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Gene Transfer of Multiple Flowers and Pubescent Leaf from *Capsicum chinense* into *Capsicum annuum* Backgrounds

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Abstract. The inheritance of multiple flowers and leaf pubescence resulting from the crosses between accessions from pepper species *Capsicum annuum* L. and *C. chinense* Jacq. was examined. Hand cross- and self-pollinations were made in a glass greenhouse. Only eight normal F₁ plants were obtained from crosses between the two species when *C. annuum* L. was the female parent. F₂ and backcross generations obtained from the F₁ and the two parents were grown in the field. Two field studies indicated that multiple flowers and leaf pubescence were controlled by dominant genes. A three-gene model leading to an F₂ segregation ratio of 45:9:10 and a two-gene model leading to an F₂ segregation ratio of 13:3 were suggested for the inheritance of multiple flowers and leaf pubescence, respectively. Epistasis was evoked in the interpretation of the data. No linkage was found between the two characters. The inconsistencies between F₂ and backcross data might be due to selective elimination of genes from one or the other parent in an interspecific hybridization. Segregation ratios from intraspecific crosses for leaf pubescence supported a two-gene model and gave an F₂ ratio of 13 pubescent leaf : 3 glabrous leaf progeny.

Although pepper plants have often been studied for their agricultural value, the inheritance of certain morphological traits has not been well established (Lippert et al., 1966). Because of the interest in transferring useful genes from wild-type peppers into widely grown cultivars, it is desirable to have genetic information on important morphological traits.

C. annuum L., the most widely grown pepper species on a world basis, sets a single flower at each node, whereas *C. chi-*

nense Jacq., a popular pepper species grown in Latin America, sets two or three flowers at each node. The character of two or three flowers set at each node was defined as the multiple-flower trait. Multiple flowers may be potentially useful to increase yield and enhance uniform maturity, which may make mechanical harvesting feasible.

Subramanya (1983) reported a possible gene introgression for the multiple-flower trait from *C. chinense* (PI 159236) into *C. annuum* ('Delray Bell'). He suggested that three major dominant genes may control double flowers at each node, and that additional genes may be involved in the expression of more than two flowers at each node. Tanksley and Iglesias-olivas (1984) employed co-segregation of isozyme genes as markers and concluded that at least five independently segregating chromosomal segments are involved in the multiple-flower inheritance of PI 159234 in crosses with the *C. annuum* cultivar NM 6-4. Greenleaf (1986) cited an unpublished conclusion by J.E. Watson and

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W.H. Greenleaf that seven additive genes determine the multiple flower in *C. chinense* Acc. 1555.

Most pepper genotypes have glabrous leaves with or without pubescence on the abaxial veins, petioles, or stems. Two contradicting results were reported regarding the inheritance of leaf and stem pubescence in peppers. Ikeno (1913) found that pubescence of stems, petioles, and leaves segregated in a 15:1 F₂ ratio, with individuals exhibiting hairs varying in degrees of pubescence. Holmes (1934) observed that a smooth stem was dominant over a hairy stem.

If one considers the transfer of a useful gene from a wild plant into a cultivated plant, it is possible to simultaneously introduce genes that are responsible for unacceptable traits. Therefore, pepper breeders need to have an understanding of the genetics of certain morphological traits in *Capsicum*. The objectives of this study were to 1) examine the inheritance of multiple flowers in *C. annuum* × *C. chinense* crosses and 2) determine the inheritance of leaf pubescence in interspecific and intraspecific hybrids.

Materials and Methods

In this study, No. 178, from the pepper selection program, Dept. of Horticulture, Louisiana State Univ., was used as the *C. chinense* parent (P₁). This entry is homozygous for multiple flowers and glabrous leaf. 'Serrano Chili', which is homozygous for single flowers and pubescent leaves, was used as the *C. annuum* parent (P₂).

