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Plant structure and the searching efficiency of coccinellid larvae

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Summary. 1. To determine the effect of plant structure on the searching efficiency of *Coccinella septempunctata* L. larvae, their functional response on pea and bean plants was compared.

2. The attack coefficient a′ was lower on pea than on bean plants.

3. This was not due to a difference in the coincidence of prey distribution and predator searching effort, but was due to larvae falling off the smooth leaves of pea plants significantly more frequently than off bean plants.

4. It was concluded that plant structure is an important factor in determining the quality of a habitat for coccinellids.

Introduction

Many invertebrate predators of aphids search along the prominent contours of plants. The structure of the plant is important in determining whether or not this behaviour leads a predator to the preferred feeding site of its prey (Fleschner 1950; Banks 1957; Dixon 1959; Boldyrev and Wilde 1969; Dixon and Russell 1972; Wratten 1973; Evans 1976a). Similarly, the rate at which a predator encounters prey can also be determined by characteristics of a plant such as hairiness and waxiness. Banks (1957) found that larvae of *Propylea quatuordecimpunctata* (L.) moved more slowly on hairy potato leaves than on glabrous bean leaves. Similarly, Arzet (1973) found that the movement of *Chrysopa carnea* Stephens larvae was hindered by the hard waxy layer of some cabbage varieties and by the strong, felt-like hairs of plants such as *Pelargonium* and tobacco. *C. carnea* larvae are also irritated by the glandular hairs of cucumber (Scopes 1969).

Recent theoretical and experimental studies on predator foraging strategies has revealed that many predators forage in response to the average quality of the habitat (Charnov 1976; Pyke et al. 1977; Cook and Cockrell 1978; Hubbard and Cook 1978; Townsend and Hughes 1981; Carter and Dixon 1982). For predators confined to a habitat with one plant type, quality is primarily determined by the density of prey. For a predator that searches for a variety of prey types in disparate habitats, however, the quality of a habitat and thus the predators' foraging strategy, will also be determined by the characteristics of the plant host. Few studies have investigated this aspect of habitat quality.

This paper presents results on the effect of plant structure on the searching efficiency of a predator found in a wide range of habitats, the larvae of the seven-spot coccinellid beetle.

Materials and methods

Coccinella septempunctata L. larvae were reared on the pea aphid, *Acyrthosiphon pisum* (Harris), cultured on broad bean, *Vicia faba* (L.). Rearing and experiments took place at $20 \pm 1°$ C, 70–75% RH and a photoperiod of 16 h.

1. Plant structure and searching efficiency

The effect of plant structure on searching efficiency was investigated by comparing the functional response of larvae on two plant species, broad bean, *V. faba*, and pea, *Pisum sativum* (L.). To reduce variability in the surface area of the plants, one hundred seeds of each species were weighed and a weight range selected that represented 20% of the seeds on either side of the mean (*V. faba*: mean $= 1.59 \pm 0.03$ g (SE), range used $= 1.47$–1.72 g; *P. sativum*: mean $= 0.39 \pm 0.01$ g, range used $= 0.36$–0.42 g). At 20° C the surface area of bean and pea plants was found to be similar after 13 and 15 days, respectively (*V. faba* $= 116.7 \pm 9.57$ cm^2, $N = 10$; *P. sativum* $= 115.8 \pm 8.52$ cm^2, $N = 10$; Mann-Whitney $U = 48$, N.S.).

The seeds were germinated singly and allowed to grow through a hole in an inverted plastic cone, the inner surface of which was coated with Fluon® to direct fallen aphids and larvae back onto the plant. First instar pea aphids were placed on the plants and allowed at least 2 h to move to and settle on their preferred feeding sites. Prey densities used were 2, 4, 8, 12, 16, 32 and 64 aphids per plant, with five replicates at each density. A third instar larva that had moulted the previous day and had been starved for 6 h prior to the experiment was placed on each plant and allowed to forage for 2 h. The number of prey that survived was recorded.

2. Plant structure and the distributions of prey and predator searching effort

The preferred feeding sites of *A. pisum* were determined by placing two adult apterous aphids on each of eight pea

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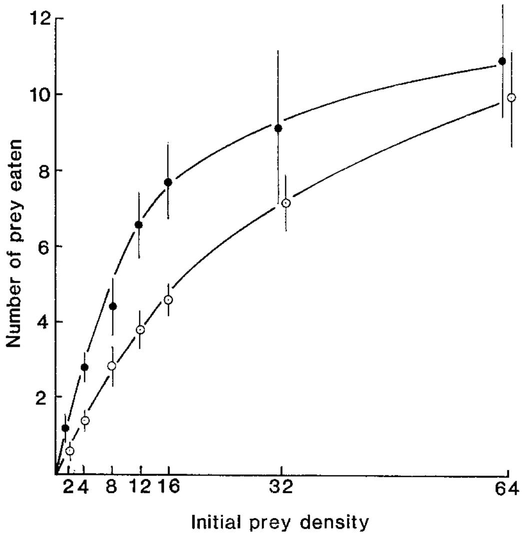

