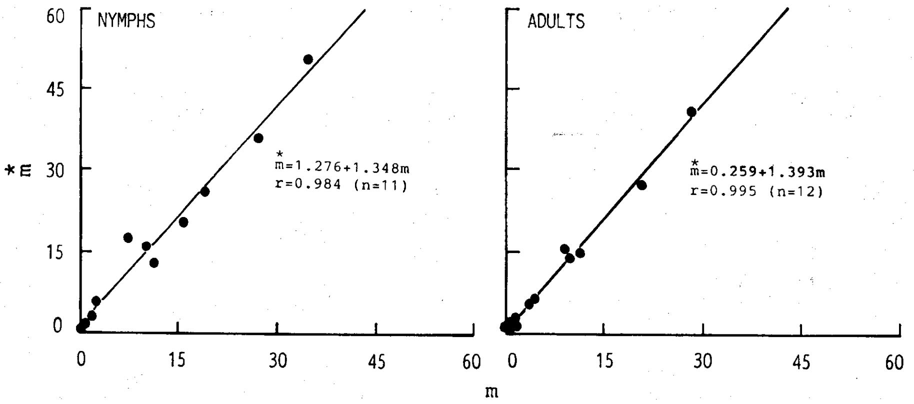

Fig. 4. Relation of the mean crowding ($\overset{*}{m}$) to the mean (m) of BPH at Karawang 1 during the wet season.

developmental stage have a consistent tendency to distribute themselves patchily.

In the second approach, quantitative feature of the overall distribution pattern is described by Bliss and Owen's (1958) method in terms of a single parameter, 'common C_A' ($1/k$), which can be obtained as the slope of the linear regression of y' on x' passing through the origin, where y' is s^2-m and x' is m^2-s^2/n. The use of this simpler and statistically more strict approach to summarize the overall feature of distribution of a given population becomes really meaningful when, as in the present case, the parameter α in the linear $\overset{*}{m}$-m relationship is nearly zero, since this condition implies that the C_A-value ($=\beta-1$) has a general tendency to remain fairly stable despite varying mean density (see Fig. 3). The weighted estimates of common C_A ($1/k$) with their 95% fiducial ranges thus obtained for both nymphs and adults in different locations and seasons are given in Table 5.

Variations of the Distribution Pattern within and among Populations

Table 5 shows that there are consistent variations in the degree of aggregation among different developmental stages in both the seasons. In most locations the values of common C_A for nymphs were higher than those of adults. The average mean values of C_A in the wet and dry seasons for nymphs were 1.026 and 1.102 respectively, whereas those for adults were 0.785 and 0.707.

Variations in distribution pattern were also observed among different wing forms. Except in some experimental fields, the values of common C_A for macropterous form were either similar to or lower than those for the brachypterous form. The average values of common C_A for the macropterous form in both the seasons, however, were higher than that of brachypterous form.

Large differences in the degree of aggregation were found between the wet and the following dry season in some experimental fields. For example, at Cirebon 1 the value of C_A for each developmental stage in the wet season was much lower than that in the

Table 3. Values of α and β with their fiducial ranges for $P=0.95$ of the $\overset{*}{m}$-m regression for each developmental stage in wet season estimated by the method of Iwao (1968).

