Inheritance of Abaxial Leaf Pubescence in Beans

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Abstract. Genetic variation for abaxial leaf pubescence was detected among dry bean (*Phaseolus vulgaris* L.) cultivars/lines. Inheritance of pubescence (long, straight hairs) was studied in the dry bean crosses of pubescent 'Pompadour Checa-50' (Dominican Republic) × eight glabrous cultivars/lines. Segregation for pubescence vs. glabrousness indicated that pubescence was determined by a single major gene or by duplicate recessive epistatic genes, depending on the cross involved. Trichome density (number trichomes per mm²) was a quantitative trait. Thus, pubescence was a discrete trait, but trichome density ranged from low to high.

Cultivars of dry beans commonly grown in the United States lack long, straight leaf hairs. However, some dry bean cultivars in the tropics possess long, straight leaf hairs at high density. Genetic variation for trichome type and density occurs in many plant species and has been shown to be associated with insect resistance (Levin, 1973; Ramalho and Ramos, 1979; Rogers, 1979; Webster, 1975). Shaik (1985) first reported negative correlations between leaf pubescence and low intensity of rust, pustules caused by *Uromyces appendiculatus* (Pers.) Unger var. *appendiculatus* [= *U. phaseoli* (Pers.) Wint.], in dry beans. Steadman and Shaik (1988) later reported a negative correlation of long, straight hairs on the abaxial leaves of adult plants with rust intensity. The protection offered by the long hairs is greatest when the leaves have not expanded. At such early stages, the leaf hairs are close enough to form a mat over the abaxial surfaces, upon which droplets of water rest without making contact with the leaf epidermis. This phenomenon of water droplets condensing first on the leaf hairs and later forming a water layer was demonstrated by Burrage (1969). Thus, on hairy leaves, the rust germ tubes would be unable to make contact with the leaf epidermis (Alten, 1983).

Rust is among the most destructive of the leaf diseases of dry bean (Kelly, 1982). The bean rust fungus is one of the most variable pathogens known (Vargas, 1980). Breeding of cultivars with race-specific resistance to all the known races of the pathogen and to maintain stability of resistance is difficult. There is a need to explore alternative types of resistance, particularly those that would operate against all races of the fungus (Coyne and Schuster, 1975; Zaumeyer and Harter, 1941; Christ and Groth, 1982).

We found no report on the inheritance of leaf pubescence in *P. vulgaris*, but quantitative inheritance was reported in *P. lunatus* L. (Lyman and Cardona, 1982). The objectives of this study were to investigate genotypic variation and the inheritance of the abaxial leaf pubescence trait in a wide array of dry bean crosses.

Materials and Methods

Plant materials. Greenhouse-grown plants of two pubescent cultivars [Pompadour Checa-50 (PC50) (P₁) and Jose Beta 83-21 (P₂)] were crossed in 1987 with eight glabrous cultivars/lines—'Chichara' 83-109 (P₃), A-55 (black bean) (P₄), 'Agate' (Pinto) (P₅), EP-1 (Pinto) (P₆), 'Harris' [Great Northern (GN)] (P₇), 'Spinel' (GN) (P₈), 'EZ Pick' (snap bean) (P₉), and 78631 (white bean) (P₁₀). Seeds from single-plant selections (SPS) of each parent were used in crosses. F₁ plants of each cross (Table 1) were subsequently grown in greenhouse plantings to produce F₂ plants. Two pubescent and seven glabrous dry bean cultivars/lines, F₁ of all crosses, and F₂ plants of P₁ × P₆ and their reciprocals, were grown in the greenhouse in Lincoln, Neb., in Oct. 1987. Pots (1.5-liters) were filled with a potting mixture consisting of equal parts of vermiculite, sand, and soil. Seeds were nicked and sown, and pots of the various populations were arranged in a completely randomized design on a greenhouse bench. The greenhouse was held at 23-26°C with a 12-hr day/night photoperiod. All plants were evaluated for abaxial leaf pubescence. Seeds of the F₂ of the remaining crosses and four F₅ lines derived from single F₄ plants from the cross P₁₀ × P₁ were planted on 1 Dec. 1987 in rows 55 cm apart and 5 m long in the field at the Univ. of Puerto Rico, Fortuna Substation, and evaluated for leaf pubescence.

