

# Inheritance of A and B Glandular Trichome Density and Polyphenol Oxidase Activity in Diploid Potatoes

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**Abstract.** Glandular trichomes from some *Solanum* species have suppressed infestation by insects including green peach aphid, which is a main vector of potato virus Y (PVY) and potato leaf roll virus (PLRV), both of which contribute to a serious loss in potato production. Eight *Solanum phureja* Juz. et Buk.–*S. stenotomum* Juz. (Phu–Stn), three *S. berthaultii* Hawkes (Ber), nine F<sub>1</sub> [(Phu–Stn) × Ber], fifteen backcross (BC) [(Phu–Stn) × F<sub>1</sub>], and seventeen reciprocal BC (BC<sub>R</sub>) [F<sub>1</sub> × (Phu–Stn)] families were evaluated to determine the genetic variability and heritability of A and B glandular trichome density and polyphenol oxidase (PPO) activity. Experiments were carried out in completely randomized and randomized complete-block designs in the greenhouse. Genetic analysis was done using half-sib family and parent–offspring regression analysis. Phu–Stn showed a higher density of A trichomes than Ber and F<sub>1</sub>, while the BC and BC<sub>R</sub> had densities of A trichomes similar to Phu–Stn. B trichomes were not observed in Phu–Stn. Ber showed a high B trichome density, which was transmitted to the F<sub>1</sub>. In the BC, B trichomes were almost absent, but, in the BC<sub>R</sub>, the density of B trichomes was higher than that of BC. Ber and F<sub>1</sub> had similar or higher PPO activity than Phu–Stn. PPO activity decreased in the BC, but, in the BC<sub>R</sub>, it was high and similar to Ber and F<sub>1</sub>. Broad-sense heritability estimates for A and B trichome density and PPO activity were from medium to high (0.48 to 0.77) in Phu–Stn, Ber, and F<sub>1</sub>. Narrow-sense heritability estimates for A and B trichome density and PPO activity were very low (0.04 to 0.24) in BC and BC<sub>R</sub>. In the BC families, additive genetic variance was very low for A and B trichome density and PPO activity. Half-sib family selection based on progeny testing and combined with BCs to Phu–Stn in subsequent generations would be a suggested breeding procedure to improve these traits. Phenotypic correlations between A and B trichome densities were 0.26 (F<sub>1</sub>) and 0.44 (BC<sub>R</sub>), between A trichome density and PPO activity 0.20 (F<sub>1</sub>) and 0.31 (BC<sub>R</sub>), and between B trichome density and PPO activity 0.04 (F<sub>1</sub>) and 0.27 (BC<sub>R</sub>). Positive associations found between traits might facilitate simultaneous improvement for high levels of A and B trichome density and PPO activity.

The wild, tuber-bearing potato species *Solanum berthaultii*, *S. polyadenium* Greenm., and *S. tarijense* Hawkes are of interest in potato breeding for their ability to suppress infestation by insects including green peach aphid (*Myzus persicae* Sulzer) (Dimock and Tingey, 1988; Gibson, 1971, 1978; Gibson and Turner, 1977; Tingey and Gibson, 1978; Tingey and Laubengayer, 1981), which is a main vector of potato virus Y (PVY) and potato leaf roll virus (PLRV), both of which contribute to a serious loss in potato production.

Resistance to aphids in these wild potatoes is due mainly to the presence of two types of foliar glandular trichomes. Type A is short (≈120 to 210 μm long) with a tetralobulate membrane-bound gland (50 to 70 μm in diameter) at its apex. Type B is longer (≈600 to 950 μm long) with an ovoid gland at its tip, which continuously discharges a clear, sticky, viscous exudate (Tingey, 1985).

