scattering. In this case we would not necessarily expect to get very good agreement between calculations and experimental results, but those calculations could be used as an upper limit for the effect of nonsphericity on scattering characteristics of interest. The result of such calculations, as shown in Fig. 3, can be useful in many applications. For example, in deducing the physical properties of atmospheric aerosols or cosmic dust particles from scattering data, one can use first the Mie calculation assuming spherical particles and then the modified Mie calculations with $n_1 = 1$. Regardless of the shape of aerosol particles, the correct values of physical properties should be somewhere between the two sets of results, as in Fig. 3.

We again emphasize that our approximation should be used only for ensembles of randomly oriented and arbitrarily shaped nonspherical particles. Whenever all particles are oriented in a definite direction or whenever the scattering occurs on a single particle, specific effects depend on a particle's exact shape; since these effects are not included in our approximation, it should not be used. In addition, our intercomparisons were made for particles in the Mie size range $x < 30$. This adequately covers the size range, for example, of the normal background aerosol particles in the earth's atmosphere; further studies will be required before the procedure can be applied to larger sizes.

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Hooked Trichomes: A Physical Plant Barrier to a Major Agricultural Pest

Abstract. *Hooked epidermal appendages (trichomes) on leaves of field bean cultivars effectively capture nymph and adult leafhoppers. Frequency of capture and capture mortality are highly correlated with trichome density. Hooked trichomes inserted at angles less than 30° are ineffective in capture.*

Breeding crop plants for genetic resistance to insect pests is an ecologically compatible alternative to the use of chemical pesticides. Selection of resistant cultivars can be accelerated if specific resistance mechanisms are identified. Although the role of secondary chemicals in plant resistance to herbivore attack has received much emphasis (*1*), considerably less is known about physical defensive barriers in plants. Recent review articles (*2*) have brought attention to the involvement of glandular and nonglandular plant hairs (trichomes) in insect resistance.

Numerous attempts have been made to establish a statistical correlation between the degree of crop pubescence and resistance to leafhoppers of the genus *Empoasca* (Walsh) (*3*), major worldwide pests of cotton, soybeans, alfalfa, clover, field beans, and potatoes. In North America *Empoasca fabae* (Harris), the potato leafhopper, is a serious pest of field beans, *Phaseolus vulgaris* L. In South America and Central America a closely related species, *Empoasca kraemeri* Ross and Moore, is a primary limiting factor in the production of this vital protein crop (*4*). Although there have been anecdotal reports of arthropod capture by hooked trichomes of *P. vulgaris* (*5–7*), the specific impact of pubescence in different cultivars of field beans on the population biology of leafhopper pests does not appear to have been determined (*8*). In this report, we describe a direct relationship between the hooked trichomes of *P. vulgaris* and mortality of *E. fabae* and report the basis for intraspecific and interspecific variation in the effectiveness of this defense mechanism.

During studies of feeding damage of *E. fabae* on field beans, we observed leafhopper nymphs and adults clinging to leaves of certain cultivars. Using a dissecting microscope at 60×, we observed leafhoppers physically impaled on leaf hairs. Closer examination revealed large numbers of hooked trichomes on the undersurface of the leaves. These specialized hairs ranged from 0.06 to 0.11 mm in length; hairs over the leaf veins were slightly longer. As leafhoppers are very active, we concluded that the insects had become entangled in the hairs as they moved rapidly over the leaf surface.

To document the various methods of capture, we examined captured leafhoppers on bean leaves by scanning electron microscopy (*9*). Both nymphs and adults were found to be impaled through the intersegmental membranes of the abdomen by hooked trichomes (Fig. 1, a and b), to our knowledge a previously unreported phenomenon. Insects were also captured by trichomes impaled in the tarsal segment of the leg or entangled in the tarsal claws, as reported for other insect species (*6, 7*). Figure 1c illustrates yet another form of capture, by a trichome embedded in the membrane between the tibia and the tarsus.

