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Spatial Distribution of *Tetranychus urticae* Koch (Acari: Tetranychidae) with Special Inferences from its Behavior of Collective Egg Deposition, Life Type, and Dispersal Activities **【Research report】**

二點葉蟎 *Tetranychus urticae* Koch (Acari: Tetranychidae) 之空間分布 與其聚集性產卵行為、生命型、分散活動力之探討 **【研究報告】**

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Abstract

Aggregate spatial distribution of the population of *Tetranychus urticae* Koch (TSM) in a carambola (*Averrhoa carambola* L.) orchard was evaluated by the index of dispersion (ID), Green's coefficient of dispersion (Cx), Lloyd's mean crowding index (mc), Leoyd's patchiness index (mc/m), Morisita's coefficients of dispersion (I, I), Taylor's power law(a, b), and Iwao's patchiness regression (a, b). The magnitudes of the fluctuation of ID, Cx, and mc values were positively correlated with the incremental densities of TSM, but I, and I were negatively or independently correlated. The estimated slopes, b from the regression analyses with Taylor's power law on variances over means were larger than 1, indicating that each stage-specific population of TSM was an aggregate one. Iwao's patchiness regression analyses on mean crowding over means of TSM showed that the TSM population is aggregate within and among the patches. The high degrees of aggregation of TSM and patchiness of egg and larval populations of TSM were inferred to be the results of life type and collective egg deposition behavior of the females within the patch; The discrepant processes of distribution patterns represent the consequences of the dispersion behaviors of the high active stages of nymphs and adults that are very different from those of the immobile egg and larval stages.

摘要

二點葉蟎 (*Tetranychus urticae* Koch (Acari:Tetranychidae)) 於楊桃 (*Averrhoa carambola* L.) 園內之族群密度資料·依分散指數 (Index of Dispersion, ID) · Green's 分散係數 (Green's coefficient of dispersion, Cx) · 平均擁擠指數 (Lloyd's mean crowding index, mc) · 聚落度指數 (Lloyd's patchiness index, mc/m) · Morisita's 分散係數 (Morisita's coefficient of dispersion, I, I) 等·均顯示二點葉蟎於楊桃園中呈聚集型之空間分布。ID、Cx及MC值大小與其密度呈正相關·但 $I\alpha$ 及 $I\beta$ 值則與其密度呈負相關關係或無關。由泰勒乘幂定律 (Taylor's power law) 所獲之斜率 (b) 值均大於一·二點葉蟎各期於楊桃園中屬聚集型分布。依Iwao聚落度迴歸 (Iwao's patchiness regression) 獲二點葉蟎各齡期之 α 、 β 值判定·二點葉蟎之卵、幼蟎、若蟎及雌成蟎之族群基本組成單位為聚落或群體 (patch or colony) ·且各聚落間成聚集型之。二點葉蟎雌成蟎巢絲結網及產卵行為·為影響其卵及幼蟎族群呈現聚集型聚落分布型之主因。若蟎及成蟎期空間分布之聚集程度變化·為該等齡期受密度影響而呈現其分散行為之表徵。

Key words: *Tetranychus urticae*, spatial distribution, dispersion index, dispersion coefficient, behavior.

關鍵詞: 二點葉蟎、空間分布、空間指數、分散係數、行為。

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Spatial Distribution of *Tetranychus urticae* Koch (Acari: Tetranychidae) with Special Inferences from its Behavior of Collective Egg Deposition, Life Type, and Dispersal Activities

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ABSTRACT

Aggregate spatial distribution of the population of *Tetranychus urticae* Koch (TSM) in a carambola (*Averrhoa carambola* L.) orchard was evaluated by the index of dispersion (ID), Green's coefficient of dispersion (Cx), Lloyd's mean crowding index (mc), Leoyd's patchiness index (mc/m), Morisita's coefficients of dispersion (I_b , I_p), Taylor's power law(a, b), and Iwao's patchiness regression (α , β). The magnitudes of the fluctuation of ID, Cx, and mc values were positively correlated with the incremental densities of TSM, but I_b and I_p were negatively or independently correlated. The estimated slopes, b from the regression analyses with Taylor's power law on variances over means were larger than 1, indicating that each stage-specific population of TSM was an aggregate one. Iwao's patchiness regression analyses on mean crowding over means of TSM showed that the TSM population is aggregate within and among the patches. The high degrees of aggregation of TSM and patchiness of egg and larval populations of TSM were inferred to be the results of life type and collective egg deposition behavior of the females within the patch. The discrepant processes of distribution patterns represent the consequences of the dispersion behaviors of the high active stages of nymphs and adults that are very different from those of the immobile egg and larval stages.

Key words: *Tetranychus urticae*, spatial distribution, dispersion index, dispersion coefficient, behavior.

Introduction

Tetranychus urticae Koch (TSM) (Acari: Tetranychidae) is one of the major pests on *Averrhoa carambola* L. in Taiwan. TSM on the host was generally ignored due to its microscopic size. Mites with short generation times and high net reproductive rates (Laing, 1969; Shih *et al.*, 1976; Lo and Ho, 1979; Carey and

Bradley, 1982; Lo, 1984) can increase to levels causing economical injury under suitable weather conditions. TSM of active stages pierce and suck the leaf tissues and cells causing them to turn whitish or yellowish and producing leaf-falls. Therefore, early estimates of TSM population occurrence and accurate density assessment through detecting its spatial distribution and a precision sam-

pling scheme are good methods to control TSM damage.

Spatial distribution and characteristic of the species (Taylor, 1984) is one of the most important pieces of information for understanding the species. The characteristics of TSM and other tetranychid mites vary through their age-stages (Jones and Parrella, 1984; Chen *et al.*, 1989), host species (Margolies *et al.*, 1984; Zahner and Baumgaertner, 1984; Raworth, 1986; Jones 1990a, b), locality, and mosaic of microhabitats (Zahner and Baumgaertner, 1984; Chen *et al.*, 1989; Ho, 1993). The spatial distribution of TSM can be used to understand population dispersion behavior, for establishing a precision sampling scheme and sequential sampling (Margolies *et al.*, 1984) or binomial sampling (Binns and Bostanian, 1990; Jones, 1990b; Hepworth and MacFarlane, 1992) in order to obtain a precise and time-and-labor saving process. The major ways to estimate the spatial distribution of a species population includes: 1. Index of dispersion, ID (Patil and Stiteler, 1974); 2. Green's coefficient of dispersion, C_x (Green, 1966); 3. Lloyd's mean crowding index, mc (Lloyd, 1967); 4. Lloyd's patchiness index, mc/m (Lloyd, 1967), 5. Morisita's coefficients of dispersion, I_s and I_p (Morisita, 1959, 1962); 6. Taylor's power law, $\log a$ and b (Taylor, 1961, 1984), 7. Iwao's patchiness regression, α and β (Iwao, 1968, 1977a, b). Although Mayer (1978) and Taylor (1984) discussed the best detecting index or coefficient to evaluate and determine the distribution pattern, divergence of opinion exists among specialists. Binns and Bostanian (1990) and Hepworth and MacFarlane (1992) demonstrated the distribution of TSM on strawberry and developed a binomial sampling scheme while Margolies *et al.* (1984) reported the distribution pattern with fixed-precision sequential sampling for TSM on peanut. Zahner and Baumgaertner (1984) tested the distribution pattern of apple TSM and

