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Tomato Stem Trichomes and Dispersal Success of *Phytoseiulus persimilis* Relative to its Prey *Tetranychus urticae*

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ABSTRACT

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Tomato varieties used at present for commercial production in Dutch glasshouses have a high density of glandular trichomes on the stem, but a very low density on the leaves. The two-spotted spider mite, *Tetranychus urticae* Koch, and the predatory mite, *Phytoseiulus persimilis* Athias-Henriot, usually disperse from leaf to leaf via the stem, thereby incurring high risks of entrapment (and death) in the exudate of the glandular trichomes. These risks have been quantified on the tomato cv. 'Turbo' and an accession of *Lycopersicon peruvianum* almost free of glandular trichomes. The possible consequences for biological control are discussed and new perspectives for predator release strategies and for plant breeding are considered.

INTRODUCTION

The foliage and stems of tomato varieties are covered with a dense vesture of glandular trichomes. Luckwill (1943) described the glandular hairs of *Lycopersicon* spp. and showed that they differ largely between species of this genus.

Using Luckwill's classification, type VI trichomes can be distinguished that physically entrap tiny arthropods, such as aphids and spider mites, in their secretions (Gentile et al., 1969; Rasmy, 1985). Similar phenomena have been reported for other solanaceous plants (Gibson, 1976; Rasmy, 1985).

Usually entrapment results in mortality due to starvation and possibly also due to contact with toxic compounds in the exudate of glandular trichomes (Aina et al., 1972), e.g. type VI trichomes (Snyder and Carter, 1984; Good and Snyder, 1985). Such a toxic compound has been found in *L. hirsutum glabra-*

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tum and identified as 2-tridecanone (Williams et al., 1980), but its effect on spider mites is yet to be investigated. Avoidance responses to the glandular defense in general have been observed; especially the trichome VI exudate has been demonstrated to contain materials repellent to different stages of *Tetranychus urticae* Koch. (Cantelo et al., 1974; Snyder and Carter, 1984). Because correlations between trichome density and spider mite fecundity have frequently been reported (Stoner and Stringfellow, 1966; Gentile et al., 1969; Stoner et al., 1968; Snyder and Carter, 1985), the exudate may be an important factor in determining reproductive success of spider mites on tomato.

In Dutch glasshouses biological control of spider mites on tomato is not very successful; predatory mites are used in less than 1% of the tomato crop area to control spider mites (Ravensberg et al., 1983). In view of the above-mentioned deleterious effects of glandular trichomes on spider mites and other tiny arthropods, it may be questioned whether the predatory mites are also affected in this respect and how the trichomes are distributed over tomato varieties presently used. *L. esculentum* cv. 'Turbo' is one of these varieties. The trichome density on the leaves is very low, whereas a dense vesture of type VI trichomes is present on the stems. Consequently the trichomes will interfere with leaf-to-leaf dispersal rather than prey searching on the leaves. Our main objective was to assess the dispersal success of predator and prey as affected by trichomes on the stem.

MATERIALS AND METHODS

The walking behaviour of young females of the predatory mite *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae) and of *Tetranychus urticae* Koch (Acarina: Tetranychidae) was studied on the stem of *Lycopersicon esculentum* 'Turbo' (Es) and the *L. peruvianum* accession IVTGB 1084 (Pe), which is almost free of type VI trichomes. Predatory mites were observed: (A) on stems of young (4–10 weeks) tomato (Es); (B) on the stems of young tomato (Es) with web, produced by eight female *T. urticae* during 2 days preceding the experiment; (C) on full-grown (5 months) tomato stems (Es); (D) on *L. peruvianum* stems with very few glandular trichomes (Pe). Two-spotted spider mites were observed: (E) on stems of young tomato (Es); (F) on webbed stems of young tomato (just as in B).