Leafhoppers captured by the tarsus or tibia terminate feeding and struggle to free themselves from the trichomes, fre-

Table 1. Relationship between density of hooked trichomes and capture mortality of leafhopper nymphs caged on leaves of field beans and lima beans. Means followed by the same letter within a column are not significantly different at $P = .05$ by Duncan's multiple range test.

Cultivar	Node	Leaf surface	Hooked trichome density (No. per cm²)	Capture (%)	Capture mortality (%)
Phaseolus vulgaris	Terminal	Lower	14,241 a	59.8 a	36.8 a
'California Light	4	Lower	1,955 b	50.0 b	31.5 ab
Red Kidney'	2	Lower	1,593 b	36.4 c	26.8 b
	2	Upper	244 e	5.7 ef	2.6 d
Phaseolus vulgaris	4	Lower	435 d	16.9 d	12.4 c
'Brasil 343'	2	Lower	362 de	13.2 de	7.6 cd
	2	Upper	11 f	0.5 f	0.0 d
Phaseolus lunatus 'Henderson Bush Lima'	2	Lower	841 c	4.5 ef	2.0 d

quently becoming impaled on other trichomes during the struggle. If unable to escape, the insect usually dies from dehydration and starvation. We observed cast skins attached to the leaf by a trichome, indicating that some nymphs escape by the process of molting. Abdominal capture is a more lethal form of plant defense. As the insect struggles to escape, the abdominal wall frequently ruptures and death soon follows from loss of hemolymph or from starvation and dehydration.

To relate trichome density to capture efficiency, we examined the field bean cultivars *P. vulgaris* 'California Light Red Kidney' and *P. vulgaris* 'Brasil 343' with respectively high and low densities of hooked trichomes. A lima bean, *Phaseolus lunatus* 'Henderson Bush,' was also included, as this species is susceptible to damage by leafhoppers (*10*). The bean plants were raised in a controlled-environment glasshouse (*11*), maintained at a constant temperature of 27°C and a 16-hour photoperiod.

Thirty-one days after seeding, first and second instar nymphs of *E. fabae* were aspirated from stock plants of broad bean, *Vicia faba* L.; they were anesthetized with CO_2 and confined to leaf surfaces by using small cages made of Plexiglas tubing (inner diameter, 23 mm) (*12, 13*). Ten nymphs were placed in each cage and two cages were used per leaflet, for a total of 20 nymphs per treatment (cultivar and leaflet) for each replication. After caging and infestation, a leaf sample was taken from another leaflet of the same trifoliolate leaf, cleared of all pigmentation in 70 percent ethanol, and examined at 100× under a compound microscope. Ten counts of the number of hooked trichomes in a 1.56-mm^2 field of the leaf surface were made randomly to provide an average hooked trichome density for the whole leaf. Twenty-four hours after infestation, the leaves were examined and the numbers of captured and dead nymphs determined. A nymph was recorded as captured only if a trichome was actually observed entering the body wall or leg.

The density of hooked trichomes is highly correlated with capture frequency and nymphal mortality of *E. fabae* on the two field bean cultivars (Table 1). The lower leaf surfaces have higher densities than the upper surfaces. As leafhoppers feed almost exclusively on the underside of the leaves, the trichomes are ideally located for defensive purposes. Within cultivars, mature leaves on the lower nodes have fewer hooked trichomes than mature leaves on the upper nodes. This difference is consistent with increased capture and capture mortality on the upper nodes. Trichome density and capture mortality were at a maximum on the unexpanded terminal leaves. The number of trichomes is fixed early in leaf development (*14*); thus, the density of

