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Short communication

Effectiveness in defense against phytophagous arthropods of the cassabanana (*Sicana odorifera*) glandular trichomes

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Glandular trichomes commonly occur throughout dicotyledonous angiosperms. Several authors have demonstrated that the secretions (i.e., secondary metabolites) produced by these structures are effective in discouraging various types of phytophagous arthropods because of their odor, taste, stickiness, or toxicity. As a result, the secretions inhibit feeding, but may also prohibit oviposition or impair larval development (Levin, 1973; Stipanovic, 1983; Duffey, 1986). In general, two modes of protection involving glandular trichomes may be distinguished: (1) trichomes may permanently exude secretions soon after their production (e.g., Gregory et al., 1986), or secretions are discharged at the death of the trichome (Fahn, 1979), resulting in an enrichment of the plant surfaces with non-volatile and/or immediate vicinity with volatile repellent(s), or (2) trichomes are 'touch-sensitive' and release the secretion only when the secretory cells are ruptured by contact (Levin, 1973). The latter mode (which is widespread in the Cucurbitaceae [Gourd family] and Solanaceae [Nightshade family], among other families) is of special interest, since it represents a rather complex plant-arthropod interrelationship: when ruptured, the 'touch-sensitive' trichomes rapidly release an exudate that eventually deters the animal. The effectiveness of this defense is often based on a multitude of specific interactions, which include physical and chemical factors (Gentile & Stoner, 1968; Duffey, 1986 and literature cited therein; Gregory et al., 1986; Musetti & Neal, 1997; Malakar & Tingey, 2000). The mechanisms, with which 'touch-sensitive' glandular trichomes physically obstruct the performance of phytophagous arthropods have been addressed in numerous studies, based primarily on experiments with the Solanaceae. The arthropods may be immobilized by becoming entangled in a sticky secretion, and often eventually cemented to the leaf surface or the trichomes (Zimmermann, 1922; Gentile et al., 1968; Gibson, 1971, 1974, 1976a, b; Rasmy, 1985; Farrar & Kennedy, 1991; Tingey, 1991; van Dam & Hare, 1998), or they are disabled by a quickly solidifying secretion that encases the distal parts of the legs (McKinney, 1938; Gibson & Turner, 1977; Tingey & Gibson, 1978; Duffey, 1986). One aspect that has rarely been addressed concerns the susceptibility of different types of arthropods to physical obstruction by quickly solidifying secretions. Here we present observations on the behavior of four arthropod taxa on leaves of *Sicana odorifera* (Cucurbitaceae) with 'touch-sensitive' trichomes releasing quickly solidifying secretions, which suggest that particular morphological features and behavioral patterns of the visiting animals are important factors related to the success of this defense mechanism.

Sicana odorifera (Vellozo) Naudin (Cucurbitaceae), the cassabanana, is a large vine, believed native to Brazil but today found spread throughout tropical America (e.g., Lira, 1991). All young aerial parts of the plant are densely covered with 'touch-sensitive' trichomes. The trichomes are up to 0.2 mm long, and consist of a stalk of 3–6 cells and a two-celled head, consisting of an enlarged, secretion-filled cell on top of which a second, small papillate cell is present, which also is incorporated in the mechanism of rapid exudation when the secretory cell is ruptured. After complete exudation, the head usually separates from the stalk. The stalk, however, does not atrophy immediately, but maintains turgor for some period and, as a result, may function as a mechanical obstacle. When the leaves mature, unruptured 'touch-sensitive' trichomes and the stalks of exuded trichomes are shed from the epidermis.

Sicana odorifera was grown from seeds in the laboratory over a period of 2–3 months. Individuals of four arthropod species, including Oleander aphids (*Aphis nerii* Boyer de Fonscolombe; Homoptera: Aphididae), Striped flea beetles (*Phyllotreta striolata* [Fabricius]; Coleoptera: Chrysomelidae), Boxelder bugs (*Boisea trivittata* [Say]; Heteroptera: Rhopalidae), and Two-spotted spider mites (*Tetranychus urticae* Koch, Acari: Tetranychidae), were placed on freshly harvested leaves in closed petri-dishes, so as to be exposed to the glandular trichomes. Their behavior was observed continuously over a period of up to 24 h.