Raworth (1986) developed a distribution-free sampling method for TSM on strawberry. The twigs and branches of carambola trees in the test orchard were trimmed and pressed on a flat-shaft at 2 m above the ground so that the fruit tree formed an upside down cone shape and all the leaves were pressed on the same level. Therefore, the influences of vertical distribution were not considered for the estimation of distribution pattern of TSM. We focus on the evaluations of horizontal distribution patterns of TSM in the carambola orchard with the 7 indices or coefficients. The discrepancies of distribution patterns represent the consequences of the dispersal behaviors of the active stages of TSM.

Materials and Methods

Sampling methods: A total of 44 five-year-old carambola trees planted in a 4-by-11 array at 5.5 m intervals were encircled by 2 rows of wind breakers. Every carambola tree was assigned a coordinate number to which Legg and Yeargan's (1985) random selection and path routes were adopted to determine each individual sampled tree in the orchard. One leaf with 10-13 leaflets in each selected tree was cut and labeled, and put into a plastic bag with absorbent cotton paper strips. The numbers of mites of each stage from every weekly sample were counted and recorded in the laboratory under the dissection binocular microscope.

Analyses of data for indices and coefficients of dispersion: Distribution of *T. urticae* in the habitat is only valid when the population exists for a certain duration on the carambola tree. Those populations containing 0 densities were not considered in analyzing distribution patterns. Therefore, the zero count samples were deleted from the data set and were not included in the analyses. Means and variances of each sample from different sampling dates were calculated. The

detection of distribution patterns of TSM using the values of means and variances to estimate the indices or coefficients were made according to the following models: 1. Index of dispersion, ID (Patil and Stiteler, 1974); 2. Green's coefficient of dispersion, Cx (Green 1966); 3. Lloyd's mean crowding index, mc (Lloyd, 1967); 4. Lloyd's patchiness index, mc/m (Lloyd, 1967); 5. Morisita's coefficient of dispersion, I_s and I_β (Morisita, 1959, 1962); 6. Taylor's power law, log a and b (Taylor, 1961, 1984); and 7. Iwao's patchiness regression, α and β (Iwao, 1968, 1977a, b). These calculated values of indices or coefficients were used to detect the spatial distribution pattern of each stage-specific group of TSM in the carambola on different sampling dates. Consequently, the most adequate distribution pattern of TSM was determined by the highest frequency of the pattern. The analytical procedures of the 7 models are introduced as follows:

Index of dispersion, ID: The theoretical random distribution of a population is detected from its variance which is estimated from the sample variance. The calculated sample variances (SS) are used to compare the means with the formula of ID (SS of sample/SS of random model) = (SS of sample/mean of sample). The estimated ID values are used to analyze the correlation coefficients between IDs and TSM densities to elucidate variations of the spatial distribution patterns under different densities.

Green's coefficient of dispersion, Cx: Green (1966) gave an equation for Cx [$Cx = ((SS/m) - 1) / (\Sigma Xi - 1)$], where SS is the sample variance; m is the sample mean; and ΣXi is the sum of numbers of individuals in i samples. Green (1966) reported that Cx values ranged from -1 to +1 which is adequate to denote the spatial distribution pattern from extremely random to extremely aggregated. Mayer (1978) reported that the variation and differentiation of Cx values were not

related to population density. When the sum of individuals in the samples is 1, $\Sigma Xi = 1$ makes the denominator equal to zero and the result is undefined. The analyses of data for the results excluded those data sets with the sum equal to 1.

Lloyd's mean crowding index, mc: The contagiousness of a population depends not only on its density but also on the individual behavioral influences. The distribution pattern is the consequence of the results of behavior changes from interaction and/or indirect physiological reaction due to contact between or among individuals. Therefore, mc calculation requires a population which does not exhibit territorial behavior and live a long time in the habitat. The evaluation of the population distribution is relevant if it meets the rules, i.e., that most individuals of the population aggregate in "patches" with random distribution but with patch-densities higher than population means. Therefore, we evaluated the population distribution of TSM including "mean numbers per individual of other individuals in the same quadrat" besides the population mean. Mean crowding index, mc, is calculated by the equation: $mc = m + (SS/m - 1)$. The estimation of each population distribution pattern depends upon the criteria of the mc values calculated.

Lloyd's patchiness index, mc/m: Lloyd's (1967) suggestions of substantiality of relative changes in mean crowding (mc) and mean density (m) to estimate the density-related nature in population dynamics and the relation of mc to m to detect the spatial distribution pattern of the species were adopted for this analyses. Values of mc and m were calculated and used to estimate the patchiness indices by the function of mc on the m.

Morisita's coefficient of dispersion, I_s and I_β : Morisita (1959) reported a hypothesis for testing the uneven distribution coefficient of I_s and I_β , I_s is calculated by the formula; $I_s = N \times (\Sigma Xi^2 -$

$\sum Xi)/((\sum Xi)^2 - \sum Xi)$; while I_p is calculated by the formula: $I_p = I_s \times (\sum Xi - 1/N) / (\sum Xi - 1)$; where N is the total sample size, and Xi is the number of individuals in the i -th sample. By this hypothesis and calculation, quadrat size does not influence I_s . Consequently, we eliminated the variation or influences of sample size and numbers of sample due to the negligence of density and different range distances reached by each individual in the habitat. In other words, we delineated the effects of behavior performances of individuals on the spatial distribution pattern. We also calculated values of I_s and I_p and assigned the corresponding populations to a distribution pattern with the values. These calculated I_s and I_p values and population densities were analyzed for their relationship to test the magnitude of the influences of individual behavior on the distributions.

Taylor' power law: Taylor's power law (Taylor, 1961; 1984) of the relation of variance to mean density was adopted for analyses using the equation: $\log SS = \log a + (b \times \log m)$. The estimated intercepts $\log a$ and slope b from the results of regression analyses were used to estimate the spatial distribution of each stage-specific population of TSM.