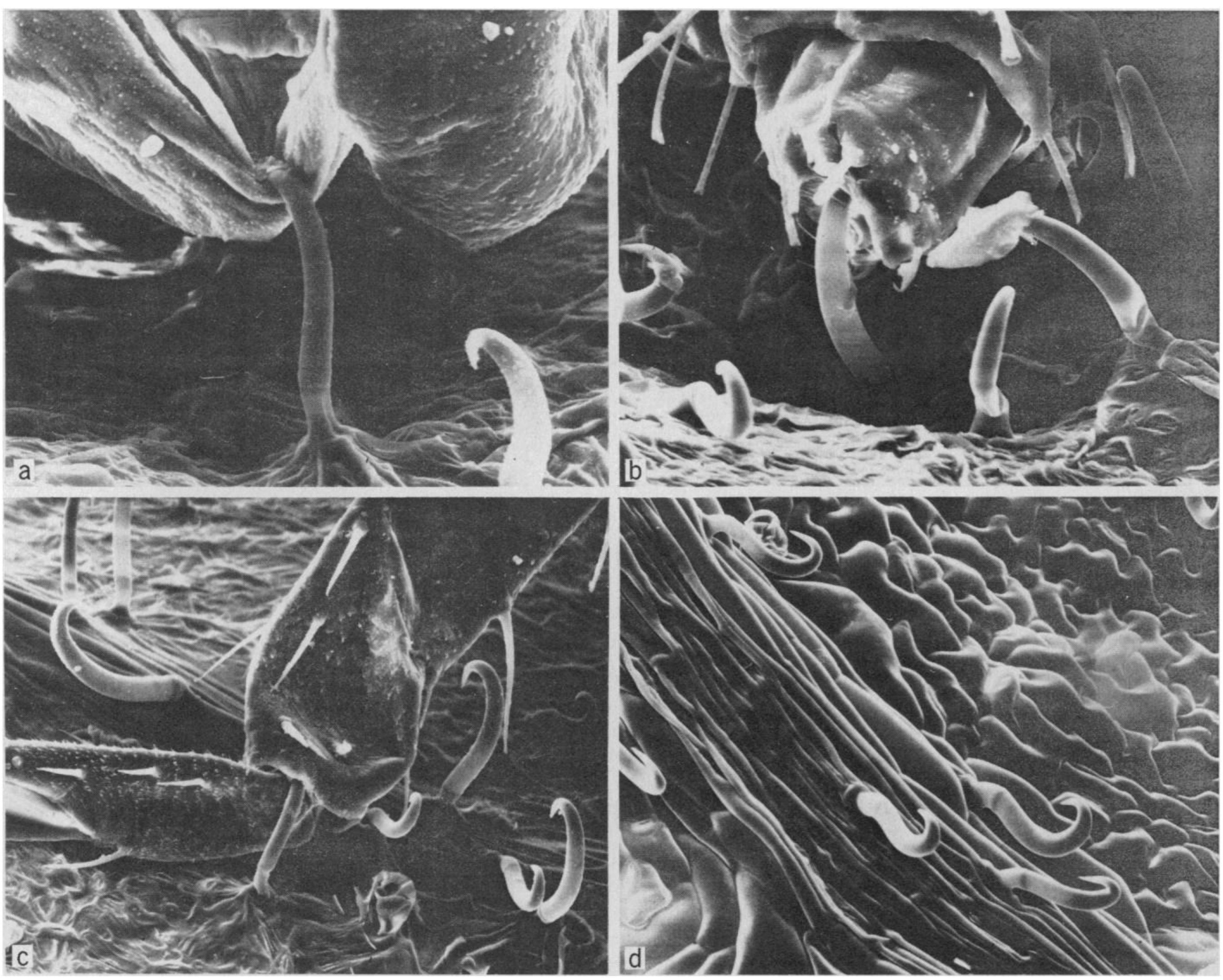

Fig. 1. (a) Trichome inserted in abdomen of a leafhopper nymph (× 700). (b) Trichome embedded in posterior of abdomen (× 700). (c) Trichome embedded in membranous tissue between leg segments (× 350). (d) Procumbent hooked trichomes of the lima bean cultivar Henderson Bush (× 350).

hooked trichomes decreases as the leaf expands. This provides the greatest insect protection for the tender and succulent plant tissues.

Intraspecific variation in nymphal mortality was also accounted for by differences in trichome density. When nymphs were confined to upper leaf surfaces (low trichome density), total mortality for the two field bean cultivars was the same. This suggests that the two cultivars, excluding trichome effects, are equally suitable as leafhopper hosts. For nymphs confined to the lower leaf surface, however, capture mortality was approximately three times greater on the cultivar with the higher density of hooked trichomes.

