GREEN PEACH APHID RESISTANCE BY GLANDULAR TRICHOMES IN *SOLANUM TUBEROSUM* X *S. BERTHAULTII* HYBRIDS[1,2]

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Abstract

Three interspecific F_3 hybrid clones of *Solanum tuberosum* L. x *S. berthaultii* Hawkes bearing both Type A and Type B glandular trichomes were assessed for resistance to the green peach aphid, *Myzus persicae* (Sulzer). In glasshouse trials, aphid mortality and population development on hybrid clones were similar to those on the aphid-resistant parent, *S. berthaultii.* Trichome exudate of the hybrid, B227-63, was as effective in aphid immobilization as that of *S. berthaultii.* Field populations of the green peach aphid on hybrids were intermediate between those on *S. berthaultii* and susceptible *S. tuberosum* cultivars.

Resumen

Tres clones F_3 de híbridos interespecíficos *Solanum tuberosum* L. x *S. berthaultii* Hawkes portando tricomas glandulares de ambos Tipo A y Tipo B, fueron evaluados en cuanto a su resistencia al áfido verde del duraznero, *Myzus persicae* (Sulzer). En ensayos de invernadero, la mortalidad y desarrollo poblacional de áfidos sobre clones híbridos fueron similares a los del progenitor resistente, *S. berthaultii.* En el híbrido B 227-63, el exudado de tricomas fué tan efectivo en inamobilizar áfidos verdes del duraznero como el de *S. berthaultii.* Las poblaciones del áfido sobre híbridos en el campo fueron intermedias a las de *S. berthaultii* y el cultivar *S. tuberosum* susceptible.

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Introduction

The wild Bolivian potato species, *Solanum berthaultii* Hawkes, is being utilized in potato breeding programs for its pest resistance. This species is defended against infestation by small, soft-bodied arthropod pests by its dense vestiture of glandular pubescence (2, 3, 5, 7). As a male parent, this diploid species has been crossed with the cultivated potato, *S. tuberosum* L., yielding fertile tetraploid progeny (1). We report here the effect of hybrid *S. tuberosum* x *S. berthaultii* clones on population biology and field infestations of the green peach aphid, *Myzus persicae* (Sulzer).

Materials and Methods

Glasshouse Studies

All hybrid germplasm used in these trials was obtained from the Cornell University potato breeding program. Three clones (B227-60, B227-63, B227-128) are F_3 interspecific hybrids of *S. tuberosum* x *S. berthaultii*. Their pedigree is given in Fig. 1. These clones and their parents were selected for high densities and large gland volumes for both Type A and Type B trichomes using the method described by Tingey and Laubengayer (7). Their quantitative trichome characteristics are summarized in Table 1. The clone, PI 310927-11, is a selection from the *S. berthaultii* accession, PI 310927, obtained from the Potato Introduction Station, Sturgeon Bay, Wisc. The epidermal morphology of B227-63, B227-128, PI 310927-11, and cv. 'Hudson', is shown in Fig. 2.

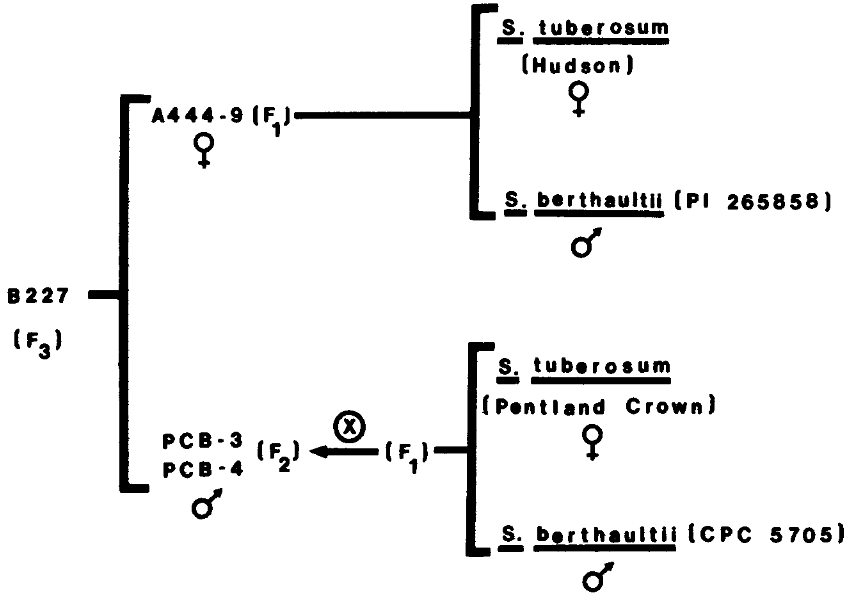

FIG. 1. Pedigree of the *Solanum tuberosum* x *S. berthaultii* family, B227.