In Spring 1986, reciprocal crosses were made between No. 178 and 'Serrano Chili' in a glass greenhouse. In Fall 1986, the F₁ seeds were harvested and planted in the same greenhouse. Only eight normal F₁ plants were obtained, all from the crosses with 'Serrano Chili' as the female parent. Self- and backcross pollinations to P₁ and P₂ were made by hand. In Spring 1987, two parents, F₂, BC₁P₁ (F₁ ♀ × No. 178 ♂), BC₁P₂ (F₁ ♀ × 'Serrano Chili' ♂), and reciprocal (r) BC₁P₂ ('Serrano Chili' ♀ × F₁ ♂) plants were grown at the Hill Farm on the Louisiana State Univ. Baton Rouge campus. A randomized block design with three replications was used. The total plant number grown for each generation was: 60 for each parental species, 117 for BC₁P₁, 149 for BC₁P₂, 35 for rBC₁P₂, and 320 for F₂. In Fall 1987, two field surveys were completed for classifying the traits under study. The first survey was completed after the flower number at the fifth node could be clearly distinguished. The second one was completed ≈ 1 month later.

A study based on intraspecific hybridization was conducted in the greenhouse to observe the pubescent leaf trait. Crosses were made between 'Serrano Chili' and several cultivars that belong to *C. annuum* and have glabrous leaves ('Keystone Resistant Giant No. 4', a bell-type pepper, 'Cayenne Large Red', and 'LSU Sport'). Two surveys for leaf pubescence were done on the plants at the seedling stage before stem bifurcation.

Results

Among the reciprocal crosses made between No. 178 and 'Serrano Chili', eight normal F₁ plants were obtained. Normal plants were only obtained when 'Serrano Chili' (*C. annuum* L.) was used as the female parent. The F₁ plants were vigorous and morphologically uniform, produced two or three flowers per node, and had pubescent leaves. All F₁ plants from intraspecific hybridizations had pubescent leaves. These observations indicated that the multiple-flower and the pubescent leaf traits are dominant.

Multiple flowers. In the F₂ population, 181 plants had the multiple-flower trait, while 37 plants had the single-flower trait (Table 1). An intermediate flowering type was defined here as plants with multiple-flowered nodes and single-flowered nodes about equally distributed on the same plant. Twenty-six plants with the intermediate flowering type were obtained.

Based on data from the F₂ population, three major genes, designated M₁, M₂, and M₃, are proposed to control the multiple-flower expression in peppers. The genotypes of P₁, P₂, and F₁ were M₁M₁M₂M₂M₃M₃ (multiple flowers), m₁m₁m₂m₂m₃m₃ (single flower), and M₁m₁M₂m₂M₃m₃ (multiple flowers), respectively. In the F₂ population, M₁ determined the expression of multiple flowers when the dominant gene was present at either the M₂ or M₃ locus, or both loci. Recessive homozygosity at the M₁ locus modified the expression and reduced the multiple-flowered nodes in spite of the dominant genes present at both the M₂ and M₃ loci. Recessive homozygosity at any two loci is epistatic to the dominant gene present at the third locus. The genetic model proposed should give an F₂ segregation ratio of multiple-flower : 9 intermediate-flowering type : 10 single-flower progeny. A χ² of 2.57 (P = 0.50 to 0.25) indicated that the goodness of fit of F₂ data for the model was nonsignificant, and, thus, the model was supported by the data. However, two BC₁P₂ populations had segregation ratios that deviated from the expected ratio based on the model. The heterogeneity test showed a significant difference between BC₁P₂ and rBC₁P₂ populations at P = 0.05, but a conclusion about the difference was difficult because of the small rBC₁P₂ population (31 plants).

Leaf pubescence. In the F₂ population of Serrano Chili × No. 178, 207 pubescent leaf and 47 glabrous leaf plants were obtained (Table 2). Based on the F₂ population, a ratio of 13 pubescent leaved : three glabrous leaved plants was apparent; a very good fit (χ² = 0.01) was obtained. However, a χ² = 6.67 in the BC₁P₁ generation indicated a poor fit to the 13:3 model we suggested.