Overall, nymphal capture and capture mortality are highly correlated ($r = .99$, $P < .01$) with hooked trichome density for the field bean cultivars (Fig. 2). Capture frequency increases rapidly with trichome density, but appears to level off beyond a density of 2000 trichomes per square centimeter. We suggest that the trichomes are so close together on terminal leaves that the nymphs are removed from most direct body contact with the leaf surface. Thus, very high densities of hooked trichomes could reduce capture and decrease the efficiency of this plant defense mechanism. Although removed from direct contact with the leaf surface, these nymphs could continue to feed, as their stylets are long enough to reach the leaf veins.

The percentage of caged leafhopper nymphs captured by the lima bean cultivar was much less than the percentage captured by either of the field bean cultivars (Table 1). This interspecific variation is not explained by differential trichome density, as lima bean leaves have moderately large densities of hooked trichomes. But the hooked hairs of *P. lunatus* are oriented at an angle of 10° to 30° (*15*) (Fig. 1d), whereas the hairs of *P. vulgaris* are relatively erect. Apparently these procumbent trichomes are oriented at such a small angle that the nymphs rarely come in contact with them. Thus the observed interspecific variability in nymphal capture for this cultivar is related to angle of trichome insertion rather than to density.

Clearly, hooked trichomes cause increased mortality of *E. fabae* on field beans. This reduction in nymphal infestation has dramatic implications for varietal plant resistance, as nymphal infestation density is generally correlated with the severity of leafhopper damage (*8*). Thus, hooked trichome density may be a valuable selection criterion in applied breeding programs for field beans, particularly if this defense mechanism can be combined with other plant factors mediating resistance to egg laying and growth of leafhoppers.

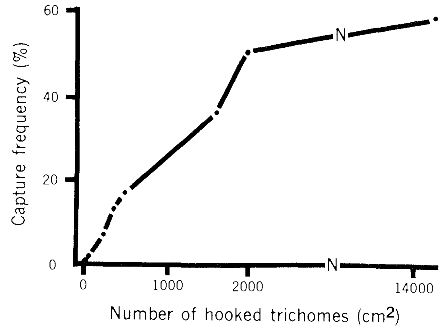

Fig. 2. Relationship between hooked trichome density and capture frequency of leafhoppers on field beans.

The role and importance of trichomes in resistance to crop pests has frequently been overlooked. In part, this may have been due to the inability of earlier workers to consistently correlate total plant pubescence with such general parameters as insect infestation level or crop yield. As our experience with *E. fabae* on field beans indicates, it is important to identify the biological impact on the pest of a specific trichome type. Other factors, including trichome density and angle of insertion, must also be considered. This knowledge should permit more effective selection of insect resistant cultivars.

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Fog Catchment Sand Trenches Constructed by Tenebrionid Beetles, *Lepidochora*, from the Namib Desert

Abstract. *Three species of coastal Namib Desert tenebrionid beetles (*Lepidochora*) build trenches on desert sand dunes. Trenches are constructed perpendicular to fog winds and concentrate moisture during fogs. The beetles return along the ridges of the trenches extracting water from them. The water content of a population of these beetles increased by 13.9 percent during one fog.*

Field observations of three nocturnal beetle species, *Lepidochora discoidalis*, *L. porti*, and *L. kahani* were made during early summer (October 1975 through January 1976), in the coastal African Namib Desert dunes. These beetles establish trenches on the vegetationless surface of the sand dunes on mornings before and during advective fogs. Trenching creates two parallel sand ridges (Fig. 1). The usual locomotory mode, however, is to walk over the surface without displacing sand (*1*). The ridges trap fog water, which is then taken up by the returning beetles.

During the early part of fogs, the beetles emerge on the barren sand dunes and move in a straight line, laying out trenches as long as a meter or more. The trenches become increasingly conspicuous as the parallel ridges trap blow-