ORIGINAL ARTICLE

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Relation between plant density and arthropod density in cabbage fields

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Abstract The relationship between plant density and the abundance of arthropods was examined by planting cabbages in four densities (0.25, 1, 4, or 8 plants per square meter). Four herbivorous species were examined: the small white butterfly Pieris rapae crucivora Boisduval, the diamondback moth Plutella xylostella (Linnaeus), the beet semi-looper Autographa nigrisigna (Walker), and the green peach aphid Myzus persicae (Sulzer). The number of spiders and the number of eggs of syrphid flies were also examined. The number of individuals per unit ground area increased curvilinearly with increasing plant density for most arthropods. To clarify the mechanism causing such a curvilinear increase, the oviposition behavior of Pieris rapae crucivora was examined. The oviposition process of a female was divided into three components: (1) entering the field, (2) alighting on a plant to bend her abdomen, and (3) attaching an egg on the leaf. The first and the second components curvilinearly increased with increasing plant density, while the third component was not influenced by the plant density. The analysis of the flight path of P. rapae crucivora indicated that the curvilinear increase in the frequency of abdominal bending behaviors occurs since a female flies at least about 1.3 m between successive abdominal bending behaviors, irrespective of the plant density, when the plant density is sufficiently high.

Key words Cabbage pests · Herbivorous density · Oviposition behavior · Pieris rapae crucivora

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Introduction

The spatial distribution of arthropods is much related to their searching behavior for their habitat. Root (1973) proposed the 'resource concentration hypothesis' whereby 'many herbivores, especially those with a narrow host range, are more likely to find hosts that are concentrated (i.e., occur in dense or nearly pure stands).' Although this hypothesis predicts that the density of herbivores per host plant increases with increasing plant density, most of the experimental results in the literature contradict this prediction; the number of herbivores per plant is smaller in densely planted fields in most cases (Luginbill and McNeal 1958; Pimentel 1961; Way and Heathcote 1966; A'Brook 1968; Farrell 1976; Solomon 1981; Latheef and Ortiz 1983; Root and Kareiva 1984; Power 1987; Segarra-Carmona and Barbosa 1990; Thompson and Quisenberry 1995). Only a few experiments supported the resource concentration hypothesis (Ralph 1977; Turchin 1988) and several experiments did not detect consistent results (Mayse 1978; Bach 1980; Boiteau 1984; Power 1989; Coll and Bottrell 1994). Therefore, it is valid to adopt the opposite hypothesis, which may be called the 'resource diffusion hypothesis': herbivores use more efficiently hosts that are diffused (i.e., sparsely distributed).

Let f(x) be the number of herbivores per plant for a given plant density x. Then, the number of herbivores per unit ground area is given by xf(x). The resource diffusion hypothesis predicts that f(x) is a decreasing function of x. In this case, it is more informative to examine the form of xf(x), because the xf(x)-curve expresses the characteristics of f(x) more clearly; for example, the shape of xf(x) becomes either the unimodal form or saturation form depending on the characteristics of f(x). In this article, I first examine the shape of the xf(x)-curve for the number of arthropods in cabbage fields to quantify the characteristics of resource diffusion. Then, I examine the oviposition behavior of the small white butterfly Pieris rapae crucivora Boisduval (Lepidoptera, Pieridae) to clarify the mechanism yielding the xf(x)-curve, because *P. rapae crucivora* is most

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suitable for observation among the arthropods living in cabbage fields.

Materials and methods

The experiments were conducted at the National Institute of Agro-Environmental Sciences, Tsukuba, Japan. Onemonth-old cabbage seedlings of the variety Rokumaru (Brassica oleracea Linnaeus) were transplanted in each plot $(10 \times 10 \text{ m})$ at one of the four levels of plant spacing: $2 \times 2m$, $1 \times 1m$, $0.5 \times 0.5m$, and $0.5 \times 0.25m$, with plant densities of 0.25, 1, 4, and 8 plants/m², respectively. The experiment was replicated by two blocks that were separated by weeded ground of 5m. The experiment was repeated twice in 1990: on May 18 (early summer experiment) and on July 19 (midsummer experiment). A compound of fertilizer 14-14-14 (N, P, K) and a compound of lime superphosphate were applied at concentrations of 5 kg and 10 kg/ are, respectively. Compost was applied before the early summer experiment at the rate of 200 kg/are. The experimental plots were weeded, and fenced with coarse wire mesh 80cm in height to avoid damage caused by hares. The seedlings that were killed by the turnip moth, Agrotis segetum (Denis et Schiffermüller), or the black cutworm, Agrotis ipsilon (Hufnagel), were replaced with undamaged plants at an early stage of the experiment.