Experimental field	α	β	$r(n)$
		Nymphs	
C1	1.400± 2.596	1.086±0.075	0.993 (12)
C2	9.551±20.401	1.191±0.317	0.926 (11)
I1	0.802± 4.438	1.673±0.237	0.979 (10)
I2	1.657± 1.811	1.249±0.068	0.996 (10)
J	5.548± 7.266	1.936±0.240	0.984 (10)
K1	1.276± 2.504	1.348±0.155	0.984 (11)
K2	1.556± 1.956	1.446±0.643	0.857 (9)
S1	−1.355± 2.654	2.442±0.902	0.870 (11)
S2	−1.736±14.162	3.273±0.749	0.934 (11)
		Total adults	
C1	1.3584± 2.408	1.308±0.098	0.991 (10)
C2	2.369± 4.652	1.337±0.108	0.992 (11)
I1	2.305± 2.018*	1.298±0.179	0.980 (10)
I2	1.319± 0.563*	1.164±0.044	0.998 (11)
J	6.069± 7.559	1.648±0.317	0.959 (11)
K1	0.259± 0.946	1.393±0.083	0.995 (12)
K2	−1.171± 0.773*	2.302±0.286	0.986 (9)
S1	0.296± 0.809	1.282±0.272	0.951 (11)
S2	2.684± 4.597	1.625±0.209	0.983 (10)
		Macropterous adults	
C1	2.078± 3.725	0.986±0.224	0.961 (8)
C2	3.288± 4.886	1.328±0.108	0.993 (9)
I1	3.686± 5.706	1.229±0.541	0.912 (6)
I2	0.493± 0.704	1.334±0.061	0.998 (8)
J	6.334± 6.678	1.964±0.462	0.922 (11)
K1	0.581± 0.929	1.502±0.090	0.997 (8)
K2	0.006± 1.231	1.953±0.892	0.927 (5)
S1	0.343± 0.496	1.288±0.839	0.866 (5)
S2	−1.373± 2.603	2.778±0.323	0.987 (9)
		Brachypterous adults	
C1	1.604± 1.172*	1. 023±0.090	0.993 (8)
C2	0.082± 1.848	1.490±0.284	0.972 (8)
I1	0.609± 0.676	1.585±0.127	0.993 (10)
I2	1.104± 0.909*	1.327±0.378	0.941 (8)
J	1.220± 2.032	1.697±0.199	0.985 (10)
K1	0.355± 0.499	1.270±0.104	0.991 (11)
K2	−0.912± 0.455*	2.315±0.168	0.995 (8)
S1	1.507± 1.697	0.943±0.576	0.794 (8)
S2	0.519± 0.756	1.578±0.045	0.999 (10)

Asterisks indicate that the confidence interval does not cover zero at $P=0.05$.

dry season. In some places, however, for example at Indramayu 1, the value of C_A for each developmental stage in the wet season was consistently higher than that in the dry season. Therefore, the effect of season on the degree of aggregation might be specific to each experimental field. However, using the average values of seasonal C_A

Table 4. Values of α and β with their fiducial ranges for $P=0.95$ of the $\overset{*}{m}$-m regression for each developmental stage in dry season estimated by the method of Iwao (1968).

Experimental field	α	β	$r(n)$
Nymphs			
C1	−0.517±0.780	1.957±0.116	0.998 (6)
C2	0.174±0.503	1.672±0.362	0.965 (8)
I1	2.054±2.373	1.128±0.039	0.998 (10)
I2	1.573±2.760	1.195±0.062	0.997 (10)
J	−8.229±5.506*	6.708±0.931	0.983 (9)
K1	0.016±3.517	1.745±0.574	0.924 (8)
K2	−1.359±1.882	3.789±0.707	0.986 (5)
S1	−0.185±0.864	1.580±0.526	0.972 (4)
S2	−0.440±0.918	2.259±0.030	0.999 (10)
Total adults			
C1	0.370±0.866	1.441±0.349	0.969 (6)
C2	0.639±1.140	1.338±0.473	0.941 (6)
I1	1.154±1.026*	1.096±0.090	0.994 (9)
I2	0.383±0.322*	0.164±0.053	0.998 (11)
J	1.075±3.594	1.749±1.606	0.628 (9)
K1	0.079±1.288	1.334±0.314	0.966 (7)
K2	−0.035±0.303	1.744±0.373	0.977 (6)
S1	0.040±0.235	1.562±0.265	0.866 (6)
S2	−1.261±1.941	2.393±0.285	0.987 (9)
Macropterous adults			
C1	0.102±0.344	1.612±0.142	0.997 (4)
C2	0.950±2.146	1.419±0.858	0.916 (4)
I1	2.954±2.074*	1.018±0.156	0.990 (5)
I2	0.512±0.347*	1.179±0.055	0.998 (7)
J	−0.614±0.954	5.692±0.941	0.986 (6)
K1	0.340±1.325	1.688±0.766	0.928 (5)
K2	0.297±0.470	1.119±0.958	0.850 (4)
S1	—	—	—
S2	−0.089±1.385	2.400±0.165	0.998 (5)
Brachypterous adults			
C1	0.950±1.648	0.867±1.262	0.613 (5)
C2	0.150±0.209	1.326±0.241	0.983 (6)
I1	0.677±0.617	1.041±0.255	0.949 (9)
I2	0.398±0.316*	1.192±0.149	0.987 (8)
J	0.384±0.708	1.460±0.366	0.953 (8)
K1	2.082±2.758	0.923±0.966	0.682 (6)
K2	−0.154±0.374	2.567±0.609	0.985 (4)
S1	0.326±0.390	1.330±0.512	0.946 (5)
S2	−0.025±1.015	1.620±0.409	0.953 (8)

