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THE INFLUENCE OF PLANT SURFACES ON THE SEARCHING BEHAVIOUR OF *COCCINELLID LARVAE*

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The behaviour of 1st- and 4th-instar larvae of *Adalia bipunctata* on leaves with different surface characters was observed. Searching success was high where single scattered hairs forced larvae to change their direction often and to cross the interveinal areas (e.g. Chinese cabbage and radish). On glabrous leaves with a thick slippery wax-layer (e.g. kohlrabi, Brussels sprout) larvae could move only along the edge or narrow protruding veins which they could clasp with their legs. Even on glabrous leaves with a thin wax-layer (e.g. broad bean, sugar-beet) the edges and the veins were the preferred parts. Larvae were unable to search leaves with dense upright or hook-shaped hairs (e.g. tomato, tobacco and bush bean).

KEY WORDS: Predation — Behaviour influence of host plant — *Adalia bipunctata* — Coccinellidae.

Spatial distribution is a major factor influencing equilibrium levels and stability in arthropod predator-prey systems (Hassell, 1978). It is governed by the behaviour of the individuals with respect to the characteristics of their habitat. The spatial distribution of coccinellid larvae is determined by, (1) oviposition behaviour of the adults, (2) the searching behaviour of the larvae.

Since coccinellid larvae cannot perceive their prey even over a small distance (Fleschner, 1950) their track is largely determined by the characteristics of the substratum, that is, of the host plant. The influence of leaf venation, branching and other morphological features of plants has been investigated by Fleschner (1950), Banks (1957), Dixon (1959) and Bänsch (1964). The following paper deals with the influence of leaf surface.

MATERIAL AND METHODS

First- and 4th-instar larvae of *Adalia bipunctata* L. from a stock culture fed on *Acyrthosiphon pisum* (Harris) served as test animals. Their searching behaviour on the leaves of 11 plant species was recorded. In Table I the plants are arranged in 6 groups, according to leaf surface. Test plants or twigs were about 20 cm long and had 2—15 leaves according to the leaf size. They were infested artificially with 100—200 *Myzus persicae* Sulz. On non-host leaves the aphids were stuck at random on the lower leaf surface with gum arabic. Coccinellid larvae after starvation for 5 hr (1st-instar) or 10—15 hr (4th-instar) were released individually in the center of a plant and observed continuously for 3 hr. Time spent on different parts of the plant and in searching, feeding and "non-productive" activities, as well as the number of aphids consumed were recorded. Resting and unsuccessful attempts at walking were recorded as "non-productive" activities.

The paths of 1st-instar larvae searching leaves of sugarbeet and Chinese cabbage were each recorded for 15 min. When a larva left a leaf it was put back on the center of the leaf. Each leaving was recorded.

In another experiment 21 *M. persicae* were stuck with gum arabic in the interveinal areas near the main veins on the undersurface of the test leaves. The time required by 1st-instar larvae to find their first prey was recorded. See also Shah (1980) for details.

RESULTS

Influence of leaf surface. The wax layer of a leaf influences the mobility of coccinellid larvae. On leaves with a thick, slippery wax-layer like those of kohlrabi and Brussels sprout 1st-instar larvae can walk only on the leaf edge and on the protruding veins which the larvae clasp with their legs. The interveinal areas are avoided. If the larvae got accidentally onto them they took a long time to leave them as their legs slipped. This "non-productive" activity took up a high proportion of the total time.

TABLE I

Plants classified according to leaf surface

Surface of leaves	Plant species	
1. Smooth (non-slippery waxy layer)	broad bean sugar-beet	*Vicia faba* L. *Beta vulgaris* L.
2. Smooth	kohlrabi Brussels sprouts	*Brassica oleracea* var. *gongyloides* L. *Brassica oleracea* var. *gemmifera* L.
3. Hairy (single, scattered hair)	Chinese cabbage summer radish	*Brassica chinensis* L. *Raphanus sativus* L.
4. Rough (leathery or soft, matted hair)	apple[1]) sour cherry	*Malus domestica* Brokh. *Prunus avium* L.
5. Hairy (long, dense, and upright trichomes and glandular hair)	tomato tobacco	*Lycopersicon esculentum* L. *Nicotiana tabacum* L.
6. Hairy (hook-shaped hair)	bush bean	*Phaseolus vulgaris* L. var. Sortex process

[1]) The uppersurface of the leaves of sour cherry and apple is similar. The under surface of apple leaves is covered with dense, soft, matted hair, on which larvae can walk. Both species are, therefore, put into the same group.

