Insect pest density per leaf area as a measure of pest load

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Abstract
The abundance of insect pests is expressed as the density per plant in most cases. This measure, however, is not always an appropriate measure of density, since the size of a plant varies greatly with its growth stage. To evaluate the importance of selecting an appropriate measure of density, the dynamics of the density of cabbage pests per leaf area was compared with that per plant. The leaf area was continuously estimated in the field in a noninvasive manner, using the allometric relationship between leaf area and leaf length. Density per leaf area and density per plant showed widely different dynamics in some herbivores. Aphid density per plant increased gradually with the growth of cabbages, while aphid density per leaf area decreased with cabbage growth, suggesting that injury by aphids was more severe in the early stages of plant growth. The larval density of the diamondback moth, Plutella xylostella (Linnaeus), per plant increased with cabbage growth, while the density per leaf area showed a peak level at 15 days after transplanting. Such differences suggest that population dynamics measured per plant may sometimes be a misleading description of actual insect-plant interactions.

Key words: Cabbage pests, density measure, leaf area, pest load

INTRODUCTION
Abundance of insect pests in the field is measured by a unit which is sometimes determined arbitrarily for convenience. When we use sex-pheromone traps to monitor the abundance of insects, for example, abundance is usually described by the number of insects per trap. When we conduct a marking-recapture experiment using sex-pheromone traps, we usually estimate the total number of individuals that exist in the experimental field (e.g., Wakamura et al., 1992; Yamamura et al., 1992; Shirai and Nakamura, 1995). In this case, we can calculate the number of individuals per unit ground area, by dividing the total number of individuals by the total area of the experimental field. If we want to evaluate the herbivore load on host plants, however, herbivore density per unit ground area will not be an appropriate measure of density. The density per host plant will be a more appropriate measure in this case, since most herbivores are gregariously distributed around the host plant.

The damage caused by an insect changes depending on the plant size. The damage will be small if the plant is large, but it will be large if the plant is small. Therefore, if we want to predict herbivore load more precisely, we should use a measure that reflects the difference in plant size. Root (1973) used the dry weight of herbivores per 100 g dry weight of consumable plant material to measure herbivore load. Pimentel (1961) used the density of herbivores per leaf area. Population dynamics measured by a different measure of density will give us a very different perspective of the population dynamics. However, such differences have not been adequately demonstrated. In this study, we compare the population dynamics of cabbage pests per leaf area with that per plant, to demonstrate the importance of selecting an appropriate measure of density.

MATERIALS AND METHODS
We examined seven pest species that are prev-
alent in early summer in cabbage fields: the small white butterfly, *Pieris rapae crucivora* (Boisd- duval) (Lepidoptera, Pieridae), the beet semi- looper, *Autographa nigrisigna* (Walker) (Lepidoptera, Noctuidae), the diamondback moth, *Plutella xylostella* (Linnaeus) (Lepidoptera, Yponomeutidae), the green peach aphid, *Myzus persicae* (Sulzer), the cabbage aphid, *Brevicoryne brassicae* (Linnaeus), the turnip aphid, *Lipaphis erysimi* (Kaltenbach), and the onion thrips, *Thrips tabaci* Lindeman. We also examined the number of spiders and the eggs of syrphid flies. The spiders belonged to the following families: Theridiidae, Linyphiidae, Araneidae, Tetragnathidae, Agelenidae, Oxyopidae, Clubionidae, Philodromidae, Thomisidae, and Salticidae. Three syrphid flies were observed in the field: *Sphaerophoria macrogaster* (Thomson), *Epiophyes balseatus* (Degeer), and *Paragus haemorrhous* Meigen.

It is known that the density of herbivores per plant sometimes decreases with increasing host plant density (e.g., Luginbill Jr. and McNeal, 1958; Pimentel, 1961; Way and Heathcote, 1966; A’Brook, 1968; Farrell, 1976; Latheef and Ortiz, 1983; Root and Kareiva, 1984; Power, 1987; Thompson and Quisenberry, 1995). Therefore, we used four levels of plant density (0.25, 1, 4, and 8 plants per square meter) to obtain various conditions of infestation. The experimental plots (each 10 m × 10 m) were replicated in two blocks at the National Institute of Agro-Environmental Sciences, Tsukuba, Japan. One-month-old cabbage seedlings of the variety Natsubare were transplanted on May 17 in 1991. A compound of fertilizer 14-14-14 (N, P, K) and superphosphate of lime were applied at concentrations of 5 kg/a and 10 kg/a, respectively. Compost was applied at a concentration of 200 kg/a. The experimental plots were weeded, and fenced with coarse wire mesh 80 cm high to prevent damage caused by hares. Seedlings which 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.