Types of nonglandular hairs. Two types of nonglandular hairs were rated in this study—straight hairs, ≈ 1 to 2 mm long, and hooked hairs, ≈ 0.1 to 0.3 mm long. Both types of hairs were rated when colloidal leaf impressions were used. Straight hairs only were rated with rapid, unaided eye assessments.

An area ≈ 2 cm² on each leaf in the interveinal tissue of the abaxial (bottom) surface was selected and smeared with a thin layer of colloidal (Fisher Chemical). Upon drying, the colloidal was peeled off the leaf surfaces. All the details of the epidermis were thus impressed on the colloidal peels. The peel was mounted in distilled water and observed under the microscope at × 4 magnification. The number of impressions of hooked and straight hairs was estimated. Areas with small veins were avoided because of extremely uneven distribution of hooked and long hairs.

Rating scale for leaf pubescence. The nodes and the nodal leaves of 10 bean cultivars/lines were numbered sequentially from the bottom to the top of plants. Thus, the primary leaves at node 1 were both considered as leaf 0, the first trifoliate leaf as leaf 1, and the subsequent trifoliate leaves as leaf 2, 3, and 4. Only leaves 0 through 4 on each plant were studied. Trichomes of trifoliate leaf 4 were studied by means of colloidal leaf impressions (Shaik, 1985) on F₁ plants, but were rated by the naked eye for abaxial leaf pubescence of long straight hairs on F₂ plants.

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Table 1. Phenotypic classes of parents, F₁, and F₂ segregation for pubescence from crosses of two pubescent with eight glabrous bean cultivars and breeding lines.

Parent or cross	No. plants observed		Expected ratios	χ^2	P
	Pubescent ²	Glabrous			
Pompadour Checa-50 (P ₁)	14	0			
Jose Beta 83-21 (P ₂)	8	0			
Chichara 83-109	0	4			
A-55 (P ₄)	0	4			
Agate (P ₅)	0	3			
EP-1 (P ₆)	0	3			
Harris (P ₇)	0	4			
Spinel (P ₈)	0	4			
'EZ Pick' (P ₉)	0	4			
78631 (P ₁₀)	0	All			
P ₉ × P ₁					
F ₁	16	0			
F ₂	33	10	3:1	0.07	0.80-0.90
P ₁ × P ₉					
F ₁	15	0			
F ₂	26	11	3:1	0.44	0.50-0.70
P ₂ × P ₃					
F ₁	20	0			
F ₂	18	2	3:1	2.40	0.10-0.20
P ₃ × P ₂					
F ₁	22	0			
F ₂	10	7	3:1	2.37	0.10-0.20
P ₁ × P ₂					
F ₁	36	0			
F ₂	107	0	107:0		
P ₁ × P ₃					
F ₁	42	0			
F ₂	137	46	3:1	0.001	0.95-1.00
P ₁ × P ₄					
F ₁	12	0			
F ₂	58	20	3:1	0.02	0.90
P ₅ × P ₁					
F ₁	24	0			
F ₂	82	66	9:7	0.04	0.80-0.90
P ₁ × P ₆					
F ₁	33	0			
F ₂	210	138	9:7	2.37	0.10-0.20
P ₆ × P ₁					
F ₁	24	0			
F ₂	162	129	9:7	0.04	0.80-0.90
P ₇ × P ₁					
F ₁	31	0			
F ₂	154	115	9:7	0.11	0.70-0.80
P ₈ × P ₁					
F ₁	12	0			
F ₂	45	30	9:7	0.41	0.50-0.70
P ₅ × P ₆					
F ₁	0	16			
F ₂	0	65			
P ₇ × P ₆					
F ₁	0	18			
F ₂	0	116			
P ₈ × P ₆					
F ₁	0	18			
F ₂	0	90			
P ₁₀ × P ₁					
F ₅ -87-56	35	15	3:1	0.70	0.20-0.50
F ₅ -87-57	121	32	3:1	1.36	0.10-0.20
F ₅ -87-62	19	3	3:1	1.55	0.20-0.50
F ₅ -87-63	103	38	3:1	0.27	0.50-0.95

²Leaf pubescence was recorded on the abaxial side of the fourth leaf. Plants rated 1 = glabrous; 2, 3, 4, and 5 = pubescent.