Iwao's patchiness regression: Linear function of mean crowding (mc) on the mean (m) with the model, $mc = \alpha + \beta m$ of Iwao (1968, 1977b), was adopted for the analyses of values of intercept α and slope β . The results of the analyzed values of α and β were thus used to interpret TSM behavior. The additional interpretations of TSM behavior were also made according to the α value: (1) $\alpha < 0$ for mutual repulsion between individuals in the quadrat; (2) $\alpha = 0$ indicates a single individual distributed in the quadrat; and (3) $\alpha > 0$ indicates a contagious quadrat and patchy formation. The β values represent the behaviors of the overall population in terms of patchy distribution behavior of TSM.

Results

The results of analyses of data for indices and coefficients of dispersion in each specific stage are reported as follows:

Index of dispersion, ID: The results of ratios between each stage-specific variance and mean of TSM densities, i.e., index of dispersion, ID, showed that the spatial distribution of the population detected in the carambola orchard tended to be contagious. The ID values for each population of egg, larva, nymph, and adult female in most sampling weeks were greater than 1 ($ID > 1$) which means that TSM exhibited aggregate behavior in the habitat (Fig. 1). A positive correlation existed between ID values and densities for each specific stage (egg: $r = 0.533$, $p = 0.001$; larva: $r = 0.565$, $p = 0.001$; nymph: $r = 0.547$, $p = 0.001$; female: $r = 0.681$, $p = 0.001$; male: $r = 0.625$, $p = 0.001$). Densities positively affected contagiousness of the spatial distribution pattern of TSM.

Green's coefficient of dispersion, Cx: Data collected from the field with total density counts equal to 1 were not included in analyses for Green's coefficient of dispersion, C_x , due to the undefined results caused by a zero in the nominator. In February and July of 1990 to 1995 the spatial distribution patterns of TSM were determined as random to contagious which corresponds to low densities and initial phases of population increase in the field (Fig. 2).

Lloyd's mean crowding index, mc: There are no reports of territorial behavior in *T. urticae* (Liang, 1979; McMurtry *et al.*, 1970; Shih *et al.*, 1976) and its population is long living and long present in the habitat (Fig. 3) which meets the requirements for analyzing the data by Lloyd's mean crowding index, mc . The estimated values of mc of egg, nymph, and male and female adults were almost all larger than the mean (Fig. 3).

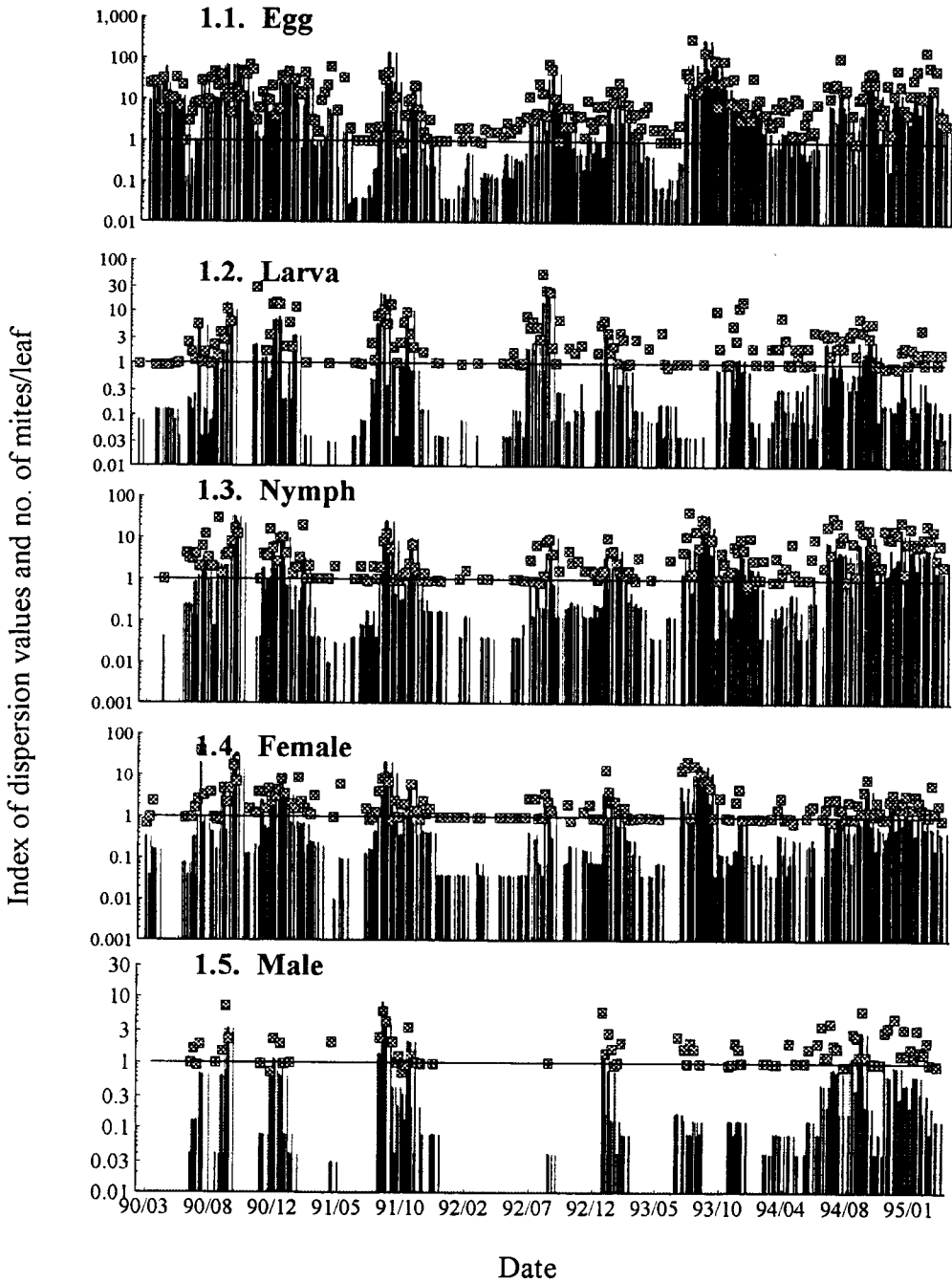


Fig. 1. Population mean densities (bars) and index of dispersion values (SS/m) (squares) of *Tetranychus urticae* in a carambola orchard

Lloyd's patchiness index, mc/m : The values of Lloyd's patchiness index, mc/m , were mostly larger than 1 (Fig. 4). The

patch or clustered colony was the basic unit for the contagious characteristics of TSM. The component of each patch