Asterisks indicate that the confidence interval does not cover zero at $P=0.05$.

calculated from all experimental fields, no large difference in the degree of aggregation was found between the two different seasons for each developmental stage.

Among the 9 experimental fields, a large difference in the value of C_A for each developmental stage was found in both the seasons (Table 5). For instance, common

Table 5. The values of common C_A ($1/k$) with their fiducial ranges for $P=0.95$ for each developmental stage in wet and dry seasons, estimated by the method of Bliss and Owen (1958).

Experimental field	Wet season	Dry season
	Nymphs	
C1	0.156±0.076	0.770±0.447
C2	0.616±0.396	0.895±0.457
I1	1.070±0.531	0.372±0.221
I2	0.593±0.270	0.332±0.131
J	1.705±0.623	2.453±2.374
K1	0.555±0.237	0.768±0.265
K2	1.490±0.939	1.893±1.813
S1	0.854±0.399	0.484±0.374
S2	2.211±0.858	1.175±0.490
Average	1.026±0.199	1.102±0.298
	Total adults	
C1	0.139±0.086	0.627±0.562
C2	0.536±0.221	0.848±0.657
I1	0.990±0.831	0.309±0.188
I2	0.495±0.292	0.267±0.078
J	1.729±0.896	1.468±1.088
K1	0.455±0.111	0.376±0.155
K2	0.687±0.472	0.757±0.623
S1	0.412±0.139	0.639±0.539
S2	0.968±0.190	0.977±0.531
Average	0.785±0.188	0.707±0.206
	Macropterous adults	
C1	0.162±0.186	0.729±0.503
C2	0.560±0.282	1.379±1.305
I1	0.493±0.204	0.427±0.592
I2	0.442±0.296	0.289±0.108
J	2.419±1.107	3.790±3.308
K1	0.615±0.249	1.039±0.523
K2	0.799±0.753	0.576±0.976
S1	0.956±0.849	(2.220)
S2	1.435±0.715	1.383±0.823
Average	1.012±0.598	1.054±0.404
	Brachypterous adults	
C1	0.237±0.161	0.596±0.789
C2	0.512±0.290	0.528±0.492
I1	0.919±0.455	0.290±0.139
I2	1.122±0.699	0.396±0.194
J	1.177±0.699	0.659±0.223
K1	0.376±0.155	0.911±0.956
K2	0.805±0.553	1.422±1.503
S1	0.507±0.249	0.808±0.670
S2	0.735±0.186	0.613±0.318
Average	0.667±0.139	0.603±0.196

Numeral in parentheses does not represent a common C_A since it is only a single value of C_A obtained from one sampling occasion.

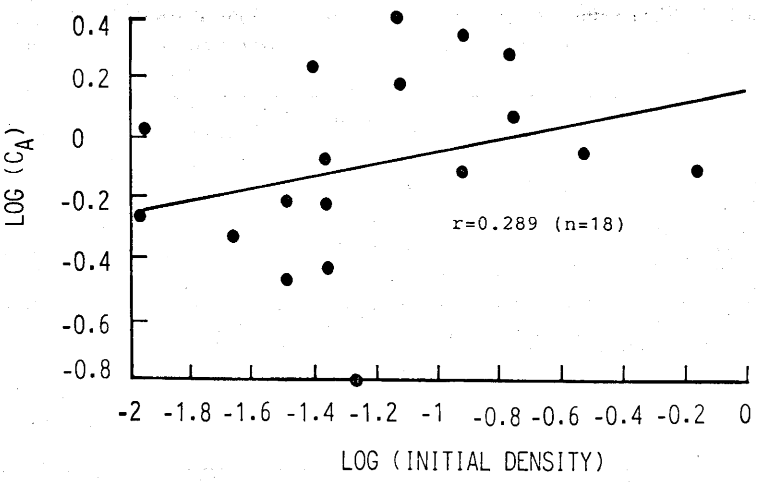

Fig. 5. Relation of the common C_A to the initial density of macropterous females.