Experiments were done in climate rooms at 25 °C and 55% RH. The predatory mites were reared using the two-spotted mites as prey and Lima bean (*Phaseolus lunatus L.*) as host plant. The spider mites used in the experiments were reared on tomato (Es). Observations were done half-way across the stem on a part with three successive leaves. The second leaf was removed and the scar left at the stalk base served as the release point. If the mites reached the first or the third leaf within 2 h the experiment was stopped and the leaf-to-leaf dispersal was recorded to be successful. If the mite was stuck to the exudate

TABLE 1

Percentage of predatory mites (P) and spider mites (S) entrapped by the glandular exudate on *Lycopersicon* stems within 2 h of release, and the mortality among the entrapped mites after one day

Treatment				*n*	Entrapment (%)	Mortality (%)
P	Es	-	Y	18	61	73
P	Pe	-	Y	15	0	0
P	Es	-	O	19	42	63
P	Es	W	Y	18	39	71
S	Es	-	Y	18	55	20
S	es	W	Y	20	35	43

P = adult female of *P. persimilis*; S = adult female of *T. urticae*; Es = stem of *L. esculentum* (high density of trichomes); Pe = stem of *L. peruvianum* (almost trichome-free stem); W = web of adult female of *T. urticae* on stem; - = no web; Y = young, 4-10-week-old tomato plant; O = 5-month-old tomato plant.

of the trichomes, their position was marked by putting a thin needle in the stem close to the site of mite entrapment. On subsequent days it was assessed whether the mites had freed themselves from the sticky exudate or whether they were still entrapped, dead or alive.

To investigate intraspecific and interspecific variation within the genus *Lycopersicon*, the exudate mass per unit stem surface was assessed on nine accessions, representing five species. Eight plants per accession were grown in a glasshouse for 10 weeks. To quantify the exudate mass two rectangular pieces (1×5 cm) of filter paper (Schut, Heelsum, no. 74-80) were pressed round the stem to absorb the exudate. The exudate mass was determined by weighing the paper pieces directly before and after stem contact. To allow interpretation of relative differences all pressings were done by the same person.

RESULTS

The results of the observations on entrapment by the trichome exudate are presented in Table 1. More than 60% of the predatory mites were entrapped on Es-stems within the 2-h observation period. Most of the entrapped predators were dead after one day (ca. 73%). The age of the tomato plant (4–10 weeks vs. 5 months) did not significantly affect the risk of entrapment ($P > 0.10$; binomial test for differences in proportions). The predators that were not entrapped required from 15 min to more than 2 h to reach the nearest leaf. On the "trichome-free" stem all predatory mites reached the nearest leaf in ca. 6 min (range: 2–13 min).

Of the spider mites 55% were entrapped. This result was not significantly different from that obtained for the predatory mites ($P \gg 0.10$). In contrast to

TABLE 2

Weight of exudate available per 10 cm^2 stem surface of different *Lycopersicon* accessions

Plant species		Mean and range of exudate mass[a] ($mg/10\ cm^2$ filterpaper)
L. glandulosum	IVT GB 1080	3.9 (3-5)
L. glandulosum	IVT GB 1079	4.3 (2-6)
L. peruvianum	IVT GB 1084	4.3 (2-6)
L. hirsutum	IVT 70826	10.4 (8-17)
L. pimpinellifolium	IVT GB 1077	11.9 (10-15)
L. pimpinellifolium	IVT GB 565	16.9 (12-22)
L. hirsutum f. glabratum	IVT 84077	17.0 (12-20)
L. esculentum 'Turbo'	IVT 84013	23.8 (20-30)
L. esculentum 'Sonatine'	IVT 84034	35.4 (27-42)

[a]Eight replications to each experiment.

the predatory mites most of the entrapped spider mites were still alive after one day, but sooner or later they died as well. The spider mites that were not entrapped needed periods ranging from 1 min to more than 2 h to get to the nearest leaf, which is approximately equal to the leaf-to-leaf dispersal time of the predatory mites.