Fig. 1. The functional response of third instar larvae to increasing prey density, on bean (●) and on pea (o) plants ±1 SE. Lines fitted by eye

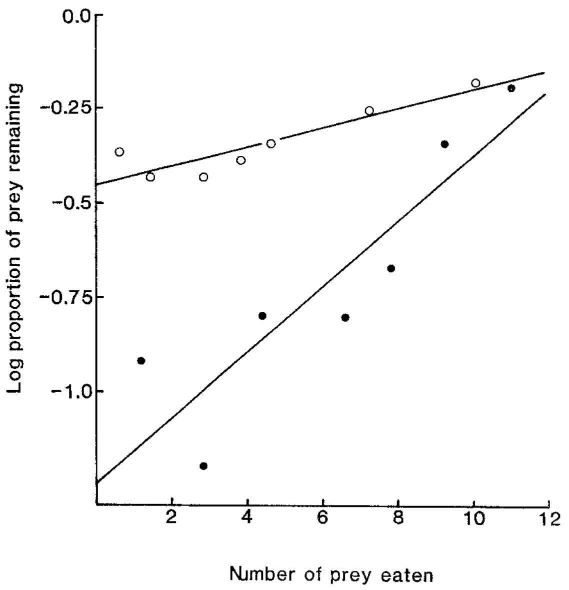

Fig. 2. Linear transformation of the functional response of third instar larvae to increasing prey density, on bean (●) and on pea (o) plants. Regression equation on bean: $y=0.0874x-1.240$; $a'=1.240$; $T_h=8.46$ min; $r=0.8937$; $df=5$; $P=0.01$; Regression equation on pea: $y=0.0259x-0.4498$; $a'=0.450$; $T_h=6.91$ min; $r=0.8980$; $df=5$; $P=0.01$

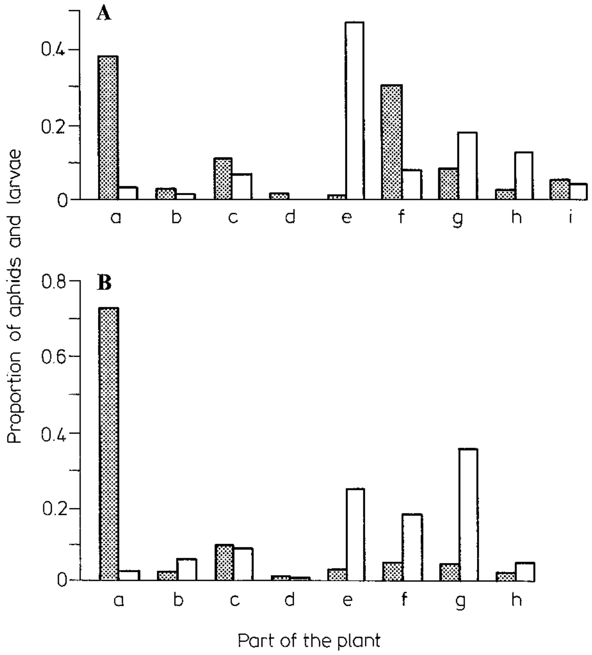

Fig. 3A, B. The distributions of aphids and larval searching effort on the different parts of pea (**A**) and bean (**B**) plants. (*a*) adaxial leaf lamina; (*b*) midrib of adaxial leaf lamina; (*c*) abaxial leaf lamina; (*d*) midrib of abaxial leaf lamina; (*e*) leaf edge; (*f*) leaflets; (*g*) stem; (*h*) petiole; (*i*) tendril of pea plants; (▨) aphid distribution; (□) larval searching effort

and bean plants and leaving them undisturbed for five weeks in a greenhouse at approximately 20° C and 16 h photoperiod. The number of aphids on each part of a plant was then recorded.

The areas of a plant searched by larvae were obtained by recording the position of 16 and 20 fourth instar larvae, unfed since moulting the previous day, every 10 min for 130 min on large uninfested bean and pea plants, respectively.

Results

1. Plant structure and searching efficiency

The functional response of larvae on pea and bean plants is shown in Fig. 1. On both species of plant a type II response resulted, with consistently higher numbers of aphids eaten at each density on bean. The attack coefficient is a measure of the searching efficiency of larvae and was calculated using Rogers (1972) random predator equation:

$$N_{eat}=N[1-\exp\{-a'(T_t-T_h\,N_{eat})\}]$$

where, N_{eat} is the number of prey eaten; N is the initial prey density; a' is the attack coefficient; T_t is the total time available; and, T_h is the handling time.