C_A for nymphs ranged as widely as from 0.156 at Cirebon 1 to 2.211 at Subang 2 in the wet season, and from 0.332 in Indramayu 2 to 2.453 in Jatisari in the dry season. A similar tendency was also found for adults in both the seasons. These facts indicate that the distribution pattern of the hopper tends to vary widely geographically.

Correlation of the Population-to-population Variation of the Distribution Pattern between Different Stages and between Wing Forms

To clarify whether the distributions of different stages and wing forms vary from field to field or from season to season in close connection to each other, correlation analyses were made between the values of common C_A among all the experimental fields in both the seasons ($n=18$). Among the relationships examined, the distribution pattern of nymphs has a significant correlation with that of both total adults ($r=0.787$, $P<0.01$) and macropterous females ($r=0.823$, $P<0.01$), but has no correlation with that of brachypterous females ($r=0.190$, ns). The correlation between the adults of different wing forms was also insignificant ($r=0.189$, ns).

Effect of Initial Density on Distribution Pattern

In Japan, it has been found that the distribution patterns of BPH in terms of C_A-index has a close negative relationship with the density of initial immigrants (Kuno, 1968). To see whether the size of initial immigrants in West Java as such affects the distribution pattern of the population, the correlation between the initial density and the value of common C_A was analyzed for all the data for different fields and seasons. Initial density here was calculated as the average number of macropterous females found within two weeks around the observed peak of initial invasion. As seen in Fig. 5, the degree of aggregation in these West Java populations of BPH did not change significantly with the changes in the initial density.

DISCUSSION

The populations of BPH in the paddy field of West Java were found to be non-randomly distributed. The distribution pattern of this insect per hill of rice plant has a general tendency to be aggregated or contagious. Kuno (1963) and Kuno and Dyck (1985) have reported similar results for the Japanese and Philippine populations of BPH. At the early stages of rice, in which density of established BPH population was still very low, however, the distribution did not show marked departure from the random expectation (Fig. 2). This does not necessarily mean that the planthopper was actually distributed randomly under these conditions, because at low densities the distribution of an organism cannot depart markedly from the Poisson expectation for statistical limitation even though the organism may have some tendency for aggregation (e.g., Iwao, 1970).

A number of mathematical models have been proposed to describe the pattern of aggregated distribution. In the present study, among other models we have exclusively considered the negative binomial distribution, because it is simplest mathematically and has been proved most widely applicable to insect distributions (e.g., Anscombe, 1950; Waters and Henson, 1959; Southwood, 1978). In fact, the distributions of both immature and mature stages of BPH were found to fit the model well. The reciprocal of k of the negative binomial or Kuno's (1968) C_A-index measuring temporal and overall distribution patterns were estimated. In addition, we also described the overall distribution pattern by Iwao's (1968) method of $\overset{*}{m}$-m regression. A general conclusion obtained from these analyses was that the distribution of BPH can be designated as "contagiously distributed individuals" ($\alpha=0$, $\beta>1$).

Contagious distribution is common in many insect populations in their natural environments (e.g., Waters, 1959; Iwao, 1970). Aggregation may be due to various causes, such as non-random deposition of eggs, heterogeneous conditions of their habitats, gregarious behavior of individuals, and limited dispersal ability of individuals (e.g., Odum, 1971).

Since the adult BPH lays its eggs as egg masses, and may usually lay several egg masses successively on the same hill, it is understandable that the distribution of offspring would become patchy, even though the initial distribution of their parents is random (see Kuno, 1968, 1977).

The contagiousness arising from habitat heterogeneity is often observed in insect populations. For BPH, however, this does not appear to be an essential cause of aggregation, since individual rice hills within an experimental field are assumed to have similar susceptibility to the insect.