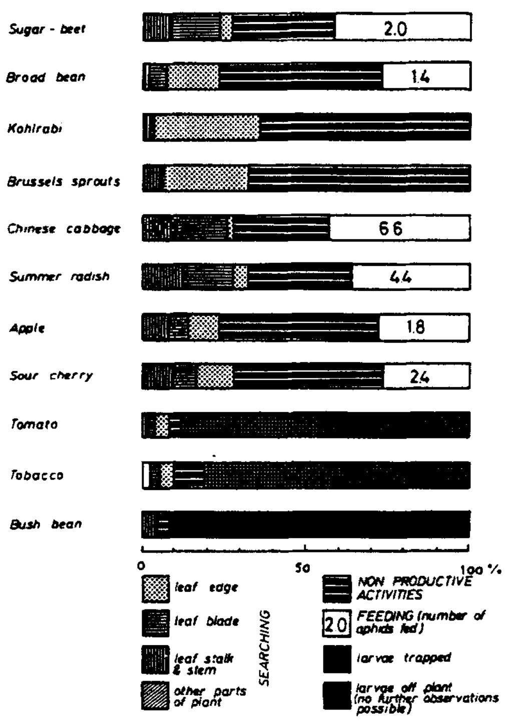


Fig. 1. Average time spent by 5 1st-instar larvae of *A. bipunctata*, each observed for 3 hr in different activities on the leaves of 11 species of plant.

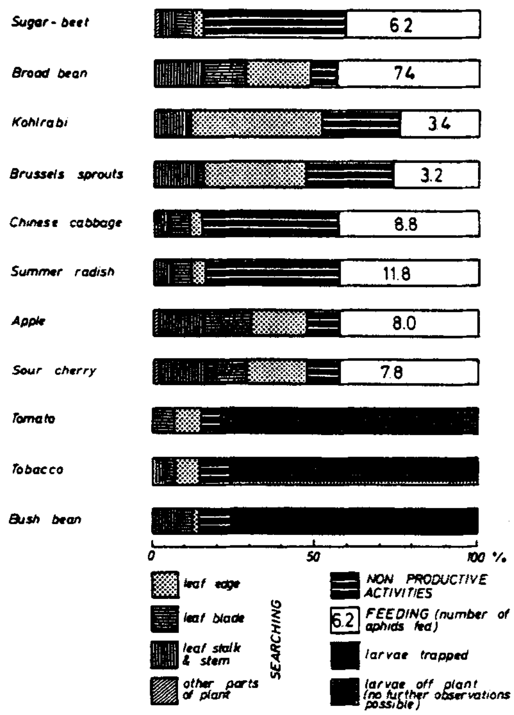
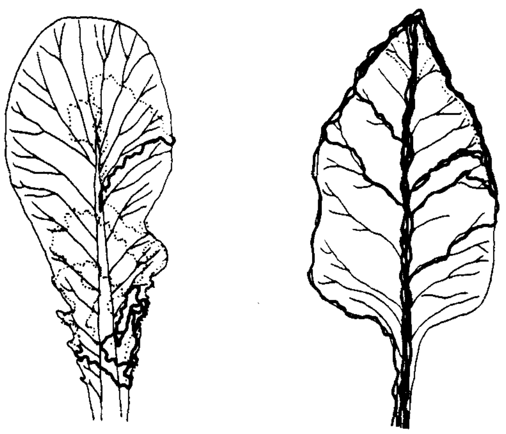


Fig. 2. Average time spent by 5 4th-instar larvae, each observed for 3 hr, in different activities on the leaves of 11 species of plant.



A B

Fig. 3. Typical track of 1st-instar larvae of *A. bipunctata* on Chinese cabbage (A) and sugar-beet (B).
under surface: ...... upper surface: ——

Since the aphids were present mainly in the interveinal areas none were captured (Fig. 1). — Fourth-instar larvae were better able to cope with this difficulty; they could walk across interveinal areas and explore them from the edge of a leaf to which they fixed themselves by their hind tarsi or anal disc. Therefore, their searching success was better than that of the 1st-instar larvae (Fig. 2).