We selected nine plants in a grid pattern of 2 m intervals in the center of each experimental plot. During the experimental period before the formation of heads (five weeks after transplanting), we counted the number of individuals on these plants twice a week. The number of eggs and larvae were counted for *P. rapae crucivora*, *A. nigrisigna*, *P. xylostella*, and syrphid flies. The numbers of alate females and apterae were counted for *M. persicae*, *B. brassicae*, and *L. erysimi*. We also measured the length and width of the longest leaf for each plant.

Allometric relations are frequently observed between plant parts (Pearsall, 1927; Hunt, 1978; Causton and Venus, 1981; Yamamura, 1997). If we have an allometric relationship between leaf area and leaf length that can be measured non-invasively, it can be used to estimate the leaf area. Thus, we conducted another experiment to examine for an allometric relationship. One-month-old cabbage seedlings of the Natsubare variety were transplanted 75 cm apart on May 16 in 1990. Fifteen plants were systematically sampled from the field every week, and the total leaf area of each plant was measured in the laboratory after measuring the leaf length and leaf width of the longest leaf in the field. Herbivorous insects were killed by spraying insecticides during the experimental period of seven weeks.

**RESULTS**

**Growth of leaf area**

A clear allometric relationship was observed

![Graph](image-url)

**Fig. 1. Allometric growth of leaf area of cabbages.**

$log_{10} (\text{leaf area}) = -4.081 + 3.054 \times log_{10} (\text{leaf length})$. $r^2 = 0.984$. 
between leaf length and total leaf area (Fig. 1). We usually apply measurement-error models to estimate allometric relationships, since both axes have errors (Causton and Venus, 1981; Jolicoeur, 1990). However, our purpose was not estimation of the allometric relationship but estimation of leaf area from the leaf length. Therefore, estimation errors of leaf area for a given leaf length should be minimized. For this reason, we used the common linear regression to obtain:

\[
\log_{10}(\text{leaf area}) = -4.081 + 3.054 \log_{10}(\text{leaf length}), \\
r^2 = 0.984. \tag{1}
\]

The coefficient is near 3. Such a cubic growth indicates that the leaf area increases similarly to volume. We also examined the relationship between total leaf area and leaf length multiplied by leaf width. The estimated equation was:

\[
\log_{10}(\text{leaf area}) = -2.793 + 1.309 \log_{10}(\text{leaf length} \times \text{leaf width}), \\
r^2 = 0.988. \tag{2}
\]

The coefficient of determination was slightly improved. Hence, we used Eq. (2) to estimate the leaf area.

Both the leaf length and width increased in a slightly accelerating manner during the experiment (Fig. 2). The results of the four plant spacings were combined in Fig. 2, since there was no significant difference among the four plant densities on any date (ANOVA after a logarithmic transformation to achieve the homoscedasticity, \(p > 0.05\)). The leaf length at the last measurement was 4 times larger than that at the first examination. The leaf area increases in a cubic manner, as indicated by Eq. (1), therefore, the total leaf area at the last examination is about \(4^3 = 64\) times larger than that at the first examination.

**Comparison between density measures**

The dynamics of the Density Per Leaf Area (abbreviated hereafter as ‘DPLA’) of herbivores was very different from the dynamics of the Density Per Plant (abbreviated hereafter as ‘DPP’). The DPP of *P. rapae crucivora* increased in an accelerating manner, while the DPLA increased gradually (Fig. 3). The DPP of larvae of *P. xylostella* increased in an accelerating manner, while the DPLA attained its maximum level at 15 days after transplanting (Fig. 4). The DPP of larvae of *A. nigrisigna* also increased in an accelerating manner, while the DPLA increased gradually (Fig. 5). The DPP of aphids increased in the later period of the experiment, while the DPLA showed a declining curve (Fig. 6). The DPP of *T. tabaci* increased gradually, while the DPLA attained a peak level at 5 or 10 days after transplanting (Fig. 7).

The DPLA of predators was also very different from the DPP. The DPP of spiders increased in

![Fig. 2. Growth of leaf length and leaf width of the longest leaf of cabbages. Each bar shows the estimated standard deviation.](image)

![Fig. 3. Difference between the population dynamics per plant and per leaf area: larval population of the small white butterfly *P. rapae crucivora* in four plant densities (0.25, 1.0, 4.0, 8.0 plants per m²).](image)
Fig. 4. Difference between the population dynamics per plant and per leaf area: larval population of the diamondback moth *P. xylostella* in four plant densities. Symbols as for Fig. 3.

Fig. 5. Difference between the population dynamics per plant and per leaf area: larval population of the beet semi-looper *A. nigrisigna* in four plant densities. Symbols as for Fig. 3.

Fig. 6. Difference between the population dynamics per plant and per leaf area: population of aphids in four plant densities. The alate and apterous density of the three species (*M. persicae, B. brassicae*, and *L. erysimi*) were combined for convenience. Symbols as for Fig. 3.