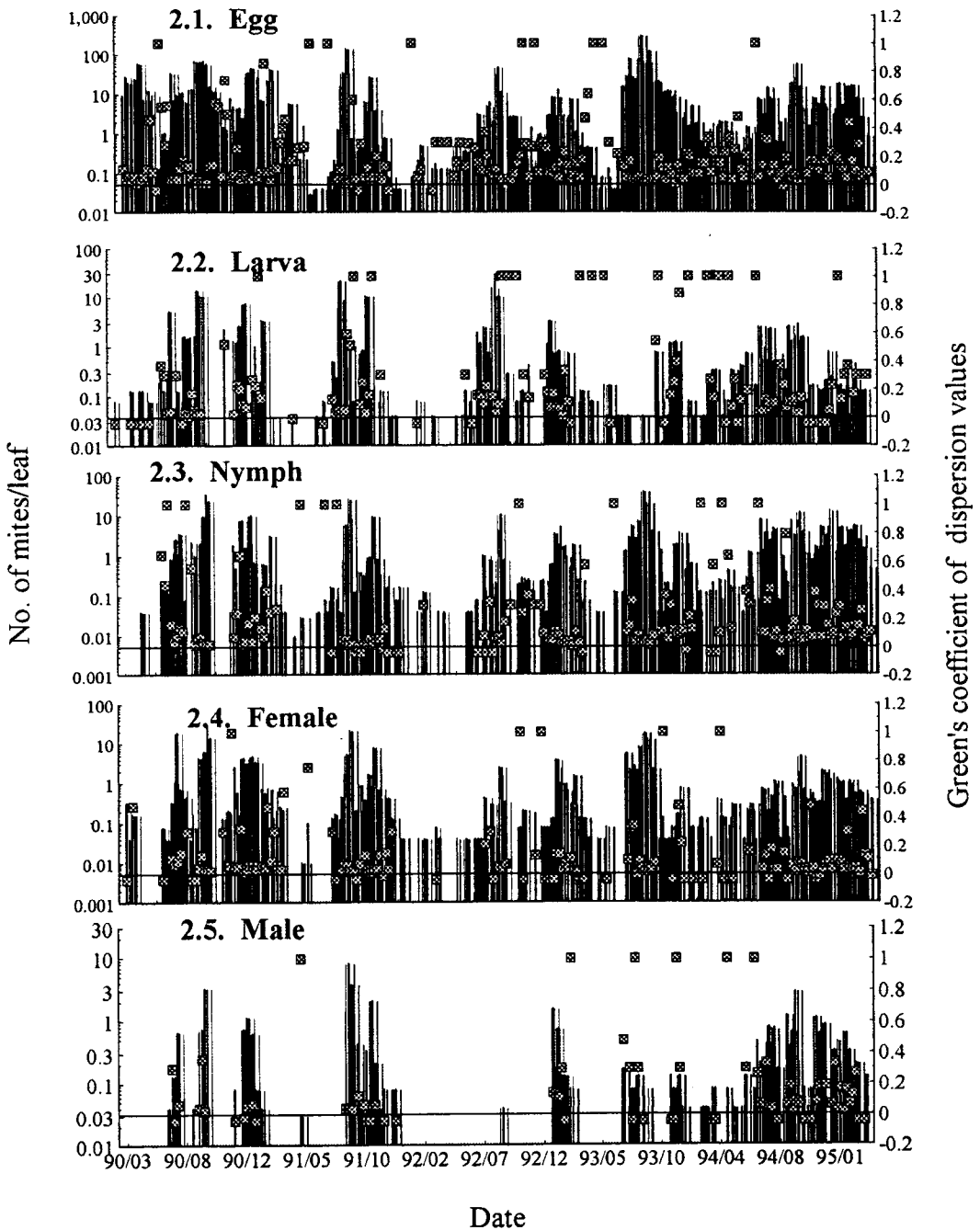


Fig. 2. Population densities (bars) and Green's coefficient of dispersion values (squares) of *Tetranychus urticae* in a carambola orchard

therefore was more than 1 individual.
Morisita's coefficients of dispersion, I_α and I_β : The estimation of Morisita's

coefficients of dispersion (I_α , I_β) shows a similar correlation to that of Cx to TSM densities, i.e., a positive relationship ex-