On leaves with a thin, non-slippery wax-layer (broad bean, sugar-beet) larvae walked across interveinal areas but preferred the leaf edge and veins (Fig. 3). On Chinese cabbage and summer radish the strong hairs of leaf edges, veins and interveinal areas acted as obstacles and forced larvae to change their direction. This resulted in a rather twisted track (Fig. 3) and a better searching success with 13 1st-instar larvae out of 20 finding prey on Chinese cabbage within 15 min and taking an average of 6.4 ± 1.1 min; on sugar-beet 7 larvae were successful taking 8.4 ± 1.2 min. Although the proportions of larvae finding prey on the two leaves were not significantly different ($\chi^2 = 3.6$) it was what was expected from the % of time spent feeding in experiment 1 (Fig. 1, 2). Larvae were more likely to walk off leaves of sugar-beet ($\bar{x} = 1.75 \pm 0.33$ times within 15 min per test animal) than off leaves of Chinese cabbage ($\bar{x} = 0.17 \pm 0.11$).

On leaves of group 4 (apple and sour cherry) searching behaviour and success were similar to those on group 1. — On tomato and tobacco leaves the dense, long and upright trichomes impaired movement; 1st- and 4 th-instar larvae found difficulty in holding on, dropped off after an average of 20 min and were unsuccessful in capturing prey.

Bush bean leaves proved to be not only an unsuitable substratum for locomotion but caused death of the larvae. The larvae became impaled on the hook-shaped trichomes and spent the rest of the time unsuccessfully trying to free themselves. Usually their soft skin was injured and they quickly died.

Similar observations were reported by Putman (1955) for *Stethorus punctillum* (Weise) on *Phaseolus lunatus*.

DISCUSSION

The chance of finding prey increases the more time a predator spends searching the preferred habitat of the prey. The searching behaviour of a coccinellid larva is influenced by the characteristics of leaf surfaces. Two features of leaves were important: the presence, density, distribution and shape of trichomes and the texture of the wax-layer. If the latter is thick and slippery young coccinellid larvae cannot hold on in the interveinal areas and are confined to narrow protruding veins or leaf edges which they can grip with their tarsi and anal disc.

The suitability of leaves for larvae of *A. bipunctata* searching for prey can be grouped as follows:

1. Leaves with dense, upright, hook-shaped or glandular hairs (e.g. bush bean, tomato, tobacco) are not suitable.
2. Glabrous leaves with a thick, slippery waxy layer impede locomotion and only aphids which have settled near to protruding veins are caught.
3. Glabrous leaves with a non-slippery surface (e.g. sugarbeet and broad bean) or leaves with soft, matted hair (apple) are a fairly good surface for hunting provided aphids concentrate near the veins. However, aphids in the interveinal areas are missed. Within this group small leaves are more favourable than large ones, because proportionally more of the leaf edge is explored.
4. Leaves with few scattered hairs along leaf edges, veins and interveinal areas (e.g. radish and Chinese cabbage) and on which aphids are distributed evenly over the leaf lamina are very suitable for foraging larvae.

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ZUSAMMENFASSUNG

Der Einfluss verschiedener Pflanzenoberflächen auf das Suchverhalten von Coccinellidenlarven.

Das Suchverhalten von Larven des 1. und 4. Stadiums von *Adalia bipunctata* L. wurde auf Blättern mit unterschiedlicher Oberflächenbeschaffenheit untersucht. Der Sucherfolg war am grössten auf Chinakohl und Radieschen; hier zwangen vereinzelte, aufrecht stehende Haare die Larven zu häufigem Richtungswechsel und veranlassten sie auf diese Weise, auch die Intercostalfelder abzusuchen. Auf kahlen Blättern mit dicker, glatter Wachsschicht (Kohlrabi und Rosenkohl) fanden die Tiere mit den Tarsen keinen Halt; sie konnten sich nur auf dem Blattrand und den vortretenden Adern, die sie mit den Beinen umklammern konnten, fortbewegen. Selbst auf kahlen Blättern mit nur dünner Wachsschicht (Zuckerrübe, Ackerbohne) wurden die Blattränder und die Adern vorzugsweise belaufen. Von Blättern mit dichter aufrechter Behaarung (Tomate, Tabak) liessen sich die Larven nach kurzer Zeit herabfallen. Die hakenförmigen Trichome der Buschbohnenblätter behinderten sie beim Laufen und führten namentlich bei den noch zarthäutigen Eilarven tödliche Verletzungen herbei.

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