Two major genes, H and Sm, were proposed to condition pubescence on the leaf surface of peppers. The genotypes of P₁, P₂, and F₁ were hhSmSm (glabrous or smooth leaf surface), HHsmsm (pubescent leaf surface, typical of 'Serrano Chili'), and HhSmsm (pubescent leaf surface), respectively. Gene pair H controls the pubescent leaf expression and is dominant for pubescent leaf of 'Serrano Chili', while gene pair Sm controls the smooth leaf expression and is dominant for the glabrous leaf of No. 178. H₋ is epistatic to Sm₋ while smsm is epistatic to

Table 1. Segregation frequency of multiple flowers in F₂ and backcross generations derived from the cross between 'Serrano Chili' and *C. chinense* No. 178.

Generation ^a	Plant number			Tested ratio	χ ²	
	Total	Observed ^b				
		MF	MS	SF		
F ₂	244	181	26	37	45:9:10	2.57 ^{NS}
BC ₁ P ₁	102	99	2	1	---	---
BC ₁ P ₂	121	8	11	102	3:1:4	60.38 ^{***}
rBC ₁ P ₂	31	1	7	23	3:1:4	15.86 ^{***}
BC ₁ P ₂ (pooled)	152	9	18	125	3:1:4	80.86 ^{***}

^aBC₁P₁ = F₁ ♀ × P₁ ♂, BC₁P₂ = F₁ ♀ × P₂ ♂, rBC₁P₂ = P₂ ♀ × F₁ ♂.

^bMF = multiple flowers, SF = single flower, MS = multiple-flowered nodes and single-flowered nodes almost equally distributed on the same plant.

NS,*** Nonsignificant or significant at P = 0.001, respectively.

Table 2. Segregation frequency of leaf pubescence in F₂ and backcross generations of the cross between 'Serrano Chili' and *C. chinense* No. 178.

Generation ^z	Plant number			Tested ratio	χ ²
	Total	Observed ^y			
		P	G		
F ₂	254	207	47	13:3	0.01 ^{NS}
BC ₁ P ₁	100	63	37	1:1	6.76 ^{**}
BC ₁ P ₂	123	123	0	---	---
rBC ₁ P ₂	30	30	0	---	---
BC ₁ P ₂ (pooled)	153	153	0	---	---

^zBC₁P₁ = F₁ ♀ × P₁ ♂, BC₁P₂ = F₁ ♀ × P₂ ♂, rBC₁P₂ = P₂ ♀ × F₁ ♂.

^yP = pubescent leaf, G = glabrous leaf.

^{NS,**} Nonsignificant or significant at P = 0.01.

Table 3. Segregation frequency of leaf pubescence in three F₂ intraspecific F₂ populations and one testcross population.

Generation	Observed plant number ^z			Test ratio	χ ²
	Total	P	G		
F ₂ (Serrano Chili × Resistant Giant No. 4)	112	91	21	13:3	0.000 ^{NS}
F ₂ (Serrano Chili × Cayenne Large Red) ^y	28	23	5	13:3	0.015 ^{NS}
F ₂ (Cayenne Large Red × Serrano Chili) ^y	100	83	17	13:3	0.201 ^{NS}
Testcross ^x	134	69	65	1:1	0.119 ^{NS}
F ₂ (LSU Sport × Serrano Chili)	189	153	36	13:3	0.011 ^{NS}

^zP = pubescent leaf, G = glabrous leaf.

^yThese two F₂s were from reciprocal crosses. We considered them as one cross, although data were not pooled.

^xTestcross = ('Serrano Chili' × 'Cayenne Large Red') × 'Cayenne Large Red'.

^{NS} Nonsignificant.

hh. In the F₂ populations studied, the combinations of *H_Sm_*, *H_smsm*, and *hhsmsm* had pubescent leaves and the *hhSm_* had glabrous leaves.