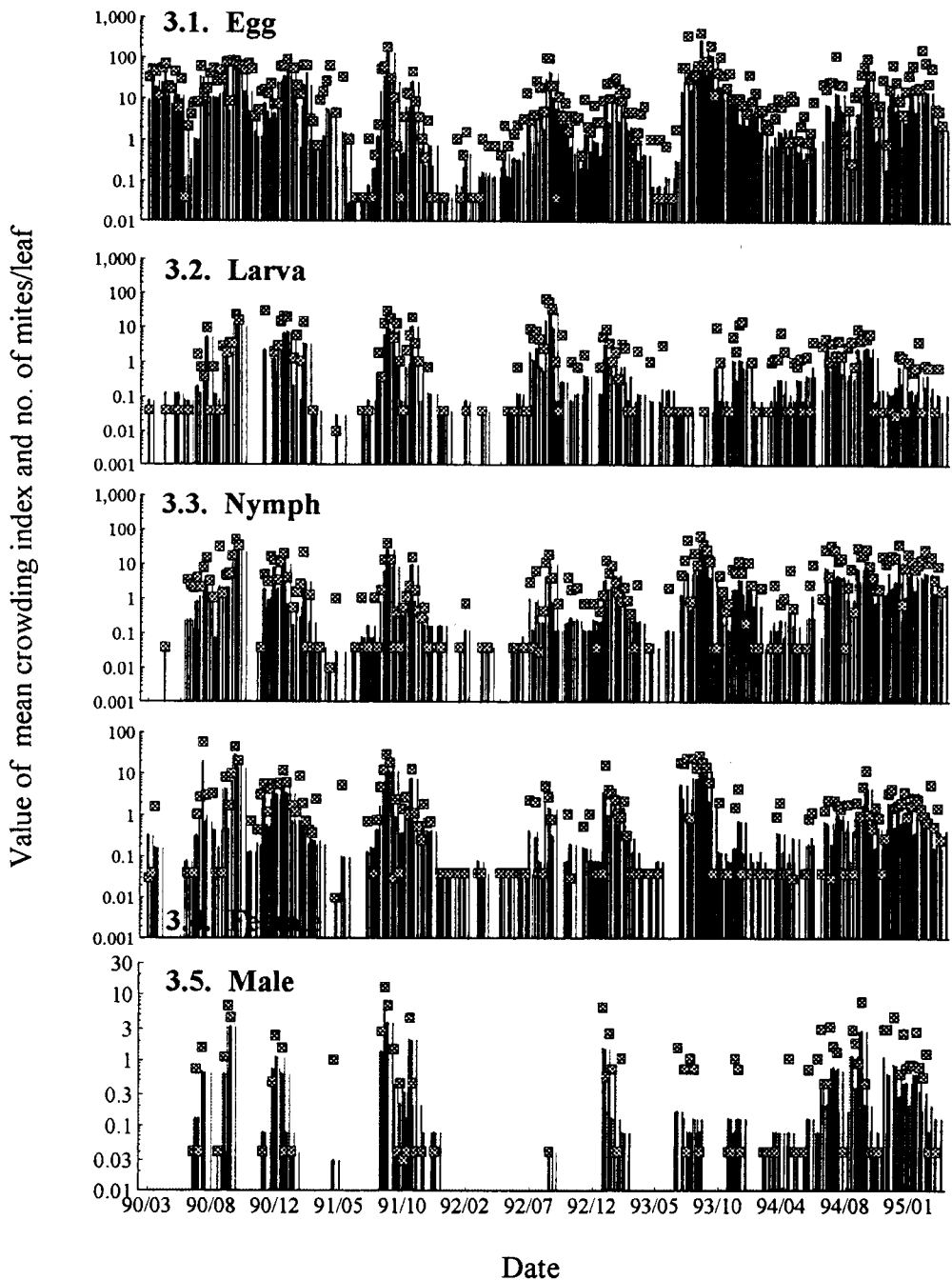


Fig. 3. Population mean densities (bars) and values of Lloyd's mean crowding index ($mc = m + (SS/m) - 1$) (squares) of *Tetranychus urticae* in a carambola orchard

ists between I_s or I_p and densities (Figs. 2, 5, 6). Values of the index of dispersion, ID, increase with TSM densities, i.e., the

correlation coefficient is found positively between the ID's and the density, but the evidence does not demonstrate the disper-

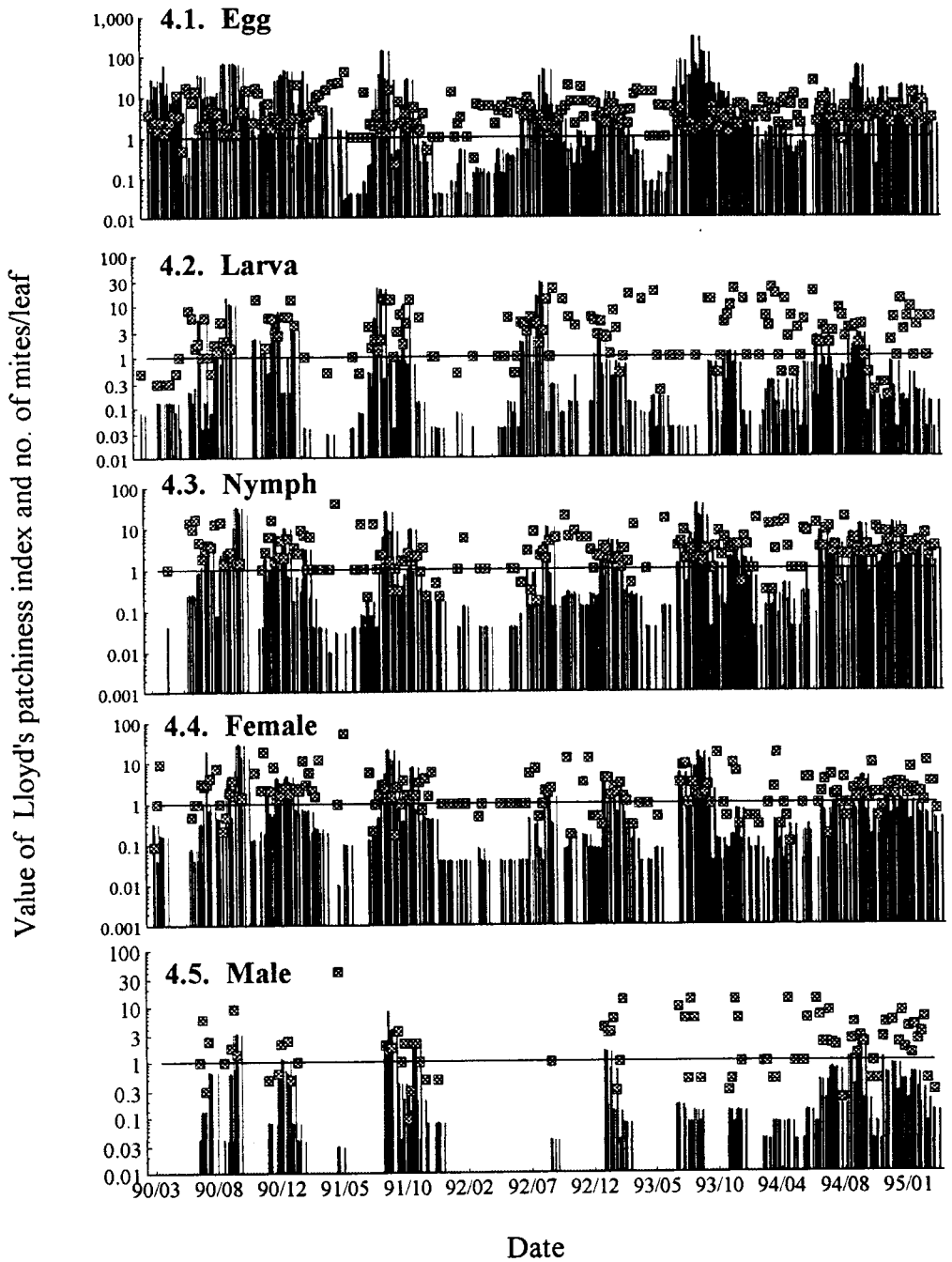


Fig. 4. Population densities (bars) and values of Lloyd's patchiness index (mc/m) (squares) of *Tetranychus urticae* in a carambola orchard

sal behavior of TSM at high densities. I_s and I_β values increased with TSM densities at the initial incremental phase of

the population but decreased at a later time of high densities. The negative correlation coefficients between I_s or I_β