Type A glandular trichomes are present on the foliage of many wild and cultivated potato species. These trichomes confer resistance to insect pests if their density, gland size, and biochemical products are similar to those of *S. berthaultii* and *S. polyadenium* (Avé et al., 1986). Selection for insect resistance was improved by

introducing an enzymic browning assay (EBA), which mass-screens potato plants for desirable trichome characteristics of a biochemical nature (Ryan et al., 1983). EBA is based on the release of exudate from type A trichomes of leaflets in a test tube with a reagent solution and reading the optical density of a spectrophotometer.

The glandular trichome-mediated resistance mechanism can be summarized as follows: a) the insect lands upon the foliage and encounters the tall type B trichomes; b) type B exudate forms an adhesive coating in the tarsi, and the sesquiterpenes in the exudate elicit a disturbance behavior; c) the insect struggles during attempts to escape and breaks the type A trichome heads; d) reaction of α- and/or β-polyphenol oxidases (PPO) released from A trichome broken heads with phenolic substrate (chlorogenic acid) occurs and an oxidative process is initiated; e) quinones are formed by enzymatic oxidation of phenols (the browning reaction); and, f) the insect becomes immobilized, ceases feeding, and dies (Gregory et al., 1986).

Mortality and immobilization of aphids increase with a rise in density of type A and type B trichomes and with increased volume of type A trichome glands. If type B trichomes are absent, fewer type A trichomes are ruptured and the expression of resistance is dramatically lowered. Thus, accessions bearing type A and B trichomes are more resistant to the green peach aphid than those with type A alone (Gibson, 1979; Tingey and Laubengayer, 1981; Tingey and Sinden, 1982).

A single dominant gene controlling the presence of sticky-tipped hair trichome (type B) was identified in *S. tarijense* and *S. berthaultii*. However, the absence of fully formed sticky tips on F<sub>1</sub> generation of *S. phureja* × *S. berthaultii* and *S. tuberosum* ssp.

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*tuberosum* Hawkes x *S. berthaultii* hybrid progenies indicates that at least one recessive gene is also involved. The fairly frequent recurrence of sticky-tipped forms in  $F_2$  generations indicates that this attribute is controlled by relatively few genes (Gibson, 1979).

The density of Type A and Type B glandular trichomes seems to be controlled by a few genes as parental phenotypes were recovered in  $F_2$  and BC generations (Mehlenbacher et al., 1983).

In a population of *S. tuberosum* ssp. *tuberosum* x *S. berthaultii* hybrids, heritability of density of type B trichomes was  $h^2 = 0.22$ . The density of type A trichomes was highly variable, with a low heritability estimate ( $h^2 = 0.18$ ) when seedling counts were used; however, a higher estimate ( $h^2 = 0.32$ ) was obtained when multiple counts on field-grown plants were used (Mehlenbacher et al., 1984).

The objectives of this research were to determine 1) the inheritance of A and B trichome density and PPO activity in *Solanum phureja*-*S. stenotomum* (Phu-Stn) and *S. berthaultii* (Ber) parents,  $F_1$  [(Phu-Stn) x Ber], backcross (BC) [(Phu-Stn) x  $F_1$ ] and reciprocal BC ( $BC_R$ ) [ $F_1$  x (Phu-Stn)] diploid potato families, and 2) the phenotypic correlations among these traits.

### Materials and Methods

**Parents.** Three *Solanum berthaultii* (Ber) plant introductions (PI265857, PI265858, and PI473331) from the Inter-Regional Potato Introduction Station, Sturgeon Bay, Wis., were used along with eight advanced *S. phureja*-*S. stenotomum* (Phu-Stn) hybrid families from the North Carolina State Univ. (NCSU) potato breeding program, Raleigh, N.C.

**$F_1$  generation.** A random sample of nine  $F_1$  progenies was generated from intercrossing the parent clones [(Phu-Stn) x Ber]. Seventeen  $F_1$  clones selected for high density of A and B trichomes and PPO activity were used as parents in a parent-offspring regression analysis. These  $F_1$  clones served as female parents to generate the  $BC_R$  population.