I examined the abundance of four herbivorous species: the number of eggs of P. rapae crucivora, the beet semilooper Autographa nigrisigna (Walker) (Lepidoptera, Noctuidae), the diamondback moth Plutella xylostella (Linnaeus) (Lepidoptera, Yponomeutidae), and the number of alate females of the green peach aphid Myzus persicae (Sulzer) (Hemiptera, Aphididae). The number of spiders and the number of eggs of syrphid flies were also examined to compare the xf(x)-curves of predators with those of herbivores. Three species of syrphid flies were found in the field: Sphaerophoria macrogaster (Thomson), Episyrphus balteatus (Degeer), and Paragus haemorrhous Meigen. The spiders belonged to the following families: Theridiidae, Linyphiidae, Araneidae, Tetragnathidae, Agelenidae, Oxyopidae, Clubionidae, Philodromidae, Thomisidae, and Salticidae. I selected nine plants in a grid pattern of 2-m intervals at the center of each experimental plot. The numbers of arthropods on these plants were counted twice a week during the experimental period of 5 weeks. The leaf length and leaf width of the longest leaf of these plants were measured to assess the plant growth.

The oviposition behavior of *P. rapae crucivora* was examined in the following way to clarify the mechanism determining population abundance. When a female entered an experimental plot, the positions of cabbages on which she alighted were recorded. I described the flight paths by a linear interpolation of the alighted positions (Root and Kareiva 1984). The observation was continued until she left the plot. The activity after alighting was recorded as either of the two behaviors: abdominal bending behavior or resting behavior. I planted numbered flat stakes (6×45 cm) in

the ground at intervals of $2 \times 2 \text{ m}$ to facilitate the recording of the flight paths. I also estimated the probability of oviposition per abdominal bending behavior in 1989 for two levels of plant spacing ($2 \times 2 \text{ m}$ and $0.5 \times 0.5 \text{ m}$) by examining the existence of new eggs at the position of leaves where a female bent her abdomen.

The variance of population usually increases with increasing population mean, which contradicts the assumption of homoscedasticity that is required for the performance of ANOVA. To test the effect of plant density, therefore, I used the likelihood ratio test based on a gamma distribution with a constant coefficient of variation. I estimated the scale parameter of the gamma distribution by Pearson chi-square (McCullagh and Nelder 1989, p. 296), and tested the effect by *F*-test. The data of two seasons were separately analyzed, because it was unlikely that the season has additive effects on the population abundance. The procedure GENMOD of SAS was used for the calculation (SAS Institute 1993).

Results

Density of arthropods

The number of lepidopterous eggs per plant, f(x), decreased with increasing plant density as predicted by the resource diffusion hypothesis (Fig. 1; P < 0.001 for all cases). The number of alate females of M. persicae per plant also decreased with increasing plant density (Fig. 1; P = 0.181 for the midsummer experiment, and P < 0.001 for the early summer experiment). On the other hand, population of herbivorous species per unit ground area, xf(x), generally increased with increasing plant density (Fig. 2; P = 0.155for Plutella xylostella of the early summer experiment, and P < 0.001 for the other cases). The population of predators showed similar trends, although the effect of plant density was not statistically significant (Fig. 3). The probability levels for the early summer experiment and the midsummer experiment were as follows: f(x)-curve; spiders, P = 0.201and P = 0.452, syrphid flies P = 0.364 and P = 0.153; xf(x)curve; spiders, P = 0.057 and P = 0.013, syrphid flies P = 0.456 and P = 0.067.