Transformation of the equation enables a' to be calculated by linear regression of the logarithm of the proportion of prey surviving and the number of prey eaten. The intercept provides an estimate of the attack coefficient while the slope provides an estimate of the product of the attack coefficient and handling time (Fig. 2). The lower attack coefficient on pea plants shows that they were searched less efficiently than bean plants.

Was the difference in attack coefficients due to a difference in the coincidence of the distributions of prey and predator searching effort?

2. Plant structure and the distributions of prey and predator searching effort

The coincidence of larval searching effort and the distribution of *A. pisum* was poor on both pea and bean plants (Pearson product-moment correlation coefficient, after an arcsin transformation of the proportion of the aphids and the proportion of the number of times larvae were found on each part of the plants: pea, $r=-0.149$, 7 d.f., N.S.; bean, $r=-0.235$, 6 d.f., N.S.; Fig. 3). There was no significant difference between pea and bean (comparing the coincidence of larval searching effort and aphid distribution as a total of all parts of each plant species, $X^2 = 0.647$, 1 d.f., N.S.). Thus, the lower searching efficiency on pea plants was not due to the effect of plant structure on the distributions of prey and predator searching effort.

However, larvae were found significantly more often off pea plants and on the soil than off bean plants (41.9% of observations compared with 10.1%, respectively; $U = 24$, $N_1 = 16$, $N_2 = 20$, $P = 0.002$). To determine the reason for this larvae were continuously observed for 2 h on pea and bean plants, and the number of times they walked or fell from the plants was recorded. Larvae searching pea plants fell off significantly more frequently than off bean plants (pea $= 3.2 \pm 1.24$ falls/2 h; bean 0.0 falls/2 h; $U = 0.0$, $N_1 = 5$, $N_2 = 5$, $P = 0.004$).

Thus, on pea plants larvae spent more time relocating the regions where prey was to be found, resulting in a low searching efficiency compared with on bean plants.

Discussion

The success with which a coccinellid larva searches for its aphid prey is significantly affected by the structure of a plant. Larvae found the smooth leaves of pea difficult to grasp and frequently fell from pea plants, resulting in the loss of searching time and a lower attack coefficient than on bean plants. For arboreal species, such as *Adalia bipunctata* (L.) and *Anatis ocellata* (L.), falling would have serious consequences and the risk is reduced as the larvae have a large anal disc for holding onto leaves (Putman 1964; Kesten 1969).

Although many insect predators have been reported concentrating their search along the veins of leaves where aphid density is generally highest (Dixon 1959, 1970; Dixon and Russell 1972; Wratten 1973; Evans 1976a), this depends on leaf structure, i.e., whether the veins are prominent or not, and on the species and instar of the predator. In this study, on both pea and bean plants, larvae searched the edge of leaves and the stem because the veins of pea and bean are not prominent and thus there was a low correlation between searching effort and aphid numbers. On bean a similar result was found by Marks (1977). However, larvae are more successful searching for *Aphis fabae* (Scopoli) on bean, as this aphid colonises the stem as well as the leaf veins (Carter 1982). Another aphid predator, *Anthocoris confusus* (Reuter), is more successful searching the veins of bean during the first instar than during the second instar (Evans 1976a), whereas on sycamore, where the veins are prominent, both stages search the veins equally well (Dixon and Russell 1972). The prominent veins of sycamore (Dixon 1970) and lime (Wratten 1973) are also successfully searched by *A. bipunctata*.

Similarly, other characteristics of a plant affect predators differently. For example, although the larvae of the coccinellid, *Coelomegilla maculata* de G., are irritated by the glandular hairs of cucumber and tend to fall from the leaves, this is not the case for the larvae of two other coccinellids, *A. bipunctata* and *Cycloneda sanguinea* L. (Gurney and Hussey 1970).

Not only the structure but the condition of a plant may also have an effect on a predators' foraging behaviour. For example, Kesten (1969) reported that adult *A. ocellata* tested pine needles with their mandibles and chose only new needles to search, presumably reducing the amount of time wasted searching areas where prey are not likely to be present. Similarly, Evans (1976b) reported that *A. confusus* females probably tested the condition of bean plants by inserting their stylets into the plant before laying eggs.

Finally, even for 'sit and wait' predators, such as the net-spinning caddis larva, the substrate can have a significant effect on the predators' feeding rate, since the type of substrate influences the mobility of the prey (Hildrew and Townsend 1977).

In conclusion, the quality of a habitat can be determined by many factors, probably interacting in a complex way, for example, the density of prey, the number of predators, competitors or mates, the availability of egg-laying sites or specific nutritional requirements, etc. Current models of predator foraging behaviour, however, regard net energy intake as by far the most important determinant of quality (Pyke et al. 1977; Townsend and Hughes 1981), and energy expenditure is usually regarded as a function of prey density. Plant structure has been shown here to have a significant effect on a predators' encounter rate, and thus the energy expended whilst searching for prey. Plant structure is, therefore, an important factor in determining the quality of a habitat and ultimately a predators' foraging strategy.

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