Tetranychus urticae (0.3–0.8 mm long) was not affected by the presence of 'touch-sensitive' trichomes, and could move around on the leaves for an indefinite time without triggering the 'touch-sensitive' mechanism. *Phyllotreta striolata* (2–3 mm long) frequently ruptured the trichomes, with secretions immediately precipitating on the legs. However, because of their mandibulate mouthpart morphology, the beetles were capable of chewing off secretions from their first and second pair of legs. They were also able to remove secretions from the third pair of legs by continuously rubbing the legs against each other (i.e., by autogrooming). *Boisea trivittata* (4–11 mm long) possesses stylate mouthpart morphology, and thus could not remove secretions from the legs by chewing. However, these arthropods eliminated secretions by autogrooming. *Aphis nerii* (1–3 mm long) was the only arthropod observed to be effectively entrapped by the glandular trichomes of *S. odorifera*. In the course of several hours, the secretion gradually accumulated on the legs, and after about 20 h on the leaf, the tarsi and pretarsi were completely encased within a thick layer of solidified secretion. Since aphids possess stylate mouthpart morphology, they are unable to clean their legs from the secretion by chewing. Interestingly, we saw no evidence of aphids removing secretions by autogrooming.

All four arthropod taxa utilized in this study are small, but display differences in morphology and behavior, which appeared to be significant relative to their susceptibility to the defense. The *S. odorifera* trichomes are selective, and the arthropods were not equally effectively deterred; only *Aphis nerii* was physically disabled by the trichome exudate. *Aphis nerii* did not display autogrooming behavior. Whether because of this, or because of differences in leg articulation (perhaps, *A. nerii* lacks the biomechanical ability to bring the legs close together), the aphids did not rub their legs together to break off the exudate, and thus the secretion rapidly accumulated. None of the aphids observed was immobilized (by becoming entangled, and eventually cemented to the leaf surface or the trichomes), but rather the secretion gradually encased the tarsi and pretarsi. This leads to reduced leg function due to: (1) decreased sensation (the trichoid sensillae on affected regions of the leg are bound by the secretion), (2) tarsi fixed in one position, and (3) decreased traction by bound pretarsi. As a result, the aphids are unable to maintain their grip on the plant surface. In nature, aphids disabled by ineffective tarsi and pretarsi easily become dislodged from the leaf by air currents over the phylloplane (cf. McKinney, 1938). Moreover, the accumulated layers of secretion inhibit the movements of the aphids by increasing the weight of the legs, and most aphids displayed difficulties in operating the extremities. In contrast to *Aphis nerii, Phyllotreta striolata* and *Boisea trivittata* were able to avoid the accumulation of secretion by cleaning their legs in either of two ways, i.e., by chewing off the secretion, or by rubbing the legs together with sufficient force in order to remove the secretion. This response of *P. striolata* and *B. trivittata* is effective against the defense of *Sicana odorifera* because the secretion exuded quickly solidifies. However, in other, previously studied cucurbit taxa, and several *Lycopersicon* and *Solanum* species with 'touch-sensitive' glandular trichomes, the exuded substances remain sticky, and phytophages are disabled by becoming entangled in the secretion, and eventually cemented to the surface (rather than by reduced leg function). With a sticky secretion, neither autogrooming nor chewing can be used effectively to reduce/prohibit accumulation; rather, chewing and feet-rubbing would result in the distribution of the sticky secretion to other body parts. Finally, the fourth taxon tested, *Tetranychus urticae*, was not affected by the defense of *S. odorifera*. These animals are obviously too small, and thus not with sufficient body mass to cause the secretory cells to rupture. If placed on geenhouse plants of *Sicana odorifera*, individuals of *Tetranychus urticae* become quickly established on the lower leaf surfaces and develop into large populations.

The experiments presented here on the effectiveness in defense against four types of small phytophagous arthropods of the 'touch-sensitive' glandular trichomes of *Sicana odorifera* indicate that the physical component of this defense mechanism only functions on those animals that (1) possess a certain minimum size, (2) are characterized by a certain mouthpart morphology, and (3) do not display particular behavioral features. Further studies are necessary in order to more fully address the nature of this defense. Perhaps, chemical analyses of the secretion and long-term observations of phytophage populations on *S. odorifera* eventually will reveal a more complex defense system, comparable to that found in members of the Solanaceae (cf. Duffey, 1986 and literature cited therein; Musetti & Neal, 1997), which does not exclusively rely on physical obstruction, but also includes other defensive properties (e.g., odor, taste, and/or toxicity) of the substances secreted.

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