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# Inheritance of potato aphid resistance in hybrids between *Lycopersicon esculentum* and *L. pennellii*

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**Summary.** The potato aphid, *Macrosiphum euphorbiae* Thomas, is an important pest of tomato, *Lycopersicon esculentum* Mill., because it transmits tomato viruses and directly reduces crop yields by its feeding. This study was conducted to determine whether the wild tomato species, *Lycopersicon pennellii* (Corr.) D'Arcy, would be useful as a source of potato aphid resistance for tomato. Type IV trichome density and aphid resistance were assessed in six generations ($P_1$, $P_2$, $F_1$, $F_2$, $BC_1P_1$, and $BC_1P_2$) from crosses between *L. pennellii* (LA 716) and two tomato cultivars, New Yorker and VF Vendor. Weighted least-squares were used in joint scaling tests to estimate the relative importance of gene effects on type IV trichome density and potato aphid resistance of the hybrids. A simple additive-dominance model adequately explained the variation in type IV trichome density. Models which included digenic epistatic effects were required to explain the variation in aphid resistance. Standard unit heritability estimates of aphid resistance in the backcross to *L. esculentum* were obtained by regression of $BC_1F_2$ offspring families on $BC_1F_1$ parents. Regression coefficients and heritability estimates varied between years with the level and uniformity of the aphid infestation. In the 1985–1986 growing seasons, when aphid infestations were uniform, aphid resistance exhibited a moderate level of heritability (29.8% ± 14.1% and 47.1% ± 11.5% in New Yorker and VF Vendor backcross populations, respectively). The non-uniform aphid infestation of 1984 resulted in lower heritability estimates in the 1984–1985 growing seasons (16.1% ± 15.7% and 21.9% ± 14.8% in the New Yorker and VF Vendor backcross populations, respectively). Selection for potato aphid resistance would probably be most efficient if it were delayed until gene combinations are fixed in later generations, because of the large epistatic effects and the low heritability of this trait in seasons with variable aphid infestations.

**Key words:** Generation means – Heritability – Insect resistance – Joint scaling tests – Tomato

## Introduction

The potato aphid, *Macrosiphum euphorbiae* Thomas, is an important pest of tomato, *Lycopersicon esculentum* Mill., when environmental conditions are favorable for rapid aphid growth and reproduction (Quiros et al. 1977; Walker et al. 1984). The potato aphid is not only damaging to tomato when high aphid populations compete with the developing fruit for nutrients and carbohydrates; even low aphid infestations can indirectly cause significant reductions in yield, since this and other aphid species are efficient vectors of many tomato viruses (Lange and Bronson 1981; Kennedy et al. 1962). Currently, chemical insecticides are the only effective means of aphid control. However, there is evidence that some aphid species are developing resistance to these compounds (Bauernfeind and Chapman 1985; McClanahan and Founk 1983; Weber 1985).

*L. pennellii* (Corr.) D'Arcy, a wild relative of the cultivated tomato native to the western slopes of Peru, is a potential source of potato aphid resistance in tomato (Gentile and Stoner 1968; Quiros et al. 1977). Aphid resistance in *L. pennellii* has been attributed to the physical entrapment of the insects in the sticky exudate of the glandular trichomes (Gentile and Stoner 1968). *L. pennellii* possesses high densities of two morphologically distinct types of glandular trichomes, the type IV and VI (Lemke and Mutschler 1984). Type VI trichomes consist of a short 1–2 cell stalk with a membrane-enclosed tetralobulate glandular head (Luckwill 1943). The type IV trichomes of *L. pennellii* are slightly longer than the type

VI hairs and secrete a naked droplet of exudate at the tip. Although the cultivated tomato possesses high densities of the type VI hairs, type IV trichomes are completely absent.

However, entrapment is not *L. pennellii*'s only mechanism of insect resistance. Aphid feeding behavior on *L. pennellii* and its $F_1$ with tomato is characterized by an increase in the pre-probe time, and decreases in both the number of probes per unit time and the total time spent probing and feeding (Goffreda et al. 1988). Removal of the glandular exudate from *L. pennellii* and the $F_1$ with 95% ethanol increased aphid feeding, and the transfer of the glandular exudate to *L. esculentum* decreased aphid feeding as measured by these three feeding parameters (Goffreda et al. 1988). The differences in feeding behavior appear to be related to the presence of sugar esters in the glandular exudate of the type IV trichomes. Glucose esters from *L. pennellii* deter aphid settling when applied to a synthetic feeding membrane (Goffreda 1988).