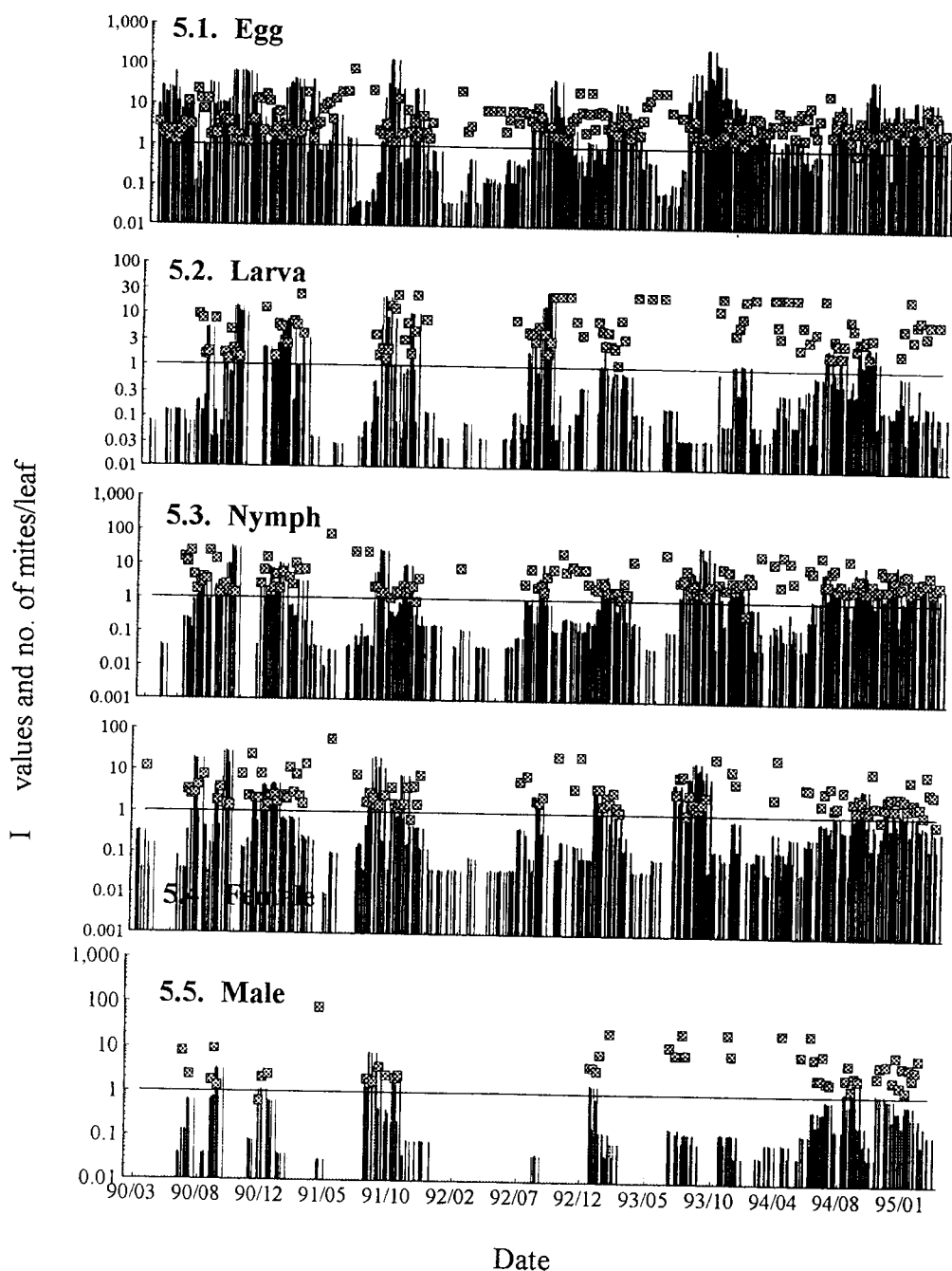


Fig. 5. Population mean densities (bars) and values of Morisita's I_{β} index (squares) of *Tetranychus urticae* in a carambola orchard

and TSM densities were evaluated for each stage (I_{β} : egg: $r=-0.184$, $p=0.007$; larva: $r=-0.210$, $p=0.203$; nymph:

$r=-0.185$, $p=0.023$; female: $r=-0.116$, $p=0.172$; male: $r=0.133$, $p=0.265$) (I_{β} : egg: $r=-0.143$, $p=0.037$; larva: $r=-0.205$, $p=0.023$;