The results of crossing 'Serrano Chili' with 'Keystone Resistant Giant No. 4', 'Cayenne Large Red', and 'LSU Sport' indicated that the F₂ data from three intraspecific crosses supported the observation on the inheritance of the pubescent leaf in the interspecific hybridization (Table 3). The goodness of fit for testcross data from F₁ of 'Serrano Chili' × 'Cayenne Large Red' backcrossed to 'Cayenne Large Red' was consistent with a 1:1 expected ratio.

Linkage. The χ² test was used to determine whether the characters under study segregated independently or were linked. The results based on the F₂ data showed a good fit (χ² = 4.31) for the independent segregation of multiple flowers and leaf pubescence (Table 4).

Discussion

Although the majority of F₁ seeds from interspecific crosses did not germinate, or the seeds germinated but produced abnormal plants, eight normal plants were obtained (Table 1). It was difficult to use the F₁ plants to produce F₂ and backcross progeny. Some early reports dealing with interspecific hybrids indicated the difficulty of obtaining viable F₁ seeds and good F₂ progeny (Rick, 1963; Rick, 1969; Stephens, 1949). In in-

Table 4. Independent segregation in F₂ population for multiple flowers and leaf pubescence.

Characteristic ^z	Frequency	Expected value ^y
M-P	147	152.45
MS-P	24	22.01
S-P	32	28.53
M-NP	40	34.55
MS-NP	3	4.99
S-NP	3	6.47
Total	249	---

^zM = multiple flowers, MS = intermediate flowering type, S = single flower, P = pubescent leaf, G = glabrous leaf.

^yχ² = 4.31, P = 0.75 to 0.50.

terspecific hybrids, deviation from the normal Mendelian segregation is common (Rick, 1963; Rick, 1969; Stephens, 1949; Tanksley and Iglesias-olvias, 1984). Such deviation also occurred in the segregating generations of 'Serrano Chili' × No. 178 crosses and was reflected by the observed inconsistencies between F₂ and backcross populations.

Inheritance of multiple flowers. In an F₂ population of 244 plants, 181 plants exhibited the multiple-flower trait. Subramanya (1983) classified 54 plants as having double flowers and one as having single flowers among the 55 F₂ individuals evaluated. Although Subramanya's (1983) population was too small to draw a definite conclusion, the data suggested that the double-flower phenotype was easy to recover in the F₂ generation. Tanksley and Iglesias-olivas (1984) indicated that the F₂ population was skewed toward the *C. annuum* parent based on the mean flower number per node (1.37 flowers per node, i.e., more F₂ plants had single flowers). Based on the F₂ data of this study, the skewness was toward the *C. chinense* parent (74% multiple-flowered plants in the F₂ population).

Subramanya (1983) suggested a three-gene model (F₂ segregation ratio of 63:1) for the double-flower expression in peppers and concluded that additional genes modified the multiple-flower trait. Tanksley and Iglesias-olivas (1984) found that at least five independently segregating chromosome segments were involved in the multiple-flower expression, according to the cosegregating data of enzyme-coding genes, and epistasis played an important role. Greenleaf (1986) mentioned that seven additive genes determined the multiple-flower trait in accession 1555. A three-gene model with epistasis was proposed to explain the genetic control of multiple flowers in No. 178. The F₂ data obtained in this study showed a good fit to a 45:9:10 F₂ segregation ratio.

The difficulty of explaining the BC₁P₂ by the suggested model is significant. Investigations of other crops reported that selective elimination of genes favored the recurrent parent genotype in interspecific backcrosses (Rick, 1963; Rick, 1969; Stephens, 1949). Subramanya (1983) and Tanksley and Iglesias-olivas (1984) also observed the deviation from the normal Mendelian segregation in the progeny of interspecific crosses of *C. annuum* × *C. chinense*.