The objectives of this study were to: (1) determine if *L. pennellii* is a strong, stable source of aphid resistance for the cultivated tomato, (2) elucidate the relationship between the type IV glandular hairs and aphid resistance in the field, (3) quantify each of the types of gene effects influencing aphid resistance in hybrids with tomato, and (4) estimate the heritability of this trait in backcross populations with tomato. An understanding about the genetic basis of aphid resistance in *L. pennellii* will facilitate the deployment of genes governing resistance in adapted tomato cultivars.

## Materials and methods

### Plant culture

Two aphid-susceptible tomato cultivars, New Yorker and VF Vendor, were hybridized to *L. pennellii* LA 716 (PI 246502) to produce $F_1$, $F_2$, and backcross progenies. Both tomato cultivars and this accession of *L. pennellii* have been selfed for numerous generations and were assumed to be homozygous.

Greenhouse-grown plants were scored for the presence and density of type IV trichomes on a leaflet adjacent to the terminal leaflet at the third node, 30 days after seeding. At this stage the seedlings were ca. 3.5 cm tall with the sixth leaf beginning to expand. Two determinations of the trichome density were made in a 6.6-mm$^2$ area, one on each side of the mid-vein, using a dissecting microscope at 60 ×. Since variances were proportional to treatment means in the non-segregating generations, variances were stabilized with a square root transformation of the trichome counts. The average of the square root of the number of type IV trichomes in each 6.6-mm$^2$ area was used in generation means analysis. Since the segregating generations contain greater genetic variation, the different generations were not equally represented. Within each replication, the non-segregating generations ($P_1$, $P_2$, and $F_1$) were represented by one plot, and the backcross and $F_2$ generations were represented by two and four plots, respectively. Each plot consisted of 14 plants. The experimental design was a split plot with two replications. Generations derived from crosses with New Yorker and VF Vendor were randomized in each replication.

Field-grown plants were evaluated for potato aphid resistance by 30-s counts of the number of potato aphids (red and green biotypes) on the plant, repeated at weekly intervals for a 4–5 week period during the season. This technique surveys a large portion of each plant for aphids, providing a relative estimate of aphid density. Since the standard deviation varied directly with the treatment mean in the non-segregating generations, a logarithmic transformation was used to stabilize the variance. Data were transformed by taking the log of the number of aphids plus one and averaging this value over the season.

In 1984, each plot consisted of 14 plants with an infestation plant (cv New Yorker) in the center of each row. Twenty apterous potato aphids (red biotype) were transferred to each infestation plant early in the season. Plots were sprayed with carbaryl (1/2–3/4 lb AI/acre) and chlorothalonil (0.5 lb AI/acre) to control aphid parasites, pathogens, and predators as proposed by Nanne and Radcliffe (1971). One plot of the non-segregating generations ($P_1$, $P_2$, and $F_1$) and two and four plots of the backcross and $F_2$ generations, respectively, were in each of four replications. The experimental design was a split plot with generations randomized within the four replications of each of the New Yorker and VF Vendor populations.

In 1985 and 1986, each plot consisted of ten plants. Aphids were not artificially introduced into the field in 1985 because there was an excellent natural infestation of potato aphids. In 1986, plants were inoculated with aphids by placing a potato aphid-infested tomato seedling (cv VFNT Cherry) on each plant in the field. In 1985 and 1986, there were two plots of the non-segregating generations ($P_1$, $P_2$, and $F_1$) and one plot of each $BC_1F_2$ family in each of two replications. Each year, either 19 or 20 $BC_1F_2$ families were evaluated in both the New Yorker and VF Vendor populations. Seed for the $BC_1F_2$ families were produced in the 1984 and 1985 field seasons by controlled self-pollinations of unopened flowers on random backcross to *L. esculentum* plants (cultivars New Yorker and VF Vendor). Plots were sprayed with carbaryl and chlorothalonil, as previously described in this section.