The innate tendency for dispersal, if intense, may of course be important in determining the pattern of distribution; the aggregated distribution pattern may be changed toward randomness as dispersal activity increases. Furthermore, in some species, intraspecific pressure, which forces individuals to occupy empty sites in the same habitat, may also be responsible for making the pattern of distribution less contagious as the population grows. But neither of these factors seems significant in the case of BPH, since the degree of aggregation was relatively stable throughout the period from transplanting to harvest (Fig. 3, Table 2). The planthopper's high tolerance to crowding together with the very limited ability of its nymphs and brachypterous adults to disperse within the habitat, has been reported in earlier studies conducted in Japan (Kisimoto,1965; Kuno, 1968, 1979; Kuno and Hokyo, 1970). For BPH, it is therefore conceivable that its aggregated distribution pattern has occurred through the population growth without marked tendency for dispersal or conspecific repulsion.

There was a tendency that nymphs distribute themselves more contagiously than adults (Table 5). Kuno (1968) reported a similar tendency in BPH population in Japan. Such a difference is not surprising, since it is likely that nymphs have much less capability than adults to migrate from the hill on which they live.

Among adults, the degree of aggregation was higher in macropters than in brachypters. This difference may be a consequence of the density-dependent manner of wingmorph determination. Namely, the proportion of brachypterous form among emerging adults would be higher in hills which have been occupied by a small number of nymphs, whereas the macropterous form would become dominant among hills with high nymphal density (see Kisimoto, 1956). This reasoning is supported by the fact that the distribution pattern of macropterous form has a significant positive correlation with that of nymphs.

The present work showed that the degree of aggregation of BPH varied remarkably among populations of different localities. These observations were consistent with those of Kuno and Dyck (1985), who found marked differences in the values of C_A-index between Japanese and Philippine populations of BPH.

Kuno (1968, 1977) suggested that differences in the spatial distribution pattern between localities are explicable by the differences in density of the initial populations, showing that the degree of aggregation decreases with increasing density of the initial population. However, there was no such close relationship for BPH in West Java (Fig. 5). This might be partly due to the erroneous determination of the initial population resulting from irregular immigration processes. But if the effect of initial population is really insignificant, some locally variable environmental conditions may act as essential factors in featuring the spatial distribution pattern.

For BPH in West Java no significant difference in the distribution pattern was observed between the wet and dry seasons. At the moment, however, it is difficult to draw any definite conclusion from this result, since the data for two-consecutive seasons only are available. Long-term studies are still needed to provide sufficient information to discuss the influence of different seasons on the distribution pattern of BPH in detail.

SUMMARY

Spatial distribution pattern of the brown planthopper (BPH) was analyzed at 9 experimental fields in the northern part of West Java during two consecutive rice cropping seasons, i.e., wet and dry seasons.

The population of each developmental stage and wing form of BPH at each location showed consistent departure from the random (Poisson) distribution, the variances of the densities in most cases exceeding their means. Namely, the distribution pattern of BPH per hill of rice plant was found to have a general tendency to be aggregated or contagious and to fit fairly well to the negative binomial model. The tendency for aggregation was further confirmed by both the β-values of $\overset{*}{m}$-m regression being larger than unity and the C_A-values being larger than zero for each developmental stage.

Although significant variations in the distribution pattern as measured by β- or C_A-value were observed between different developmental stages, between wing forms and among locations, the degree of aggregation for a given developmental stage at each experimental field remained fairly stable throughout the crop period, despite wide temporal changes in population density.

Possible factors to explain these characteristics of the spatial distribution pattern of the BPH in West Java were discussed with reference to the process generating it.

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インドネシアの西部ジャワにおけるトビイロウンカの空間分布様式

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西ジャワ北部地域の9箇所に設定した無防除実験水田において，連続する雨季と乾季の2シーズンにわたって得られたデータをもとに，トビイロウンカの空間分布様式の解析を行った．

幼虫・成虫ともに分布型は一般にポアソン分布に適合せずに集中性を示し，負の2項分布によい一致を示した．分布の一貫した集中性は，C_A 指数値 (>0), 及び $\overset{*}{m}$-m 回帰における β 指数値 (>1) によっても確かめられた．

C_A 指数で示される分布集中度は，同じ発育段階については同一シーズン，同一水田内ではほぼ安定していたが，異なる発育段階，翅型，場所，あるいはシーズン間ではある程度の変動を示した．

西ジャワにおける本種個体群の分布様式のこれらの特性が，どんな要因によって決定されているかを，分布形式過程との関連において論じた．