TABLE 1. — *Glandular trichome characteristics of mature foliage for 6 potato clones differing in levels of resistance to the green peach aphid. Ithaca, N.Y. 1979.*

		Mean no. glandular trichomes/mm^2				Mean gland diam (μm)			
		Type A		Type B		Type A		Type B	
Clone[a]	Species[b]	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial	Adaxial
B227-60	TUB x BERTH	3	3	9	3	75	75	30	30
B227-63	TUB x BERTH	4	3	10	3	75	75	30	30
B227-128	TUB x BERTH	3	3	20	6	60	75	15	30
PI 310927-11	BERTH	3	6	11	10	57	62	29	32
Hudson	TUB	1	2	0	0	75	75	-	-
Katahdin	TUB	3	2	0	0	75	75	-	-

[a] Secretions of Type A trichomes on *S. tuberosum* are not adhesive and do not harden or darken.

[b] TUB: *S. tuberosum;* BERTH: *S. berthaultii.*

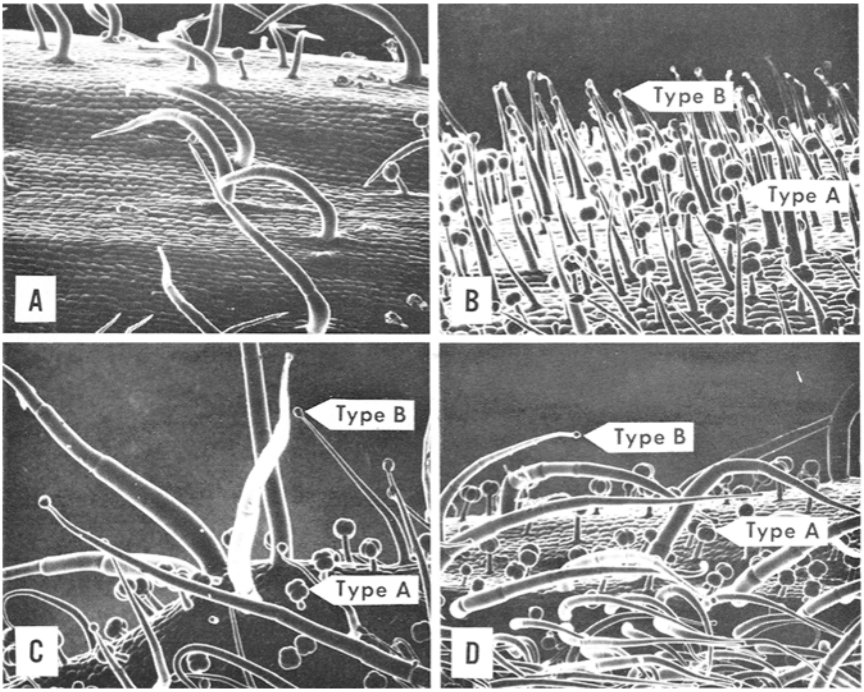

FIG. 2. Epidermal morphology of 4 potato clones. (A) *Solanum tuberosum,* cv. Hudson; (B) *S. berthaultii,* PI 310927-11; (C-D) *S. tuberosum* x *S. berthaultii* F_3, B227-63 and B227-128, respectively. (68X)

Population Development—Six plants of PI 310927-11, B227-63, and cv. Hudson were propagated by stem cuttings and established in a peat-vermiculite soil mix supplemented by Osmocote® fertilizer. All irrigation was by capillary methods. Plants were grown in a glasshouse at daily temperatures fluctuating between 12 and 16°C. Natural light was supplemented with metal halide illumination of 32,000 lux at soil level, 14h per day. Plants were caged in dacron organdy, using the method of Tingey *et al.* (8), when ca. 20 cm in height, and arranged in a randomized complete block design. Eighteen viviparous apterae were placed on each plant, in 3 groups of 6 each on leaves arising from nodes 1-2, 3-4, and 5-6. The mainstems were excised 21 days later, and all foliage was thoroughly examined for dead and living aphids. Bodies of all aphids recovered from B227-63 and PI 310927-11 were examined at 64X for evidence of trichome exudate.

Mortality and Tarsal Encasement — One plant each of the previous 3 clones, plus 2 additional hybrids (B227-60, B227-128) were propagated and grown in the manner described above. When plants were ca. 50 cm tall, 3 14-mm diam Plexiglas® ring cages (6) were placed on the abaxial surfaces of the penultimate sub-terminal leaflets of fully-expanded mature leaves. Two 4th-stadium nymphs were placed in each cage. Mortality and encasement of tarsi by trichome exudate were determined 72 h later. This procedure was repeated weekly for a total of 3 replications.