### Statistical and genetic analysis

An analysis of variance of potato aphid resistance (as measured by the transformed insect counts in the 1984–1986 growing seasons) was performed on the non-segregating generations ($P_1$, $P_2$, and $F_1$) derived from crosses with New Yorker and VF Vendor. Data were analyzed within each year since the genotype × year interaction was highly significant ($P < 0.0001$). The mean transformed aphid count from each plot was analyzed as a single experimental unit. Statistical significance between means was determined by a Bonferroni *t*-test ($P < 0.05$) (Miller 1981).

Weighted least-squares were used to estimate genetic parameters in joint scaling tests with weights that were equal to the reciprocals of the standard errors of the generation means, as proposed by Mather and Jinks (1971). The computational procedures used were those described by Rowe and Alexander (1980), using expected coefficients of the gene effects presented by Hayman (1958) (Table 1). This model defines the average effect of a gene substitution in terms of the linear regression of the genotypic value on number of alleles at a given locus as proposed by Fisher (1941), and it assumes that all the favorable alleles are in *cis* and contributed by *L. pennellii*. Transformed trichome density from the 1984 greenhouse study and aphid count data from the 1984 field study were subjected to analysis by generation means using the full 6-parameter model. The model was reduced to a simple additive-dominance model by sequential removal of gene effects from the model whenever possible. The validity of the reduced 3-parameter and 5-param-

**Table 1.** Expected coefficients of gene effects for the six generation means

| Generation | Gene effects[a] | | | | | |
|---|---|---|---|---|---|---|
| | m | [d] | [h] | [i] | [j] | [l] |
| $P_1$ | 1 | 1 | −0.5 | 1 | −1 | 0.25 |
| $P_2$ | 1 | −1 | −0.5 | 1 | 1 | 0.25 |
| $F_1$ | 1 | 0 | 0.5 | 0 | 0 | 0.25 |
| $F_2$ | 1 | 0 | 0 | 0 | 0 | 0 |
| $BC_1P_1$ | 1 | 0.5 | 0 | 0.25 | 0 | 0 |
| $BC_1P_2$ | 1 | −0.5 | 0 | 0.25 | 0 | 0 |

[a] m – mean, [d] – additive, [h] – dominance, [i] – additive × additive, [j] – additive × dominance, and [l] – dominance × dominance effects

**Table 2.** Mean potato aphid (*Macrosiphum euphorbiae*) counts per 30 s on plants of *L. pennellii* (LA 716), *L. esculentum* (cultivars 1. New Yorker and 2. VF Vendor), and their $F_1$ hybrids

| Cross/ Generation | Pedigree | Year | | |
|---|---|---|---|---|
| | | 1984 | 1985 | 1986 |
| 1 $P_1$ | *L. pennellii* (LA 716) | 2.6a | 20.7a | 3.7a |
| $P_2$ | *L. esculentum* cv New Yorker | 33.5b | 78.2c | 67.8c |
| $F_1$ | $(P_2 \times P_1)$ | 3.2a | 28.2b | 40.1b |
| 2 $P_1$ | *L. pennellii* (LA 716) | 2.0a | 7.4a | 1.8a |
| $P_3$ | *L. esculentum* cv VF Vendor | 33.8b | 91.2c | 56.0c |
| $F_1$ | $(P_3 \times P_1)$ | 2.2a | 24.9b | 28.5b |

a, b, c – Means followed by a different letter within each cross and year differ significantly by a Bonferroni *t*-test ($P<0.05$). Data were analyzed by using an analysis of variance on the transformed data (log + 1). Table presents original treatment means

eter models were tested with a Chi-square goodness-of-fit test with 3 and 1*df*, respectively.

Standard unit heritability estimates were obtained by parent-offspring regression as proposed by Frey and Horner (1957). Parent $BC_1F_1$ plants were standardized by subtracting the mean of the transformed aphid counts and dividing by the standard deviation. Offspring were grown the following year and their plot means were averaged, standardized, and regressed on their parent standard scores. The regression coefficient ($\beta_1$) overestimates heritability ($h^2$) because of prior inbreeding in the base population (Smith and Kinman 1965). Heritability estimates were calculated by dividing the regression coefficient ($\beta_1$) by two times the coefficient of parentage ($r_{xy}$). Since the coefficient of parentage between $BC_1F_1$ parents and their $BC_1F_2$ offspring is equal to 3/4, heritability estimates were calculated by multiplying the regression coefficient by 2/3. This estimate of heritability is biased upwards by both dominance and epistatic variation.