Table 2. Segregation for pubescence in F_3 families of the reciprocal cross PC50 (P_1) $\times$ snap bean 'EZ Pick' (P_9).

Crosses	No. nonsegregating for pubescence	No. segregating for pubescence	Expected ratio ²	P
$P_1 \times P_9$	9	8	1:2	0.05–0.1
$P_9 \times P_1$	5	11	1:2	0.80–0.90

²Heterogeneity test for expected ratio (1:2) families: $\chi^2 = 5.69 - 2.63 = 3.06$ (df = 3), $P = 0.30-0.50$.

A rating scale of 1 to 5 was used to describe hair density on the abaxial leaf area as follows: 1 = no hairs; 2 = 1% to 10%; 3 = 11% to 25%; 4 = 26% to 50%; and 5 = >50% of area covered. Pubescence ratings were evaluated on fully expanded leaves to eliminate density fluctuations due to leaf expansion (Pillemer and Tingy, 1976). Plants rated 1 were considered glabrous and those rated 2, 3, 4, and 5 pubescent.

Inheritance of pubescence. The χ^2 method was used to test the goodness-of-fit to particular ratios of glabrous : pubescent plants when bimodal distributions were observed, and to test expected F_3 ratios of nonsegregating pubescent : segregating pubescent progenies.

Results and Discussion

Leaf hair variation. One of the two pubescent cultivar/line sources, 'Pompadour Checa-50' (PC50 SPS) (P_1), had dense long straight hairs on the abaxial surface of leaves 2 and above. The lower leaves of PC50 had either exclusively hooked or a mixture of hooked and straight hairs and were less pubescent (data not shown). The second pubescent cultivar/line, 'Jose Beta' 83-21 (P_2), was moderately pubescent with long straight hairs on the abaxial surfaces of leaves 2, 3, and 4 but with less density than P_1 (data not shown). The other cultivars/lines used in crosses to P_1 and P_2 were highly to moderately glabrous and totally lacked long straight hairs on the abaxial leaf surfaces (Table 1).

Inheritance of pubescence. Dominance for leaf pubescence, for both long and short hairs, was expressed in all of the F_1 (pubescent $\times$ glabrous) families and their reciprocals. The parents showed little variation in pubescence, indicating little influence of environment on the expression of the trait. In contrast, variation in degree of pubescence within F_1 families indicated that heterozygotes were not as stable in the expression of this trait as the homozygous parents. F_1 families of glabrous $\times$ glabrous parents (P_5 , P_7 , and $P_8 \times P_6$) and of highly pubescent $\times$ pubescent parents ($P_1 \times P_2$) were glabrous and pubescent, respectively (Table 1); the F_2 families did not segregate. This test for allelism indicated that the parents possessed similar genes controlling this character (Table 1).

A good fit to a 7 glabrous : 9 pubescent ratio of plants occurred in the F_2 generations from crosses of Great Northern or Pinto cultivars with the pubescent parents. However, if the glabrous parent was either 'Chichara' 83-109, 'EZ Pick', A-55, or 78631, the F_2 and F_3 segregation showed a good fit to a 1 glabrous : 3 pubescent ratio of plants. In the former set of crosses, we hypothesized that this trait was controlled by duplicate recessive epistatic genes, with pubescence being expressed when both dominant genes were present in the

homozygous ($Pb-1/Pb-1$ $Pb-2/Pb-2$) or heterozygous state. In the latter set of crosses, the variation for pubescence was determined by a single gene, suggesting that these glabrous parents were homozygous-dominant at one of the loci determining this trait. We were unable to indicate which locus possessed the dominant alleles.

The F_3 segregation from the cross $P_1 \times P_9$ confirmed the hypothesis that a single major dominant gene controlled pubescence in that cross (Table 2). The number of F_3 families not segregating for pubescence and segregating for pubescence showed a good fit to a 1:2 ratio, respectively (Table 2). No heterogeneity for the F_3 1:2 segregation ratio was detected among crosses of $P_9 \times P_1$ and their reciprocals (Table 2).

All of the present Great Northern and Pinto cultivars are glabrous and lack nonspecific resistance to rust, so developing lines of these bean classes with high abaxial leaf pubescence using PC50 as a source of pubescence is warranted. Because of the simple inheritance of leaf pubescence, single plant selection for this trait should be effective in segregating progeny of early generations.

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