Fig. 7. Difference between the population dynamics per plant and per leaf area: population of the onion thrips *T. tabaci* in four plant densities. Symbols as for Fig. 3.
Pest Density per Leaf Area

Fig. 8. Difference between the population dynamics per plant and per leaf area: population of spiders in four plant densities. Symbols as for Fig. 3.

Fig. 9. Difference between the population dynamics per plant and per leaf area: population of syrphid fly eggs in four plant densities. Symbols as for Fig. 3.

an accelerating manner, while the DPLA showed a declining curve similar to that of aphids (Fig. 8). The DPP of eggs of syrphid flies increased gradually, while the DPLA showed a peak level at 10 or 15 days after transplanting (Fig. 9).

DISCUSSION

We compared the population dynamics per leaf area with that per plant, showing that the two dynamics are sometimes very different. These differences suggest that the population dynamics measured per plant may sometimes be a misleading description of actual insect-plant interactions. For example, aphid density per plant increased in the latter phase of the cabbage growth, which gives us the false impression that the damage by aphids is most severe in the later period, when in fact the aphid density per leaf area decreased with plant growth. This indicates that the injury by aphids was most severe just after transplanting (Fig. 6).

The density of herbivores per leaf area reflects the difference in plant size but it ignores the difference in insect size. The body size of an older stadium larva is much larger than that of a younger stadium larva in lepidopterous herbivores, and hence the damage caused by an older stadium larva is much greater than that caused by a younger stadium larva. Therefore, the density per leaf area may also provide us with misleading information about pest load if all larvae are included in the calculations. In order to avoid such problems, we should use a weighting coefficient that would reflect the leaf consumption for each stadium. Furthermore, several pest species simultaneously damage the same plant in fields, and hence a composite measure, such as a weighted sum of the density of several pest species, is needed for the precise evaluation of the total pest load. Harcourt et al. (1955) measured the relative consumption of cabbages by the three lepidopterous pests: *P. xylostella*, *Pieris rapae* (L.), and *Trichoplusia ni* (Hübner). East et al. (1989) measured the relative consumption by three species: *P. xylostella*, *Spodoptera exigua* (Hübner), and *T. ni*. The weighting coefficient should be determined based on such results.

Great effort has been expended to detect density-dependence effects since the 1960's, although it is a logical necessity that any population that persists in the environment experiences some form of density-dependent regulation (Godfray and Hassell, 1992). The detection of
density-dependence is not statistically straightforward, and various methods have been proposed to overcome the statistical problems (Kuno, 1971; Reddingius, 1971; Bulmer, 1975; Pollard et al., 1987; Reddingius and Den Boer, 1989; Dennis and Taper, 1994). However, the problem inherent to the density-measure itself appears to be seldom discussed (see Yamada, 1995, for discussion). The density measure will not always reflect detrimental effects of density, such as the deterioration or conditioning of food. In such cases, we cannot detect the density-dependence by any statistical method. Therefore, we should, instead, concentrate our efforts on choosing an appropriate density measure to clarify the mechanism of population dynamics. Strictly speaking, density per leaf area will not be the best measure of population density even for herbivorous insects feeding on leaves, since herbivores sometimes prefer restricted parts of leaves. The European subspecies of the small white butterfly, P. rapae, preferred younger leaves, while T. ni showed no preference for leaves of any particular age (Hoy and Shelton, 1987). This preference explains the intraplant distribution of P. rapae; larvae commonly live on the head and wrapper leaves. Hirata (1967) reported the difference in the intraplant distribution of the Asian subspecies of the small white butterfly, P. rapae crucivora, the cabbage armyworm, Mamestra brassicae (Linnaeus), and the beet semi-looper, A. nigrisigna. The part of leaves preferred by herbivores may contain a larger amount of resources, even if the leaf area is the same. Ideally, therefore, the density measure should be determined for each species of herbivore. Fretwell and Lucas (1970) used the term 'ideal free distribution' for the spatial pattern that individuals distribute among patches so that all individuals experience the same amount of food resources. If the distribution of herbivorous insects is near the ideal free distribution, we can evaluate the amount of food resources in different parts of a plant by using the spatial distribution of individuals. This idea was presented by Morisita (1959, 1971) under the terminology of 'theory of environmental density.' The ideal free distribution is achieved only when individuals have sufficient dispersal ability and ability to evaluate resources. The actual distribution of herbivores will differ from the ideal free distribution, since individuals do not have sufficient ability to attain the ideal free distribution. However, close examination of the distribution of individuals may provide some suggestions as to the best measure of density. We should always be aware of the danger of relying on a density measure that is not founded on the biology of the target species.

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