## Results and discussion

### *Potato aphid resistance in L. esculentum, L. pennellii and their $F_1$ hybrids*

*L. pennellii* (LA 716) appears to possess both a stable and high level of resistance to the potato aphid. Aphid populations were sparse on *L. pennellii* even in 1985 when there was an extremely high infestation of aphids (Table 2). Although alate aphids would settle on *L. pennellii* plants, the aphids were unable to establish thriving colonies as they did on both cultivars of *L. esculentum*. Resistance in the $F_1$ varied from almost complete immunity to aphids in the 1984 growing season, to moderate levels of aphid resistance in the 1985 and 1986 season. The level of aphid resistance in *L. pennellii* and the $F_1$ differed significantly from the *L. esculentum* controls in all 3 years (Table 2). Aphid resistance in *L. pennellii* and the $F_1$ differed significantly in both 1985 and 1986, but not in 1984. Data from the 1984 and 1985 seasons indi-

**Table 3.** Segregation ratios in *L. esculentum* × *L. pennellii* hybrids for the presence of type IV glandular hairs

| Cross/Generation | | Pedigree | Type IV trichomes | | | | $\chi^2$ | *P* |
|---|---|---|---|---|---|---|---|---|
| | | | Observed | | Expected | | | |
| | | | Present | Absent | Present | Absent | | |
| 1 | $P_1$ | *L. pennellii* (LA 716) | 28 | 0 | 28 | 0 | | |
| | $P_2$ | *L. esculentum* cv New Yorker | 0 | 28 | 0 | 28 | | |
| | $F_1$ | $(P_2 \times P_1)$ | 28 | 0 | 28 | 0 | | |
| | $F_2$ | $(P_2 \times P_1)^2$ | 107 | 5 | 105 | 7 | 0.609[a] | $0.5>P>0.25$ |
| | $BC_1$ | $(P_2 \times P_1) \times P_1$ | 56 | 0 | 56 | 0 | | |
| | $BC_1$ | $(P_2 \times P_1) \times P_2$ | 36 | 20 | 42 | 14 | 3.428[b] | $0.1>P>0.05$ |
| 2 | $P_1$ | *L. pennellii* (LA 716) | 28 | 0 | 28 | 0 | | |
| | $P_3$ | *L. esculentum* cv VF Vendor | 0 | 28 | 0 | 28 | | |
| | $F_1$ | $(P_3 \times P_1)$ | 28 | 0 | 28 | 0 | | |
| | $F_2$ | $(P_3 \times P_1)^2$ | 107 | 5 | 105 | 7 | 0.609[a] | $0.5>P>0.25$ |
| | $BC_1$ | $(P_3 \times P_1) \times P_1$ | 56 | 0 | 56 | 0 | | |
| | $BC_1$ | $(P_3 \times P_1) \times P_3$ | 37 | 17 | 40.5 | 13.5 | 1.210[b] | $0.5>P>0.25$ |

[a] Tested against a 15:1 ratio

[b] Tested against a 3:1 ratio

cate that aphid resistance in the $F_1$ hybrids exhibits at least partial dominance and that the level of dominance observed varies with aphid pressure. The 1986 data does not support dominance for resistance.

### *Inheritance of type IV trichomes in L. esculentum × L. pennellii hybrids*

Data from the segregating generations indicate that the presence of the type IV trichomes on the seedlings is controlled by two dominant, unlinked genes, with either gene conferring the type IV trichome in the hybrids. Data from the $F_2$ and backcross to *L. esculentum* generations in crosses with either tomato parent fit a 15:1 and 3:1 ratio, respectively (Table 3). All $F_1$ and backcross to *L. pennellii* plants examined possessed type IV trichomes. These data support the conclusions of Lemke and Mutschler (1984) that the presence of the type IV trichomes is simply inherited, controlled by duplicate gene epistasis.