Immobilization by Trichome Exudate — Two groups of 4th-stadium nymphs were prepared; i.e. those with and without adhesive tarsi. Aphids were obtained from a colony maintained on Chinese cabbage, *Brassica olearacea* L. Pekenensis Group, cv. Michihili. Those with adhesive tarsi were confined on a glandular pubescent clone for ca. 60 min. and then divided into 2 categories depending on the source of trichome exudate; i.e. B227-63 or PI 310927-11. Nymphs with and without trichome exudate on their tarsi were individually placed in the center of a 14-mm-diam arena, on the abaxial surfaces of fully-expanded, excised leaflets of B227-63, PI 310927-11, and cv. Hudson. The time spent in movement from point of confinement to edge of the 14-mm-diam arena was recorded. An aphid that terminated its movement for a period in excess of 5 sec was gently nudged with a hair brush, so that data on mobility would not be affected by resting or feeding activity. All observations were made at an ambient temperature of 25°C. Treatments were completely randomized and replicated 20 times. Aphids and leaflets were discarded following each observation period.

Field Trials

Plants were propagated by stem-cuttings and transplanted in No. 522 Jiffy-strips® to Howard gravelly loam soil at the Cornell University Vegetable Research Farm, Freeville, N.Y. in late May 1979 and 1980. Treatments (clones) were planted down the row at a spacing of 0.6 m, and arranged in a randomized block design of 4 replications. Plots consisted of 6 plants/clone in 1979 and 4/clone in 1980. Cultural practices, weed control, and fungicide treatments were similar to those used in commercial production. In 1979, no insecticides were used except for the application of diflubenzuron at 0.28 Kg AI/ha on June 19, 26, and July 6 for suppression of the Colorado potato beetle. In 1980, plots were treated weekly with carbaryl at 1.1 kg AI/ha. Both years, each plot was bordered by rows of cv. 'Superior'. These practices helped to promote a constant influx of colonizing aphids.

Populations of apterous *M. persicae* were determined by visual examination of adaxial and abaxial surfaces of fully-expanded leaves from the lower ⅓ of randomly-selected plants. In 1979, 2 leaves were examined from each of 3 plants/plot on July 18, July 30, and Aug. 14; in 1980, 10 leaves from each of 4 plants/plot were examined on July 18, Aug. 1, and Aug. 18. Data were adjusted to a base of 10 leaves/plot and processed by analysis of variance and Duncan's Multiple Range test following transformation to log (X + 1).

Results

Glasshouse Studies

The mean aphid population on cv. Hudson was 761/plant 21 days after confinement; no dead aphids were found. No living aphids were found on hybrid B227-63 or on the *S. berthaultii* clone, PI 310927-11 (Table 2). Of an initial population of 18 females/plant on B227-63 and PI 310927-11, a mean of 13 dead females/plant was recovered. Reproduction by the initial population on these clones averaged 14 and 11 nymphs/plant, respectively, but all died in the 1st stadium. Dead females on these clones did not differ in proportion of tarsi or labia encased by trichome exudate, nor in their distribution on the plant. Most were entrapped on foliage; ca. 93% were found on leaves arising from nodes 1-6, whereas aphids were widely distributed on cv. Hudson (Fig. 3).

TABLE 2. — *Effect of 3 potato clones differing in glandular pubescence on population development and immobilization of the green peach aphid. Ithaca, N.Y. 1979.*

	Mean no. aphids/plant						
	Total		Dead nymphs	% encasement		% distribution of dead aphids[a]	
Clone	Live	Dead	(1st stadia)	Tarsi	Labia	Leaves	Stems
B227-63	0	12.5	14.2	84	20	89	11
PI 310927-11	0	12.5	10.5	94	24	78	22
Hudson	761	0.0	0.0	0	0	-	-
LSD (P = 0.05)	376	4.3	7.5	8	11	-	-

[a] Clones did not differ by analysis of variance (P = 0.05).

The presence of trichome exudate on tarsi significantly hindered aphid mobility on the glandular pubescent clones, PI 310927-11 and B227-63, compared to cv. Hudson (Table 3). Aphids lacking trichome exudate on their tarsi quickly left Hudson, whereas escape times on B227-63 and PI 310927-11 were ca. 3 times longer. Exudate from B227-63 was as effective as that from PI 310927-11 in restricting movement (Table 4). Foliage of PI 310927-11 was slightly more immobilizing than that of B227-63.