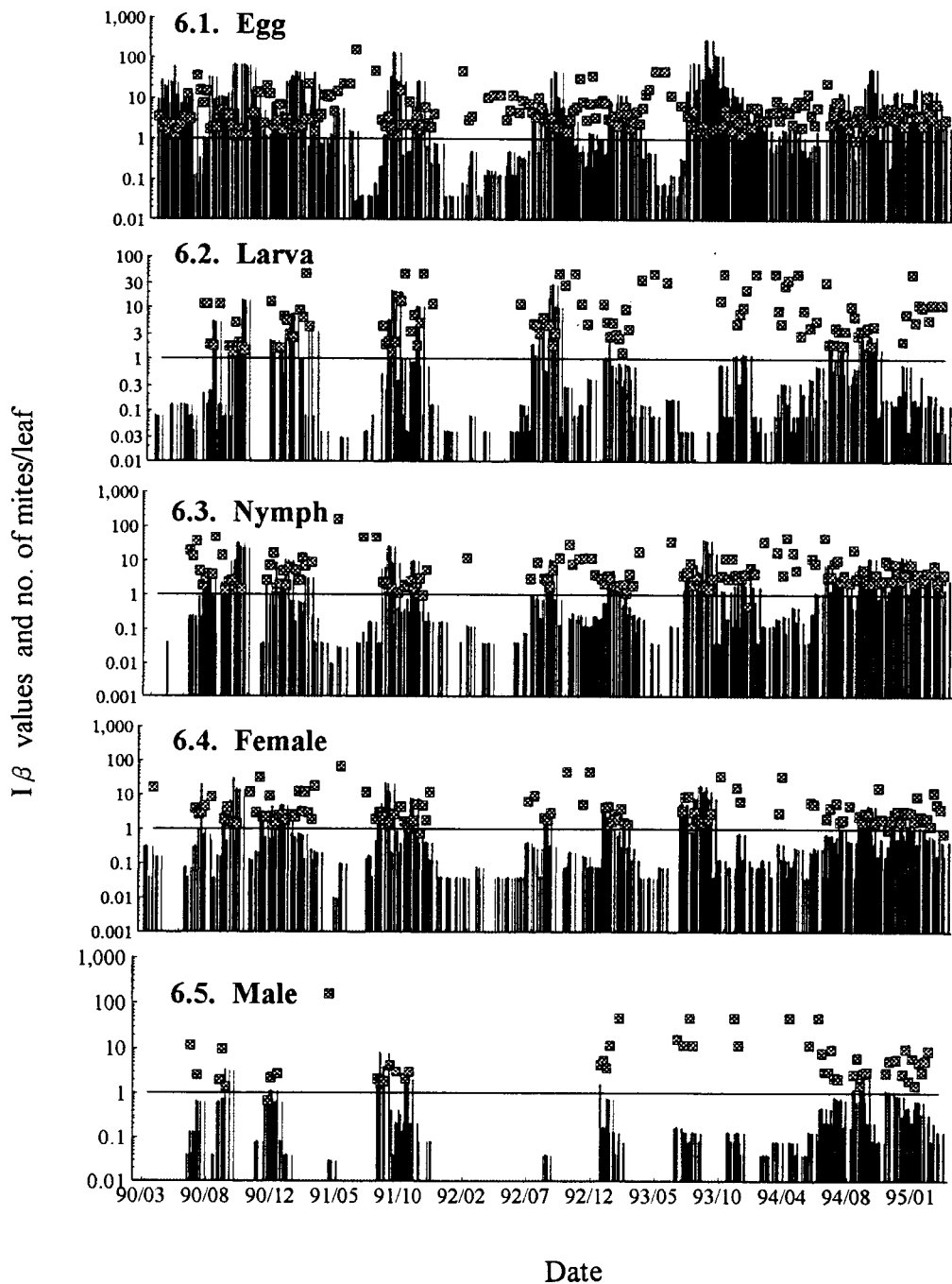


Fig. 6. Population mean densities (bars) and values of Morisita's I_{β} index (squares) of *Tetranychus urticae* in a carambola orchard

nymph: $r = -0.162$, $p = 0.046$; female: $r = -0.128$, $p = 0.131$; male: $r = -0.138$, $p = 0.247$). The estimated coefficients of

correlation values were very low which indicates that I_{β} and I_{β} are weakly dependent on or independent of the TSM

density.

The values of indices or coefficients of ID, Cx, mc, mc/m, I_s and I_b can be immediately calculated from sampled data for detecting the distribution on each sample day. The variations of the detected distribution pattern due to different sample days, population sizes, and densities represent the nature and characteristics of the species that can not be neglected from analyses and discussion. The analysis of the population distribution over a long period of time is the only integrated way to have a better understanding of TSM distribution behavior.

Taylor's power law: The estimated values of variances (SS), means (m) and mean crowding indices (mc) were analyzed with Taylor's power law and Iwao's patchiness regression for each stage of TSM. From the results of regression analyses of variances over means with

Taylor's power law model, we obtained 5 regression equations and their respective intercepts (log a) and slopes (b) (Table 1). The estimated slopes, b, are larger than 1 which indicates that TSM populations are contagious. The slope values decreased with advancing age and contagiousness was negatively related to the aging of TSM stages.

Iwao's patchiness regression: The estimates of α and β and all equations were significant at the $p=0.001$ level (Table 2). The α s of each stage were greater than 0 and the α s of the egg, larval, and nymphal stages were much larger than those of adults (Table 2). The basic unit of contagiousness being more than 1 individual of TSM is conferred by the results of $\alpha > 0$. The basic units are aggregation since the β values are estimated and proved to be significantly greater than 1. Consequently, TSM distributed in the habitat with aggregative clusters within

Table 1. Estimated values of intercepts and slopes of the different stages of *Tetranychus urticae* by regression analyses of the variances to the means with Taylor's power law model

Stage	<i>Tetranychus urticae</i>			
	log a	b	R-square	P
Egg	0.720 ± 0.020	1.544 ± 0.022	0.958	0.001
Larva	0.625 ± 0.022	1.464 ± 0.024	0.962	0.001
Nymph	0.623 ± 0.020	1.493 ± 0.024	0.958	0.001
Female	0.467 ± 0.019	1.389 ± 0.023	0.956	0.001
Male	0.406 ± 0.029	1.305 ± 0.034	0.948	0.001

Table 2. Estimated values of intercepts (α) and slopes (β) of the different stages of *Tetranychus urticae* by regression analyses of mean crowding to the mean with Iwao's patchiness regression model

Stage	<i>Tetranychus urticae</i>			
	α	β	R-square	P
Egg	10.199 ± 1.847	1.604 ± 0.064	0.737	0.001
Larva	1.485 ± 0.414	2.084 ± 0.103	0.736	0.001
Nymph	3.030 ± 0.505	1.719 ± 0.084	0.709	0.001
Female	0.824 ± 0.279	1.779 ± 0.065	0.819	0.001
Male	0.464 ± 0.125	1.769 ± 0.106	0.771	0.001

the density of TSM was significantly greater than 1.

Discussion

Index of dispersion, ID: The incremental tendency of the positive relationship of ID values of developmental stages to densities showed that density effectiveness on the contagiousness was high in male and female adults, nevertheless, it was moderated in nymphs, larvae, and eggs. A few ID values were less than 1 or equal to 1 for very low TSM densities, which may represent either a uniform ($ID < 1$) or random distribution ($ID = 1$) pattern of TSM at very low frequencies.

Green's coefficient of dispersion, Cx: In the phase of density increase, TSM population was distributed in a contagious pattern, which transformed into a random or uniform one as the density increased and approached a high level or the density peak (Fig. 2). In the decrement phase, i.e., after the density peak, Cx values increased with decreasing densities of TSM. The random distribution pattern of the first generation of TSM in February was the result of individuals distributing themselves randomly into the habitat. The reproduction of TSM increased in densities in the habitat inducing the contagiousness and patchiness within the patch that was formed by the dispersed females. The tendency of dispersal was enhanced as the density in the patch increased, and the growth and enlargement of the patch enhanced the probability of overlapping of the patches seeding a uniform or random distribution of TSM in the habitat. These transformations of aggregative to random or uniform distribution in the later parts of incremental phases are shown in Fig. 2.

Lloyd's mean crowding index (mc) and patchiness index (mc/m): The values of mc/m and mc increased with population densities (Fig. 3, 4) which indicates that the TSM population exhibit

an incremental contagiousness with increasing density. When the egg and female densities reached their highest peak in the incremental phase (Fig. 4.1, 4.4), i.e., the later parts of the population density in each population fluctuation, Lloyd's patchiness indices, mc/m, and the degree of contagiousness were lowered and weakened. The incremental rate of contagiousness in the patch was lower than the incremental rate of TSM densities in each population increasing phase (Fig. 4). However, the pattern of correlation and significance between the incremental or decremental phases of population density and degree of contagiousness shown by the mc or mc/m indices required a further analysis and interpretation of results. Consequently, TSM first aggregated to form a patch in the habitat and increased the contagiousness of the patch, and then the contagiousness of the overall population increased. In reaching the high density with increasing numbers and enlarging area and boundary of the patch, the distances among the patches were shortened and the spatial distribution pattern became less contagious ($mc/m \leq 1$) (Fig. 4). The density-dependent nature and behavior of the distribution of the TSM demand further studies.