The mean type IV trichome densities on $F_1$ and $F_2$ plants with either tomato cultivars were intermediate between tomato and *L. pennellii* (Table 4). Backcrossing to *L. pennellii* increased the mean type IV trichome density, whereas backcrossing to *L. esculentum* lowered trichome densities. In the $F_2$ populations derived from crosses with New Yorker and VF Vendor, 22% and 21% of the plants, respectively, had type IV trichome densities within the range of densities obtained on *L. pennellii.* In the backcross to *L. pennellii,* 50% and 57% of the plants in the New Yorker and VF Vendor populations had trichome densities within *L. pennellii*'s range. These data suggest that the density of type IV trichomes is simply inherited, controlled by only a few major genes. Variation in the mean density of type IV trichomes in the populations derived from crosses with New Yorker and VF Vendor was adequately explained by the 3-parameter, additive-dominance model in generation means analysis (Table 5).

### *Inheritance of aphid resistance in L. esculentum × L. pennellii hybrids*

The $F_1$ hybrids with both tomato cultivars and their backcross generations to *L. pennellii* exhibited levels of aphid resistance which were similar to that of *L. pennellii* (Table 4). However, the mean level of aphid resistance in the $F_2$ and backcrosses to *L. esculentum* generations decreased dramatically, suggesting that epistatic interactions between loci could be important in the genetic mechanism of aphid resistance. Few $F_2$ and backcross to *L. esculentum* plants possessed as high a level of aphid resistance as the $F_1$ generation, indicating that aphid resistance exhibits complex inheritance.

The additive-dominance model could not adequately explain the variation in the mean level of aphid resistance, suggesting that epistatic gene effects may strongly influence resistance ($\chi^2 = 238.7$ and 264.9, $df = 3$, New Yorker and VF Vendor populations, respectively; data not shown). In the populations derived from crosses with New Yorker, the generation means were adequately described by a 5-parameter model which also included additive × additive and additive × dominance digenic epistatic effects (Table 5). No reduced model could adequately explain the variation in the mean level of aphid resistance in the VF Vendor-derived generations.

**Table 4.** Generation means of type IV trichome densities and potato aphid (*Macrosiphum euphorbiae*) counts on *L. esculentum* × *L. pennellii*

| Cross/ Generation | | Pedigree | Trichome density (no./6.6 mm$^2$) | | $\sqrt{\text{density}}$ ($\sqrt{\text{no.}}$/6.6 mm$^2$) | | Av. aphid count (no./30 s) | | Av. transformed aphid count (Log[no. + 1]/30 s) | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| 1 | $P_1$ | *L. pennellii* (LA 716) | 172 | 27 | 13.1 | 1.0 | 2.6 | 2.9 | 0.32 | 0.24 |
| | $P_2$ | *L. esculentum* cv New Yorker | 0 | 0 | 0.0 | 0.0 | 33.5 | 19.5 | 1.21 | 0.33 |
| | $F_1$ | $(P_2 \times P_1)$ | 100 | 39 | 9.8 | 1.9 | 3.2 | 4.7 | 0.31 | 0.29 |
| | $F_2$ | $(P_2 \times P_1)^2$ | 85 | 47 | 8.7 | 2.9 | 28.5 | 24.5 | 1.12 | 0.47 |
| | $BC_1$ | $(P_2 \times P_1) \times P_1$ | 128 | 46 | 11.1 | 1.9 | 4.5 | 8.4 | 0.40 | 0.35 |
| | $BC_1$ | $(P_2 \times P_1) \times P_2$ | 34 | 37 | 4.7 | 3.5 | 31.7 | 24.1 | 1.14 | 0.38 |
| 2 | $P_1$ | *L. pennellii* (LA 716) | 194 | 29 | 13.9 | 1.0 | 2.0 | 1.9 | 0.29 | 0.20 |
| | $P_3$ | *L. esculentum* cv VF Vendor | 0 | 0 | 0.0 | 0.0 | 33.8 | 23.8 | 1.15 | 0.41 |
| | $F_1$ | $(P_3 \times P_1)$ | 88 | 15 | 9.3 | 0.8 | 2.2 | 4.6 | 0.19 | 0.26 |
| | $F_2$ | $(P_3 \times P_1)^2$ | 77 | 50 | 8.2 | 3.2 | 25.6 | 23.5 | 1.04 | 0.49 |
| | $BC_1$ | $(P_3 \times P_1) \times P_1$ | 132 | 44 | 11.3 | 1.9 | 6.4 | 10.6 | 0.47 | 0.39 |
| | $BC_1$ | $(P_3 \times P_1) \times P_3$ | 29 | 30 | 4.6 | 2.9 | 45.7 | 34.6 | 1.29 | 0.48 |