**BCs.** Two types of BC families were generated: BC families using Phu-Stn as the female recurrent parent [(Phu-Stn) x  $F_1$  bulk] and  $BC_R$  families using Phu-Stn as the male recurrent parent [ $F_1$  x (Phu-Stn) bulk]. The  $BC_R$  population served as the offspring for the parent-offspring regression analysis.

**Experimental design and statistical analysis.** All the experiments were evaluated in the greenhouses of the Dept. of Horticultural Science, NCSU, under 22 to 25C, September through March for 2 consecutive years. In the process of generating the BC populations, the Phu-Stn, Ber, and  $F_1$  families were evaluated for density of A and B trichomes and PPO activity in completely randomized designs, following an experimental hierarchical classification, i.e., families, plants/family, leaves/plant, etc. This data was used to obtain a preliminary estimate of broad-sense heritability (H). Due to limitations in the availability of genetic material, the number of families and plants per family within populations was not similar (Ber: three families, six plants/family; Phu-Stn: eight families, four plants/family;  $F_1$ : nine families, nine plants/family). To evaluate A and B trichome density, the number of leaflets per plant, and spots (5 mm<sup>2</sup>) per leaflet, were constant (three leaflets, three spots). Similarly, to evaluate PPO activity, the number of samples per plant was constant (two samples).

The BC and  $BC_R$  families were evaluated in randomized complete-block designs with 3 replications, 15 BC and 17  $BC_R$  families/experiment, 10 plants/family, 2 leaflets/plant and 2 spots/leaflet (BC experiment = 450 plants,  $BC_R$  experiment = 510 plants). Due to the particular genetic structure of the  $BC_R$  families, they were also analyzed using a parent-offspring regression ap-

proach to estimate narrow-sense heritabilities ( $h^2$ ). For this purpose, at a different greenhouse and before evaluating the  $BC_R$  (offspring), the female parent of each  $BC_R$  family (17  $F_1$  clones) was evaluated in a completely randomized design with three replications to generate the parental data of A and B trichome density and PPO activity.

The statistical analysis of all experiments was done using the least squares method in a general linear model (Proc GLM) (SAS Institute, 1985). Variance components were estimated using maximum likelihood method in a general linear model (Proc VARCOMP) (SAS Institute, 1985). In the parent-offspring regression analysis, the regression coefficients were estimated using standard procedures of linear regression (Proc REG) (SAS Institute, 1985) with the assumption that the correlation between individuals within each offspring was zero. Pearson's phenotypic correlations ( $r_{x-y}$ ) between A and B trichome density and PPO activity in  $F_1$  and  $BC_R$  populations were estimated using Proc CORR (SAS Institute, 1985).

The genetic variance components were estimated under the following assumptions: a) normal diploid and solely Mendelian inheritance; b) no environmental correlations between progenies; c) the parents are not inbred and can be considered random members of some noninbred population; d) experimental errors are independent; and e) linkage equilibrium (Cockerham, 1963). Furthermore, H (defined as the ratio of total genetic variance to phenotypic variance) and  $h^2$  (defined as the ratio of additive genetic variance to phenotypic variance) were estimated on an individual plant basis using standard procedures of quantitative traits analyses (Dudley and Moll, 1969; Hallauer and Miranda, 1988; Nyquist, 1991).

**Assessment of A and B trichome density.** Families were grown in the greenhouse and evaluated for A and B glandular trichome density 45 days after planting. Trichome density in two leaflets, sampled from the middle portion of each plant (two spots per leaflet), were assessed in a 5-mm square of abaxial surface at  $\times 64$  magnification. Spots were carefully located between secondary veins, avoiding main veins and leaflet borders.