After 72 hours of confinement, nymphal mortality on B227-63 was 94%, compared to 11% on cv. Hudson and 'Katahdin'. Two additional hybrids, B227-60 and B227-128, were equally as resistant. The proportion of tarsi encased by trichome exudate followed a similar trend, averaging ca. 60% on the hybrids and PI 310927-11. No trichome exudate was observed on tarsi of aphids confined on cv. Hudson and Katahdin.

Field Studies

In 1979, seasonal total infestations of the green peach aphid reflected the trends observed in glasshouse trials, averaging ca. 9 aphids/10 leaves on the hybrids and on PI 310927-11, and 24/10 leaves on cv. Hudson (Table 5). In 1980, infestations were far greater, ranging from 53/10 leaves on PI

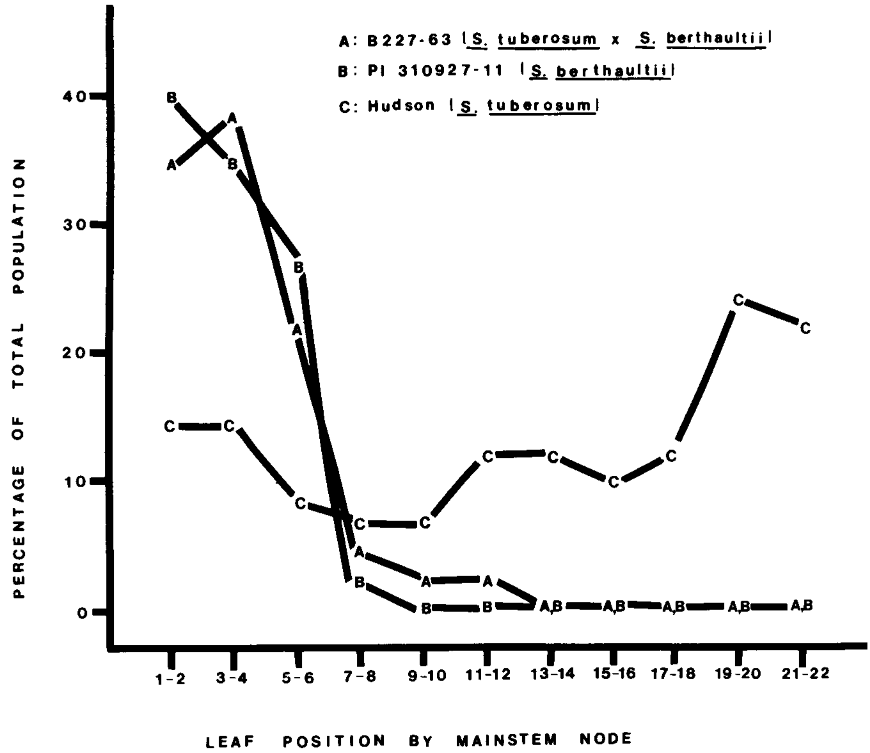

FIG. 3. Distribution of aphid population by leaf position 21 days post-infestation on 3 potato clones differing in type and density of glandular pubescence. Ithaca, N.Y. 1979.

310927-11 to 878/10 leaves on cv. Superior. The population on the 3 hybrid clones averaged 476/10 leaves, a reduction of 43% from the 3 cultivars. Reduction in infestation during 1979 between the same groups was 61%.

TABLE 3. — *Effect of tarsi encumbered by trichome exudate on escape time (sec) of 4th stadia* M. persicae *nymphs confined on foliage of 3 potato clones. Ithaca, N.Y. 1981.*

Source of exudate	Mean escape time (sec)[a] on foliage of: B227-63	PI 310927-11	Hudson
B227-63	57	69	21
PI 310927-11	83	93	10
None	24	29	8

[a] LSD (P = 0.01) for all comparisons: 12.5.

TABLE 4. - *Analysis of variance for data in Table 3. Ithaca, N.Y. 1981.*

Source of variation	DF	MS	F[a]
Source of exudate	2	17.35	193.8
Adhesive vs. nonadhesive	1	34.85	387.2
B227-63 vs. PI 310927-11	1	0.02	0.02
Substrate	2	46.54	517.1
B227-63, PI 310927-11 vs. Hudson	1	92.20	1024.4
B227-63 vs. PI 310927-11	1	0.87	9.7
Interaction	4	1.94	21.6
Error	171	0.09	

[a] Critical values of F-distribution (P = 0.01): 1 df = 6.63, 2 df = 4.61.