### *Relationship between type IV trichomes and aphid resistance*

Previous research has demonstrated that compounds secreted from the type IV trichomes of *L. pennellii* and the $F_1$ strongly deter potato aphid settling and feeding (Goffreda 1988; Goffreda et al. 1988). However, we have not detected a significant relationship between type IV trichome densities on seedlings and field resistance to aphids in segregating $F_2$ and backcross generations (data not shown). It is possible that seedling determinations of trichome densities may not be highly correlated with trichome densities of adult, field-grown plants. Although a simple additive-dominance model could explain the variation in type IV trichome densities on 30-day-old seedlings in this study, Lemke and Mutschler (1984) found that epistatic gene effects were necessary components for the model to explain the variation in generation means of 50-day-old seedlings. The principal difference between the two studies was the age of the plants at the time of trichome determination; perhaps genes involved in differential rates of leaf expansion as the plants mature are responsible for the significant epistatic gene effects detected in the study by Lemke and Mutschler (1984).

Another possible explanation for the lack of correlation between trichome density and aphid resistance is that the trichomes of many hybrids may lack or have substantially reduced quantities of the compounds responsible for the insect resistance. Resistance in *Nicotiana* spp. to the green peach aphid, *Myzus persicae* Sulzer, increases as the plant matures, which parallels an increase in the amount of trichome exudate (Abernathy and Thurston 1969). In the present study, droplet size of the type IV trichomes in the $F_2$ and backcross to *L. esculentum* generations was very variable between plants and also appeared to be strongly influenced by the age of the plant and environmental conditions. The large magnitude of epistatic effects on aphid resistance, as indicated by the generation means analysis, could result from the interaction between genes governing the presence of the type IV trichomes and those responsible for the production of the biologically active compounds.

### *Estimation of heritability by parent-offspring regression*

Potato aphid infestations were not uniform in 1984, resulting in poor evaluation of the level of aphid resistance of the parental $BC_1F_1$ base population grown in 1984. Consequently, the regression coefficients and standard unit heritability estimates calculated from the 1984 parental data were lower than those in 1985, when aphid infestations were high (Figs. 1 and 2). In the 1985–1986 growing seasons, potato aphid resistance exhibited a moderate level of heritability (29.8% ± 14.1% and 47.1% ± 11.5% for the New Yorker and VF Vendor backcross populations, respectively). Heritability estimates were generally low in 1984–1985 growing seasons (16.1% ± 15.7% and 21.9% ± 14.8% for the New Yorker and VF Vendor backcross populations, respectively). Consequently, single plant selections based on the repeated aphid counts will only be effective in years of uniformly high aphid infestations.

**Table 5.** Estimates of gene effects for type IV trichome density and aphid resistance in *L. esculentum* × *L. pennellii* hybrids

| Cross[a] | Component[b] | Trichome density | | Aphid resistance | |
|---|---|---|---|---|---|
| | | 6-parameter | Reduced model (±SE) | 6-parameter | Reduced model (±SE) |
| 1 | m | 8.74 | 8.22±0.035 | 1.12 | 1.09±0.003 |
| | [d] | 6.48 | 6.47±0.065 | −0.74 | −0.74±0.008 |
| | [h] | −0.06 | 3.26±0.253 | −1.85 | −1.60±0.035 |
| | [i] | −3.33 | – | −1.40 | −1.14±0.021 |
| | [j] | −0.07 | – | −0.30 | −0.30±0.011 |
| | [l] | 4.40 | – | 0.47 | – |
| $\chi^2$ ($df$=1 or 3) | | | 5.47[NS] | | 3.48[NS] |
| 2 | m | 8.16 | 8.11±0.002 | 1.04 | 1.10±0.012 |
| | [d] | 6.74 | 6.91±0.004 | −0.82 | −0.78±0.046 |
| | [h] | 1.62 | 2.38±0.012 | −1.17 | −1.75±0.122 |
| | [i] | −0.77 | – | −0.65 | −1.24±0.086 |
| | [j] | −0.20 | – | −0.39 | −0.34±0.058 |
| | [l] | 1.44 | – | −1.06 | – |
| $\chi^2$ ($df$=1 or 3) | | | 0.98[NS] | | 13.72** |