The leaf length increased with increasing plant density (Fig. 4; P < 0.001 for both experiments). However, the absolute difference in the leaf length was small as compared to the total leaf length. The absolute difference in the leaf width was also small as compared to the total leaf width (Fig. 4; P = 0.405 for the early summer experiment, and P = 0.584 for the midsummer experiment). Therefore, the difference in plant growth was unlikely to contribute much to the difference in the population abundance of arthropods.

Oviposition process of P. rapae crucivora

I divided the oviposition process of a female *P. rapae crucivora* into three components: (1) entering the field, (2)

Fig. 1. Effects of plant density on the number of herbivores per plant (f(x)-curve). The egg density is shown for *Pieris rapae crucivora*, *Plutella xylostella*, and *Autographa nigrisigna*, and the density of alate females is shown for *Myzus persicae*. *Open circles* and *solid circles* indicate the population means of the early summer experiment and the midsummer experiment, respectively. *Vertical bars*, asymptotic standard errors



Fig. 2. Effects of plant density on the number of herbivores per unit ground area (m^2) (xf(x)curve) (symbols as for Fig. 1). *Vertical bars*, asymptotic standard errors

alighting on a plant to bend her abdomen, and (3) attaching an egg on the leaf. If these components are mutually independent, we can express the expectation of the total number of eggs, which is denoted by E_{egg} , by a simple form:

$$E_{\rm egg} = E_{\rm ent} \cdot E_{\rm bend} \cdot E_{\rm ovi} \tag{1}$$

where E_{ent} is the expectation of the total number of females entering the field, E_{bend} is the expectation of the number of abdominal bending behaviors per entrance, and E_{ovi} is the expectation of the number of eggs oviposited per abdominal bending behavior. E_{ovi} was first estimated for two levels of plant density. Number of eggs/number of abdominal bending behaviors was 119/149 for the 2 × 2m plot and 276/346 for the 0.5 × 0.5 m plot. The 95% exact confidence interval of the oviposition probability was 0.744–0.852 for the 2 × 2m plot, and 0.762–0.833 for the 0.5 × 0.5 m plot, indicating that the difference in $E_{\rm ovi}$ was very small, if any. Hence, I calculated a common estimate of $E_{\rm ovi}$ by using the data of two plant densities: $\hat{E}_{\rm ovi} = (119 + 276)/(149 + 346) = 0.80$. $E_{\rm bend}$ was estimated by the average number of abdominal bending behaviors per entrance. The effect of plant density was significant (Fig. 5a; Kruskal–Wallis test, $\chi^2 = 47.6$, df = 3, P < 0.001). $E_{\rm egg}$ was estimated for the early summer experiment by multiplying the population per

Fig. 3. Effects of plant density on the abundance of predators. *Upper graphs:* f(x)-curve; *lower graph:* xf(x)-curve (symbols as for Fig. 1). *Vertical bars*, asymptotic standard errors



Fig. 4a,b. Effects of plant density on plant growth. a Mean leaf length of each plant during the experiment. b Mean leaf width of each plant during the experiment (symbols as for Fig. 1). *Vertical bars*, asymptotic standard errors

Fig. 5. a Effect of plant density on the number of abdominal bending behaviors of *P. rapae crucivora* per entrance (E_{bend}). *Vertical bars*, asymptotic standard errors. **b** Estimate of the number of entrances (E_{ent})

square meter (open circles in Fig. 2) by $10 \times 10 \text{ m}^2$. Then, I estimated E_{ent} by substituting $\hat{E}_{\text{ovi}} = 0.80$, \hat{E}_{egg} , and \hat{E}_{bend} into Eq. 1. Both \hat{E}_{bend} and \hat{E}_{ent} curvilinearly increased with increasing plant density (Fig. 5), indicating that both components contributed to the curvilinear increase in the egg density of *P. rapae crucivora*.