**Assessment of polyphenol oxidase (PPO) activity.** A modified enzymic browning assay (Avé et al., 1986) was used to quantify PPO activity. Filter paper discs (Whatman no. 1) 8 mm in diameter were dipped into the reagent solution and blotted on dry filter paper to remove any excess solution. A moist filter paper disc was placed on a rubber stopper and gently pressed onto leaflets of different leaves from the middle portion of the plant. Two samples from each plant were assessed (two leaflets/sample) 60 days after planting. The paper disc was placed in a test tube containing 3 ml of the reagent solution and shaken in a 37C water bath for 20 min, during which time a violet color developed. Optical density (OD) of the assay solutions was measured on a spectrophotometer (Coleman 575; Perkin-Elmer, Norwalk, Conn.) at 470 nm. High OD values indicated high enzymic activities (Avé and Tingey, 1986). The reagent solution used in the browning assays (Ryan et al., 1983) was composed of 70 mM sodium phosphate dibasic, pH 7.0 and 0.075% (w/v) p-phenylenediamine.

### Results and Discussion

**Trichome density and PPO activity means in parents,  $F_1$ , and  $BC$  families.** The advanced Phu-Stn hybrid families showed a higher density of A trichomes than the Ber families (Table 1). The  $F_1$  families showed a higher density of A trichomes than the Ber but a lower density than that of the Phu-Stn. The BC families showed levels of A trichome density similar to that of the Phu-Stn families.

The tetralobulate membrane-bound glands of type A trichomes were noticeably smaller in the Phu–Stn families than in the Ber, F<sub>1</sub>, and BC families. The density of A glandular trichomes is only one component of insect resistance, while the other is the diameter of the gland size and the amount of the biochemical product (Avé et al., 1986). Thus, the smaller-sized glands in the Phu–Stn families could indicate a lower insect resistance potential.

B glandular trichomes were not observed in Phu–Stn (Table 1). Ber showed a high level of B trichome density, which was transmitted to the F<sub>1</sub> families. In the BC families, the B glandular trichomes were almost absent. However, in the BC<sub>R</sub> families, the B trichome density was higher than that of the BC families (Table 2). Interestingly, within each BC<sub>R</sub> family, almost five to six individuals per family (plants/family = 30, BC<sub>R</sub> families = 17) showed a high density of B trichomes (15 to 20 trichomes/5 mm<sup>2</sup>). Thus, the high standard error found in the BC<sub>R</sub> population reflects the high degree of dispersion or variability observed in B trichome density values.

It has been proposed that the complete loss of B trichomes in BC populations might be due to structural genomic differentiation in interspecific crosses (Rick, 1969; Stephens, 1949; Zamir and Tadmor, 1987). Similarly, Kalazich and Plaisted (1991) evaluating hybrid progenies of *S. tuberosum* (L.) × *S. berthaultii* reported that the expression of B trichomes was lost in BC populations but was recovered when intercrossing either F<sub>1</sub> or BC individuals.

The F<sub>1</sub> cytoplasm had a very small contribution of the male parent Ber, because male and female gametes supply equal quantities of chromosomal material, with the female parent usually contributing more cytoplasm than the male (Beale and Knowles, 1979). Based on previous reports that the effects of structural genomic differentiation were present in both BC populations, it is likely that the small component of Ber present in the F<sub>1</sub> cytoplasm, could have caused the increased density of B trichomes in the BC<sub>R</sub> families. However, inheritance based on genes in the cytoplasm could be distinguished from maternal effects only by making a series of repeated backcrosses using Phu–Stn as a male recurrent parent (Beale and Knowles, 1979).

Ber had higher PPO activity than Phu–Stn and Ber probably conferred increased PPO activity to the F<sub>1</sub> families (Table 1). It is important to note that, even though Ber had a lower density of A glandular trichomes than Phu–Stn, it had a higher PPO activity. This may be due to the slightly larger size of the A glandular trichomes of Ber than those of Phu–Stn. It also may be due to the intrinsic characteristic of Ber to produce higher levels of PPO enzymes and phenolic substrates than other wild *Solanum* species. In the BC families, the PPO activity was decreased, which may be due to the almost complete absence of B trichomes. Conversely, high levels of PPO activity were observed in the BC<sub>R</sub> families. This was expected due to the increase of B trichome density and the positive correlation between B trichome density and PPO activity ( $r_{B-PPO} = 0.27$ ) in this population.