In this study, BC₁P₂ populations favored the recovery of single-flowered plants (32% higher than expected) and showed a selective elimination of multiple-flowered plants (84% lower than the expected recovery). These BC₁P₂ data may imply that multiple-flower genes are located on chromosomes that are easily eliminated in interspecific backcrosses. From the standpoint of breeding, early selection in an F₂ population may be an acceptable method of introducing the multiple-flower genes into commercial cultivars (Tanksley and Iglesias-olivas, 1984).

Inheritance of leaf pubescence. Ikeno (1913) reported that pubescent stems, petioles, and leaves in peppers had a 15 pubescent : 1 glabrous F₂ segregation ratio with individuals in the dominant pubescent class exhibiting different degrees of pubescence. Holmes (1934) observed that the smooth stem is dominant over the hairy stem. The results of this study agreed with those of Ikeno's and indicated that pubescence in peppers is dominant and controlled by two genes. Our results disagree with Ikeno's 15:1 segregation ratio. In the F₂ generation of 'Serrano Chili' × No. 178, a 13 pubescent leaf : 13 glabrous leaf segregation ratio was found. The gene model supported by the F₂ ratio did not explain the BC₁P₁ (testcross for pubescent leaf trait) segregation we noted. The number of pubescent leaf plants recovered in the BC₁P₁ implied that 'Serrano Chili' had a selective advantage in the cross and deviated from the usual observation of selective elimination of donor-parent (No. 178) genotype. This result was probably caused by segregation and recombination of modifier gene(s) originating 'in the 'Serrano Chili' parent and independent of the major pubescent leaf genes. A second explanation is that an unidentified genetic mechanism was related to the No. 178 leaf phenotype. Plants of No. 178 have a shiny, glabrous (or smooth), and wavy wrinkled leaf surface but a short-type of hairs on their stems and leaf veins (particularly abaxial veins). Therefore, the same pubescence genotype in BC₁P₁ may express a glabrous leaf surface when the modifiers are lacking; but a pubescent leaf surface when the modifiers are present.

The results from the intraspecific hybridization supported the gene model suggested by the interspecific cross. Three F₂ populations all showed a 13 pubescent : 3 glabrous ratio. One testcross of 'Serrano Chili' × 'Cayenne Large Red' backcrossed to 'Cayenne Large Red' was obtained; the segregation ratio (1:1) in the testcross was consistent with the suggested gene model.

We noted the interesting phenomenon that different degrees of pubescence appeared not only among individuals within F₂ populations but also between F₂ populations. The gene model proposed for leaf pubescence assumes that *H*₋ (pubescence) was epistatic to *Sm*₋ (smooth) and *smsm* (pubescence) was epistatic to *hh* (smooth). Dominance and epistasis may not be complete, thus different degrees of pubescence are common within the population. Among different F₂ populations, the F₂ population derived from 'LSU Sport' × 'Serrano Chili' had a majority of plants with 'Serrano Chili' type of pubescence compared to the

other populations. This leads us to speculate that there are possibly multiple alleles existing among the different pepper cultivars with glabrous leaves.

We confirmed gene transfer of the multiple-flower trait and hypothesized a gene model for its inheritance. Since no linkage was found between multiple flowers and leaf pubescence., multiple flowers can be introduced into some pepper cultivars (e.g., 'Serrano Chili') without changing leaf pubescence. However, because the selective elimination of multiple-flowered plants occurred in the interspecific backcross population, an early F₂ selection may be a useful breeding strategy.

The gene model for leaf pubescence was proposed based on both interspecific and intraspecific hybrid data. The intraspecific F₂s and backcrosses were included to avoid the disadvantages derived from interspecific hybridization, such as the deviation from the normal Mendelian segregation ratio in F₂ or backcross populations. The results for leaf pubescence in two hybridizations were consistent. This result may suggest that the genetic combinations in the F₂ population of 'Serrano Chili' × No. 178 can serve to predict the genetic models for the characters of these two cultivars.

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