I next examined the mechanism yielding the curvilinear relationship between E_{bend} and plant density. The flight pattern of female butterflies was described by two components

for convenience: (1) the flight direction between alighting and (2) the flight distance between alighting. I estimated the proportion of reverse movements defined as the turning movement with an angle larger than 90°. I ignored rightangled turns because we cannot judge the reversal in such a case. The proportion of reverse movement was about 0.2 irrespective of the plant density (Fig. 6a). The effect of plant density was not significant (P = 0.4127) by the likelihood ratio test based on the binomial distribution. On the other Fig. 6. a Effect of plant density on the proportion of reverse movements (more than 90° in turning angle) of *P. rapae crucivora. Vertical bars*, exact 95% confidence intervals. b Mean flight distance between successive abdominal bending behavior of *P. rapae crucivora. Vertical bars*, asymptotic standard errors





Fig. 7. Mean flight distance between successive abdominal bending behaviors of *P. rapae crucivora* plotted against plant spacing. *Vertical bars*, asymptotic standard errors. The *line* was calculated by a linear regression (flight distance) = 1.33 + 0.53 (plant spacing) ($r^2 = 0.966$)

hand, the flight distance between successive abdominal bending behaviors significantly decreased with increasing plant density (Fig. 6b; Kruskal–Wallis test, $\chi^2 = 128.4$, df = 3, P < 0.001). When the flight distance between successive abdominal bending behaviors is plotted against the plant spacing, however, we find that the flight distance does not decrease enough to compensate for the decrease of plant spacing (Fig. 7). If the flight distance is roughly extrapolated in Fig. 7, it approaches about 1.3 m with decreasing plant spacing.

Discussion

Increase in the optical stimulus or the olfactory stimulus may be the cause of the curvilinear increase in the frequency of entrance with increasing plant density in Fig. 5b. Stanton (1983) discussed the diffusion of host plant odor and calculated the area in which the concentration of the odor is higher than the threshold of attraction. Her calculation showed that the relationship between the area of attraction and the plant density is curvilinear, which provides an explanation for the curvilinear increase in the number of entrances shown in Fig. 5b.

The curvilinear increase in the frequency of oviposition per entrance has been studied for several other butterflies. Rausher (1983) showed that the curvilinear increase in the oviposition rate of Battus philenor butterflies with increasing plant density is caused by a decrease in postalighting probability of oviposition and not by a plateauing of alighting rates. The curvilinear increase in the oviposition rate of *P. rapae crucivora*, in contrast, is caused by a plateauing of the number of abdominal bending behaviors but not by a change in the probability of oviposition. The plateauing of the number of abdominal bending behaviors is caused by the characteristics of the flight behavior of females: they fly at least about 1.3m between successive abdominal bending behaviors on average (Fig. 7). If the plant density is sufficiently high, therefore, they fly over many plants without laying eggs. Such an egg-dispersing behavior was also reported by Root and Kareiva (1984) and Stanton (1983) for the European subspecies of *P. rapae* and the sulfur butterfly *Colias philodice eriphyle*, respectively. Capman et al. (1990) reported similar behavior for the wing skipper Pholisora catullus on lamb's quarter, Chenopodium album.

If a female disperses her eggs sparsely, her offspring obtain two advantages. First, her offspring can avoid mortality caused by the detrimental effect of their density, such as the consumption of food. Second, her offspring are favored by the 'spreading of risks' of Den Boer (1968), by avoiding local stochastic extinction. Root and Kareiva (1984) considered that the latter advantage was the major cause of the evolution of the egg-dispersing behavior of females. As suggested by Kuno (1981), however, the condition yielding the effect of spreading risks may be rather limited: the effect emerges only if females disperse their eggs over an area in which mortality is not synchronized. If we want to clarify the evolutional cause of the eggdispersing behavior of females, therefore, it will be necessary to quantify the spatial unit of environmental fluctuation as well as the spatial unit of egg dispersion.

The analysis of the oviposition behavior of *P. rapae crucivora* indicated that the xf(x)-curve is determined by two components, E_{ent} and E_{bend} , and that the latter is more influential (Fig. 5). Similar arguments may be applicable to other herbivores, although the relative importance of these components may differ depending on the species. As for the xf(x)-curves of predators, however, the interpretation is not straightforward, because the density of predators will be

influenced by prey density as well as by plant density. For example, female adults of syrphid flies may lay their eggs near the colonies of aphids. Hence, the curvilinear increase in syrphid density per unit ground area may be a result of the curvilinear increase in the aphid density. It will, therefore, be important to separate the effect of prey density from plant density by another experiment if we want to elucidate the mechanism responsible for the xf(x)-curves of predators.

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