It is conceivable that spider mites profit from their ability to spin a silken mat over the trichomes. When numerous spider mites have attempted to reach nearby leaves via the stem, such a mat can be formed and its significance for dispersal success is evident to anyone who has ever observed a spider-mite infestation in tomatoes. It is more interesting to assess the change in effectiveness when only few dispersers have attempted to pass the stem. As shown in Table 1, the mortality during leaf-to-leaf dispersal tends to become lower when only eight female spider mites had previously crossed the stem. However, the effect was not very significant ($0.05 < P < 0.10$). The same effect was found when the entrapment of predatory mites was determined on tomato stems previously visited by a low number of spider mite females ($0.05 < P < 0.10$). Thus, once predatory mites are on a plant infested by spider mites, they might profit from the ability of their prey to reduce the effectiveness of the plant's glandular defense system.

There is a need to quantify the exudate mass produced per unit stem surface. Firstly, the exudate production of plants within a particular accession may be variable both in time and space; several authors have shown the strong influence of external conditions, such as daylength and light intensity, on 2-tridecanone levels (Kennedy et al., 1981) and trichome density (Good and Snyder, 1985). Secondly, the variation in exudate production between accessions may be relevant for breeding varieties better adapted to biological control. Therefore, the exudate mass was determined by weighing standard pieces of filter paper before and after having pressed it round the stem. Differences due to individual perspiration appeared to be negligibly small (0.1–0.3 mg; $n=8$). In the experiments on mite dispersal and mortality on Es the mean exudate mass was 27 mg per 10 cm^2 filter paper ($n=8$, range=24–29 mg). Applying the method to assess differences between nine accessions representing five species of *Lycopersicon* gave the results presented in Table 2. Therefore, rather than counting the number of these trichomes per unit stem surface it seems more easy and relevant to use the weighing method proposed here.

DISCUSSION

Our experiments show that the glandular trichomes of *L. esculentum* provide a rigorous defense against phytophagous spider mites which acts also against one of the natural enemies of these phytophages. Especially the trichomes on the stem are an important barrier to dispersal, as predatory mites and spider-mites usually move from leaf to leaf by walking.

Because the glandular exudate of type VI trichomes accumulates under a membrane (Luckwill, 1943), the mites are only caught after touching and breaking this cuticle. If the secretions were not protected in this way, their stickiness would soon become ineffective as a consequence of dust particles falling on the sticky material. Thus, the protective but breakable cuticle can be regarded as an adaptation increasing the effectiveness of the plant's glandular defense against arthropods.

Our results on prey and predator mortality during dispersal via the stem provide good reasons to modify the method of predator release by regular distribution, as currently employed in Dutch tomato glasshouses. By releasing predatory mites on every other plant, i.e. irrespective of the position of the spider-mite colonies, most of the predatory mites would die before reaching their prey. It would be much more effective to release them on the leaves that are infested by spider mites. In this way, the predators suffer less mortality before reaching a prey colony, and their dispersal could be improved by the presence of a silken mat over the trichomes on the stems connecting spider mite-infested leaves. Pest-site directed release is therefore to be preferred to the regular distribution method presently used in the Netherlands. Other release strategies – such as the pest-in-first method or the full supply method proposed by Hussey and Scopes (1985) – lead to a rather homogeneous distribution of prey and predator. Therefore, we expect that in that release strategy predators also run less risk of entrapment before finding their prey.

Although leaf-to-leaf dispersals of spider mites and predatory mites are hampered in similar ways, there are good reasons to suppose that the predatory mites are more affected by the glandular defense than the spider mites, because: (1) due to obvious differences in the amount of food available per leaf, predatory mites disperse more frequently than do spider mites; (2) spider mites may be more successful in reaching fresh food resources by their ability to descend to lower leaves on silken threads, thereby bypassing the sticky trichomes on the stem.

The consequences of the differential effect of the stem trichomes on predatory mites should be evaluated in future biological control experiments on trichome-free and trichome-dense tomato varieties. These experiments are decisive for starting research on breeding tomato varieties that carry less or no trichomes. In some of the wild relatives of the cultivated tomato there is sufficient genetic variation, although the two promising species *L. glandulosum* and *L. peruvianum* are difficult to cross with *L. esculentum*. Another option would be to breed for increased trichome density from *L. hirsutum* (Carter and Snyder, 1985) in order to prevent heavy infestations by spider mites. However, this approach is incompatible with biological control with predatory mites and is less acceptable for growers, who dislike the tomato stickiness.

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