Morisita's coefficients of dispersion, I_s and I_p : Owing to the short duration of TSM egg and larval stages and the inability of the almost immobile larvae to disperse out of the web-nest unit made by the maternal female, similar results are found in the correlation coefficients and significance levels between I_s or I_p values and TSM densities of eggs and larvae. Therefore, we took the egg and larval stages as 1 combined group to contrast with the nymph and adult groups to discuss the relationship between I_s or I_p values and TSM densities. The results showed that the senior and aged groups of TSM nymphs and adults demonstrated a lower degree of correlation and sig-

nificance to the aggregativeness. In other words, the values of the correlation coefficients and the significance level between the values of I_s or I_β and TSM densities may decrease with the age and seniority of TSM. Consequently, the elder the TSM stage, the higher the tendency of dispersal behavior observed. A negative or independent relation between coefficients of dispersion and animal densities was also reported by Mayer (1978). In conclusion, the stage-specific spatial distribution of TSM in the habitat is the result of the influences of their behavior performances. However, the diverse range of behaviors that influences TSM dispersion due to the variations of stage and aging need further intensive studies.

Taylor's power law and Iwao's patchiness regression: The basic components of egg, larval, and nymphal stages are patches or clustered colonies. Estimated β values larger than 1 represent the aggregative pattern existing among the patches (Table 2). According to the values of α , the highest numbers of individuals among all test stages were in egg patches followed by nymphal, larval, female, and male patches. Consequently, the effects of decremental contagiousness in the patch due to the seniority and aging of TSM reveal the following: (1) collective egg deposition behavior of the females aggregating eggs in the same patch; and (2) incremental activity and dispersal behavior by seniority or aging.

Stage-specific populations of TSM distributed in an aggregation pattern were verified by calculated values of ID , mc , and mc/m , and estimated values of slope b and intercept α , and slope β by regression analyses. However, Cx values varied with the incremental and decremental phases and seasonal variation of the TSM population, but the other indices or coefficients showed that TSM was distributed in an aggregative pattern in the field. TSM spatial distribution may be transformed to random, aggregative, ran-

dom, and / or uniform patterns depending on the processes of population development in the field. In other words, distribution pattern is density and time dependent. Therefore, we suggest that character of species in distribution pattern of TSM is not a "fixed and mono type".

The estimation of distribution patterns of TSM depending on the calculated values of ID , Cx , mc and mc/m revealed that variations of estimated values for pattern-assessment existed due to the different hypotheses. Furthermore, calculations of Cx values by discarding samples contained 1 individual per sample influenced the probability of the estimation of randomness of the TSM population.

Lloyd's mean crowding indices and Iwao's regression estimated values of α and β showed the TSM was distributed contagiously within and among the patches. The evaluated cluster formation of TSM is associated with the egg laying behavior of females and the life type of the species. Collective egg laying behavior of females is the character of the TSM female which is evident by the interpretation of α and β values.

Table 1 and Table 2 demonstrate the influences of the components in the web-nest formation of complex life type (Saito, 1977a, b, 1979) in the micro-environment to support the life and activities of a TSM population by which a clustered TSM patch is formed and the attack rate from the predators is minimized (Sabelis, 1981). The contagious distribution and the high degree of patchiness created by the aggregative behavior of TSM enhances the advantages of a complex life type - a fitness of survival and reproductive strategy of TSM. The presence of an individual of a TSM egg or larva in a unit increases the chance of other individuals being in the same unit which induces patchy formation as detected from results of $\alpha > 0$ and $\beta > 1$ (Table 2). That the degree of contagiousness is

larger than the mean density ($\alpha > 0$, $\beta > 1$ and $mc/m > 1$) also means that TSM females did not move out of the unit or patch before laying a batch of eggs. The magnitude of the negative feedback mechanism from intraspecific competition on space and resources increasing with seniority and competition duration as well as the high tendency of dispersal behavior of elder stages are proved from the results of the positive relation between the decrement values of the indices of basic contagion (α) and/or the density-contagiousness coefficients (β) and incremental aging of TSM (Table 2). In conclusion, the diverse results of contagiousness in a patch and the values of dispersion indices or coefficients (α , β and slope b) to aging manifested in the spatial distribution of TSM varied with age-specific groups. The spatial distribution pattern is influenced by the behavior of TSM including the collective egg deposition of parental females, the complex life type, the incremental tendency of dispersal, and activity behavior which are an age-dependent function of TSM. Discrepancies of the spatial distribution patterns due to the density, season, and stage with specific sequential transformation of distribution patterns depending on the densities represent the species characteristics and behavioral consequences of *T. urticae* which require further study.

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二點葉蟎 *Tetranychus urticae* Koch (Acari: Tetranychidae) 之空間分布與其聚集性產卵行爲、生命型、分散活動力之探討

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摘 要

二點葉蟎 (*Tetranychus urticae* Koch (Acari: Tetranychidae)) 於楊桃 (*Averrhoa carambola* L.) 園內之族群密度資料，依分散指數 (Index of Dispersion, ID)，Green's 分散係數 (Green's coefficient of dispersion, C_x)，平均擁擠指數 (Lloyd's mean crowding index, mc)，聚落度指數 (Lloyd's patchiness index, mc/m)，Morisita's 分散係數 (Morisita's coefficient of dispersion, I_b , I_p) 等，均顯示二點葉蟎於楊桃園中呈聚集型之空間分布。ID、 C_x 及 MC 值大小與其密度呈正相關，但 I_b 及 I_p 值則與其密度呈負相關關係或無關。由泰勒乘冪定律 (Taylor's power law) 所獲之斜率 (b) 值均大於一，二點葉蟎各期於楊桃園中屬聚集型分布。依 Iwao 聚落度迴歸 (Iwao's patchiness regression) 獲二點葉蟎各齡期之 α 、 β 值判定，二點葉蟎之卵、幼蟎、若蟎及雌成蟎之族群基本組成單位為聚落或群體 (patch or colony)，且各聚落間成聚集型之空間分布。二點葉蟎雌成蟎巢絲結網及產卵行爲，為影響其卵及幼蟎族群呈現聚集型聚落分布型之主因。若蟎及成蟎期空間分布之聚集程度變化，為該等齡期受密度影響而呈現其分散行爲之表徵。

關鍵詞：二點葉蟎，空間分布，分散指數，分散係數，行爲