Discussion

In the sheltered glasshouse environment, the expression of resistance by hybrid clones was dramatic, equalling that of *S. berthaultii.* Virtually all of the females caged on B227-63 and PI 310927-11 were found on the same group of leaves on which they were originally placed (Fig. 3), indicating rapid entrapment. Our observations on escape behavior support this contention, and highlight the disabling effects of trichome exudate on aphid mobility.

Under field conditions, the expression of resistance was less striking, particularly in 1980, although the reduction in infestation of 43% compared to *S. tuberosum* is still noteworthy considering the overwhelming size of the population. Aphid infestations of such magnitude are rarely observed in commercial practice, and typically follow seasonal depletion of natural enemies by indiscriminate use of non-selective insecticides (4).

We are unable to explain the discrepancy in the expression of resistance between glasshouse and field environments, but several possibilities bear consideration. Tingey and Laubengayer (7) demonstrated that Type A and B trichomes interact to produce greater levels of resistance than that afforded by Type A hairs alone. That is, adhesiveness conferred on tarsi by Type B exudate accelerates the discharge of Type A hairs, leading to increased encasement of tarsi and subsequent entrapment. Once discharged, however, the immobilizing properties of Type A hairs are lost, because the tetralobulate gland is not renewed. Under the repeated influx of colonizing aphids in field trials, the population of Type A trichomes may be depleted, thus eliminating this line of defense. Depletion probably occurs rapidly on mature, senescent foliage — the preferred tissue for colonization by the green peach aphid. Furthermore, mature leaves have fewer trichomes per unit area than younger, incompletely expanded foliage. Other possible mechanisms causing this phenomenon are precipitation or overhead irriga-

TABLE 5. — *Populations of the green peach aphid on 7 potato clones differing in glandular pubescence. Freeville, N.Y. 1979-80.*

Clone	Species[a]	Season total no. aphids/ 10 leaves[b]		Mean no. apterous M. persicae/10 leaves[b]					
				1979			1980		
		1979	1980	July 18	July 30	Aug. 14	July 18	Aug. 1	Aug. 18
PI 310927-11	BERTH	9.8 b	53a	4.6a	2.1a	22.9 c	2.0a	1.3a	157a
B227-60	TUB x BERTH	8.2a	392a	8.4 b	2.2a	13.8 b	3.3ab	19.8a	1154 b
B227-63	TUB x BERTH	8.5ab	581 bc	5.0a	10.9 b	9.6a	1.5a	17.0a	1725 bc
B227-128	TUB x BERTH	10.5 b	456 b	5.9ab	14.1 b	11.6ab	5.3ab	79.8ab	1284 b
Katahdin	TUB	-	805 cd	-	-	-	4.8ab	193.0 c	2280 c
Hudson	TUB	23.5 c	810 d	24.9 c	46.3 c	6.3a	7.0 b	143.5 bc	2498 cd
Superior	TUB	-	878 d	-	-	-	3.5ab	131.5 bc	2692 d

[a] TUB: *S. tuberosum;* BERTH: *S. berthaultii.*

[b] Means within a column followed by the same letter are not significantly different at $P = 0.05$ by analysis of variance and Duncan's Multiple Range test.

tion directly discharging and washing away trichome secretions, or driving soil particles at high velocity into the abaxial leaf surface resulting in rupture and discharge of Type A hairs. Alternatively, finely divided particulate matter, e.g. soil particles or inert substrates used in wettable powder and flowable formulations of pesticides, may adhere to trichome glands, altering adhesiveness and entrapment properties. Finally, our field methods tended to underestimate levels and expression of resistance, since clones of *S. tuberosum* x *S. berthaultii* and *S. berthaultii* were transplanted at 8-20 cm height, whereas those of *S. tuberosum* were planted as tubers. This procedure resulted in a 3-4 week difference in availability of foliage for aphid colonization. Alate viviparous *M. persicae* were frequently found on transplants within 2-6 days after planting, well before sprouts of cultivars emerged from the soil.

Despite the apparent buffering effect of the field environment on levels of resistance, our results indicate that hybrids of *S. tuberosum* x *S. berthaultii* exhibit substantial defense against the green peach aphid, compared to their cultivated parent. Season-long reductions in aphid populations of 40-60% will not eliminate the need for other control measures, but may allow reduction in the frequency or rates of aphicide treatments. Furthermore, the relatively rapid entrapment and immobilization of aphids by glandular trichomes may reduce virus spread by decreasing plant to plant movement of viruliferous apterae or alatae. Finally, as knowledge of the inheritance and chemical properties of glandular pubescence increases, it may be possible to develop clones better defended than those studied here.

Acknowledgments

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