**Inheritance of A and B trichome density and PPO activity.** In the process of generating BC families for the present study, trichome density and PPO activity in Phu–Stn, Ber and F<sub>1</sub> families were determined. Preliminary H estimates were obtained using these data (Table 3). H estimates for A and B trichome density and PPO activity were from medium to high (0.48 to 0.77) in Phu–Stn, Ber, and F<sub>1</sub> populations. These estimates indicate that there were acceptable levels of genetic variability for the density of A and B glandular trichomes and for PPO activity in these populations; however, these estimates might be biased upward due to the size of the experiments and the confounding environmental effects.

In the BC populations, h<sup>2</sup> for A and B trichome density and PPO

Table 1. Mean estimates of A and B trichome density<sup>y</sup> and polyphenol oxidase (PPO) activity in diploid potato populations.

Population <sup>y</sup>	Mean ± SE		
	A	B	PPO <sup>x</sup>
Phu–Stn	21.7 ± 15.9	0.0	0.26 ± 0.08
Ber	2.3 ± 2.1	27.0 ± 6.2	0.42 ± 0.23
F <sub>1</sub>	6.3 ± 6.3	21.0 ± 7.3	0.39 ± 0.17
BC	23.7 ± 6.5	0.1 ± 0.16	0.159 ± 0.026
BC <sub>R</sub>	17.9 ± 4.9	1.2 ± 2.0	0.416 ± 0.064

<sup>y</sup>Number of glandular trichomes per 5 mm<sup>2</sup>.

<sup>y</sup>Phu–Stn = hybrid *Solanum phureja*–*S. stenotomum*, Ber = *S. berthaultii*, F<sub>1</sub> = hybrid: [(Phu–Stn) × Ber], BC = backcross: [(Phu–Stn) × F<sub>1</sub> bulk], BC<sub>R</sub> = reciprocal BC: [F<sub>1</sub> × (Phu–Stn) bulk].

<sup>x</sup>Optical density at 470 nm.

Table 2. Family means of B glandular trichome density in backcross (BC) and reciprocal backcross (BC<sub>R</sub>) diploid potato families.<sup>z</sup>

Family	BC	Family	BC <sub>R</sub>
1	0.09	2	0.76
2	0.07	3	0.45
3	0.12	6	0.16
4	0.11	9	0.64
5	0.13	10	0.24
6	0.06	12	1.16
7	0.11	13	0.27
8	0.17	14	2.08
9	0.07	16	0.77
10	0.06	17	2.38
11	0.21	19	3.27
12	0.11	21	0.16
13	0.12	23	1.99
14	0.04	24	0.08
15	0.05	25	1.85
		26	0.28
		27	3.95
SE	0.16		2.00

<sup>z</sup>BC = [(Phu–Stn) × F<sub>1</sub> bulk]; BC<sub>R</sub> = [F<sub>1</sub> × (Phu–Stn) bulk].

Table 3. Broad-sense heritability (H) estimates for A and B trichome density and PPO activity in Phu–Stn, Ber, and F<sub>1</sub> diploid potato populations.<sup>z</sup>

Population <sup>z</sup>	H ± SE		
	A	B	PPO
Phu–Stn	0.62 ± 0.23	---	0.48 ± 0.26
Ber	0.52 ± 0.32	0.63 ± 0.33	0.69 ± 0.38
F <sub>1</sub>	0.74 ± 0.15	0.73 ± 0.22	0.77 ± 0.17

<sup>z</sup>Phu–Stn = hybrid *Solanum phureja*–*S. stenotomum*; Ber = *S. berthaultii*; F<sub>1</sub> = hybrid [(Phu–Stn) × Ber].