[NS], ** Not significant and significant at the 1% level, respectively

[a] Cross 1 – New Yorker × LA 716 hybrids; cross 2 – VF Vendor × LA 716 hybrids

[b] m – mean, [d] – additive, [h] – dominance, [i] – additive × additive, [j] – additive × dominance, and [l] – dominance × dominance effects

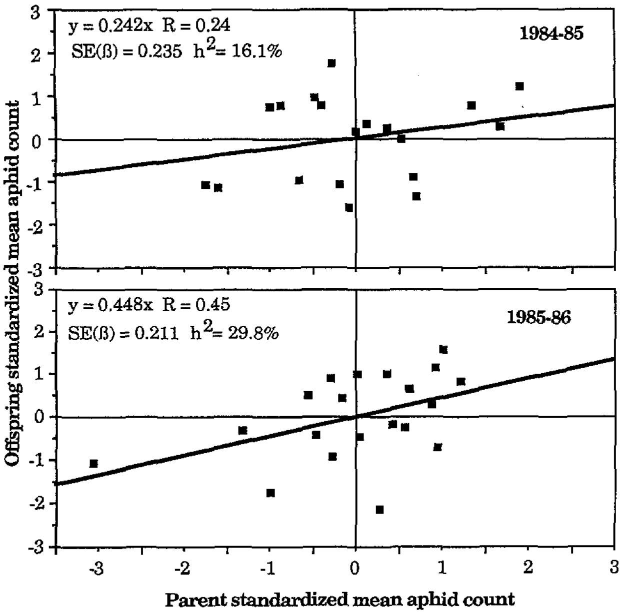

**Fig. 1.** Regression of standardized aphid count data from $BC_1F_2$ families on $BC_1F_1$ parents derived from backcrosses to *L. esculentum* cv New Yorker

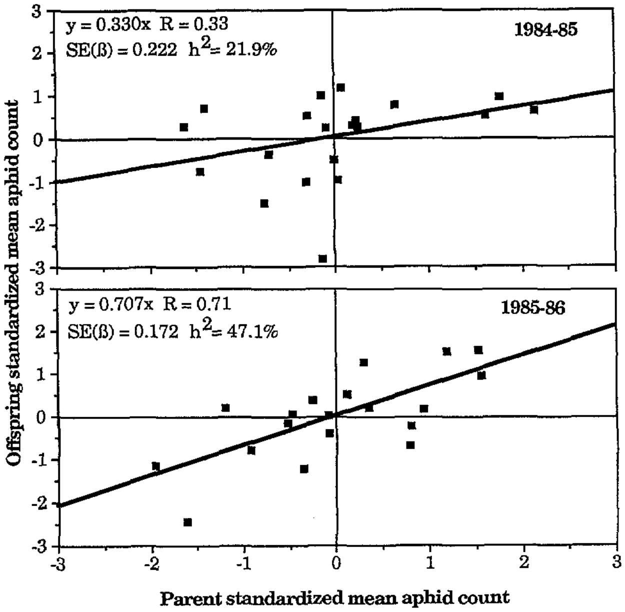

**Fig. 2.** Regression of standardized aphid count data from $BC_1F_2$ families on $BC_1F_1$ parents derived from backcrosses to *L. esculentum* cv VF Vendor

These data suggest that selection for potato aphid resistance will be more efficient if delayed until later generations because of the large epistatic effects and the low heritability of this trait in seasons with reduced aphid infestations. However, trichome characteristics can be selected in early generations since they appear to be simply inherited. Selection for type IV trichome density alone may not be effective, because the trichomes on different plants in segregating populations may vary in their ability to produce biologically active compounds. Sugar esters present in the type IV exudate strongly deter aphid settling and feeding (Goffreda 1988; Goffreda et al. 1988). We have developed a technique to quantify the level of sugar ester production on the leaf surface and are determining whether this technique could be an effective selection tool in the development of aphid resistant tomato varieties.

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