Table 4. Narrow-sense heritability (h<sup>2</sup>) estimates for A and B trichome density and polyphenol oxidase (PPO) activity in BC and BC<sub>R</sub> diploid potato populations.<sup>z</sup>

Population	Genetic analysis	h <sup>2</sup> ± SE		
		A	B	PPO
BC	Half-sib family	0.15 ± 0.11	0.0	0.08 ± 0.19
BC <sub>R</sub>	Half-sib family	0.04 ± 0.08	0.09 ± 0.06	0.12 ± 0.12
BC <sub>R</sub>	Parent–offspring regression	0.05 ± 0.06	0.17 ± 0.06	0.24 ± 0.50

<sup>z</sup>BC = backcross population: [(Phu–Stn) × F<sub>1</sub> bulk]; BC<sub>R</sub> = reciprocal backcross population: [F<sub>1</sub> × (Phu–Stn) bulk].

activity were from very low to low (0.04 to 0.24) (Table 4) when using half-sib family and parent-offspring regression analysis. Half of these estimates are lower than their standard errors, which indicates that these estimates were extremely low or statistically equal to zero.

These  $h^2$  estimates suggest that there is very little additive genetic variance for A and B trichome density and PPO activity in these BC populations. Therefore, the high estimates of broad-sense heritability found in previous generations, e.g., Phu-Stn, Ber, and  $F_1$ , are mostly due to nonadditive genetic effects. Furthermore, the narrow-sense heritabilities found in the present study were lower than those reported by Mehlenbacher et al. (1983), who estimated an  $h^2$  of 0.18 and 0.32 for the density of A trichomes and 0.22 for the density of B trichomes.

*Phenotypic correlations between A and B trichome density and PPO activity.* Low positive correlations between A and B trichome density ( $r_{A-B} = 0.26$ ) and A trichome density and PPO activity ( $r_{A-PPO} = 0.20$ ) were found in the  $F_1$  population. There was no association between B trichome density and PPO activity. Conversely, in the  $BC_R$  population, the associations between A and B trichome density ( $r_{A-B} = 0.44$ ), A trichome density, PPO activity ( $r_{A-PPO} = 0.31$ ), and B trichome density and PPO activity ( $r_{B-PPO} = 0.27$ ) were positive and even slightly higher than those found in the  $F_1$  population.

In breeding potatoes for resistance to aphids, it is important to consider the apparent complementary interaction between A and B glandular trichomes. Plants bearing both types have been reported to be more resistant to green peach aphid than those with A trichomes alone (Gibson, 1979). Therefore, the positive associations found between these traits might facilitate simultaneous improvement for high levels of A and B trichome density and PPO activity.

In general, the results suggest that additive genetic variance was very low for density of A and B trichomes and PPO activity in these BC populations. However, the low levels of additive genetic variance may not be such a problem when dealing with the improvement of a vegetatively propagated species. To develop potatoes expressing high levels of A and B trichome density and PPO activity and recover desirable agronomic traits of the advanced Phu-Stn population, a suggested breeding procedure would be to use a half-sib family selection, based on progeny testing, combined with BCs to Phu-Stn in subsequent generations, provided that there would be a limited amount of epistatic variance, while using broad genetic base populations.

Finally, in developing insect-resistant potato populations, PPO activity and A and B trichome density should be emphasized as a selection criteria due to the following considerations: 1) there exists a positive correlation between PPO activity and aphid resistance (Ryan et al., 1983), 2)  $h^2$  estimates of PPO activity are slightly higher than those of A and B trichome density, 3) there is high consistency and precision in measuring PPO activity (lower cv values than when counting trichomes), 4) assessing PPO activity is faster and less tedious than counting trichomes, and 5) the PPO activity measures the amount of phenolic substrates related to the insect entrapment properties.

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