

Capsaicinoid Inheritance in an Interspecific Hybridization of *Capsicum annuum* x *C. chinense*

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ABSTRACT. Pungency, caused by the presence of capsaicinoids, is a major quality-determining factor in chile (*Capsicum* L. sp.) The inheritance of nordihydrocapsaicin, capsaicin, dihydrocapsaicin, isomer of dihydrocapsaicin, and homodihydrocapsaicin has not yet been determined. Generations mean analysis revealed that additive, dominance, and interaction effects were significant for capsaicin, dihydrocapsaicin, and isomer of dihydrocapsaicin in an interspecific hybridization of *C. annuum* L. x *C. chinense* Jacq. A simple additive-dominance model was sufficient to explain the genetic variation for nordihydrocapsaicin and homodihydrocapsaicin. Except dihydrocapsaicin and isomer of dihydrocapsaicin in the BCP₁ family, the values of backcross families shift toward the recurrent parents. Because of the significant additive gene effect and the tendency of the values of the capsaicinoids at backcross families to shift toward the recurrent parents, repeated backcrossing and selection will increase and decrease (depending on the recurrent parent) the capsaicinoid content. Positive genetic correlations were observed between the capsaicinoids and the values ranged from 0.4 to 0.8. The estimated number of effective factors were 0.4 for nordihydrocapsaicin, 0.6 for homodihydrocapsaicin, 0.9 for isomer of dihydrocapsaicin, 1.1 for dihydrocapsaicin, 2.8 for total capsaicinoids, and 6.2 for capsaicin. Different gene actions and a different number of effective factors involved in the capsaicinoids inheritance imply that different genes are controlling the synthesis of each capsaicinoid.

Pungency is a major quality-determining factor in chile (*Capsicum* sp.) and is caused by the presence of one or more of the 14 capsaicinoids (Kobata et al., 1998). A chile sample may contain partially or all these capsaicinoids. Krajewska and Powers (1988) reported a linear relationship between pungency and the total amount of capsaicinoids. Therefore, the total pungency value of a given sample is obtained by adding the pungency values of the individual capsaicinoids. Total capsaicinoid content in chile varies from zero to more than 300,000 Scoville Heat Units depending upon genotype (DeWitt and Bosland, 1993).

Krajewska and Powers (1988) reported that humans perceive each capsaicinoid differently, i.e., capsaicin, dihydrocapsaicin, and homodihydrocapsaicin cause a very irritating sensation in contrast to nordihydrocapsaicin which causes the least irritating sensation. Therefore, depending on the proportion of specific capsaicinoid present in the chile sample, the sensation of the product could vary. These marked differences in the perception of the capsaicinoids signify the importance of considering each capsaicinoid separately. The array and relative quantity of individual capsaicinoids in a given chile sample is defined as a capsaicinoid profile.

Capsaicinoids are important in both the pharmaceutical and food industries. Capsaicin is a counter-irritant against pain (Sicuteri et al., 1990) and dihydrocapsaicin protects against increased cholesterol levels in guinea pigs (Negulesco et al., 1989). Specific pungency levels must be maintained for food manufacturers to reliably label food products as mild, medium, and hot. Therefore, cultivars must have a pungency level within a specific range to have commercial value. Moreover, progress in improving or manipulating the pungent property depends on the knowledge of the genetic mechanisms for this trait.

A genetic mechanism for capsaicinoid content has not yet been determined (Ishikawa et al., 1995). Early study using organoleptic tests suggested that the presence or absence of pungency is controlled by a single dominant gene (Deshpande, 1935). Studies quantifying the amount of pungent compounds (total capsaicinoids) using chromatography revealed that the inheritance of the total capsaicinoid content is under polygenic control with transgressive segregation in the F₂ generation (Gill et al., 1973; Ohta, 1962). Ishikawa et al. (1995) reported 10 times greater total capsaicinoid content in F₁ plants than the pungent parent. In the F₁ generation, high capsaicinoid level was a dominant trait (Ahmed et al., 1982; Ohta, 1962). Using generation mean analysis, Ahmed et al. (1982) reported that the estimate of gene effects for additive, dominance, and dominance x dominance components were significant for total capsaicinoid content.

Genetic studies for individual capsaicinoids have not been conducted. Understanding the mode of inheritance for individual capsaicinoids will enable breeders to manipulate capsaicinoid profiles more effectively. Knowledge of the inheritance of the trait and factors (genotypic and environmental) influencing its expression is important for successful breeding of chile for capsaicinoid content. Therefore, the objective of this research was to determine the mode of inheritance for nordihydrocapsaicin, capsaicin, dihydrocapsaicin, isomer of dihydrocapsaicin, and homodihydrocapsaicin in a *C. annuum* x *C. chinense* hybridization.

Materials and Methods

PLANT MATERIAL. A highly pungent parent (200,000 Scoville Heat Units (SHU)), *C. chinense* 'Habanero', was hybridized to a very low pungent parent (420 SHU), PI 298646 *C. annuum* from Spain. Because the generation mean analysis is used to analyze hybrids between two parents that differ as much as possible for the character under analysis (Cherif and Harrabi, 1990), these two genotypes, that are extremes for high and low capsaicinoid content, were selected for hybridization.

HYBRIDIZATION AND POPULATION DEVELOPMENT. In a climate-

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controlled greenhouse with an average daily maximum temperature of 29 °C and average daily minimum temperature of 18 °C, plants of PI 298646 and 'Habanero' were grown and evaluated to confirm capsaicinoid levels and to observe the uniformity of each line. A single plant of each selected parent was grown in a 1.25-L white plastic pot and used for hybridization. The growing medium was 1 peat : 1 silica sand : 1 sandy loam soil (by volume). In each pot, 18 g of a slow-release fertilizer (Osmocote 14N-4.2P-11.6K; Scott's-Sierra Horticultural Products, Marysville, Ohio) was topdressed at transplanting and again at flowering. At the white bud stage, flowers were emasculated and hand-pollinated on the same day. The pollinated flowers were labeled with the hybridization date and parent names. The F₁ and the parental lines were grown in the greenhouse to produce F₂, BCP₁ (F₁ × high parent), and BCP₂ (F₁ × low parent) seeds. Because of sterility, poor seed set, and poor seed germination, obtaining large numbers of plants was difficult in this interspecific cross and the experiment was conducted with limited numbers of plants in each family. Although reports (Subramanya, 1983; Tanksley and Iglesias-Olivas, 1984) suggested that the deviation from the normal Mendelian segregation is common in interspecific crosses of *Capsicum*, Shuh and Fontenot (1990) reported an agreement between the results of interspecific and intraspecific hybridization of *Capsicum* for inheritance of leaf pubescence. Therefore, it was assumed in this experiment that inheritance of capsaicinoids can be determined by using interspecific hybrids.

SCREENHOUSE EXPERIMENT. In 1997, P₁, P₂, F₁, F₂, BCP₁, and BCP₂ populations were evaluated in a randomized complete block design under a screen house at the Fabian Garcia Science Center, Las Cruces, New Mexico. The average daily maximum temperature of the screen house during the growth period was 33 °C and average daily minimum temperature was 18 °C. Irradiance in the screen house was 50% of the open field. Seeds of each family were sown in the greenhouse and seedlings were transplanted to 1.25-L white plastic pots in the screen house 4 weeks after sowing. Each treatment was planted in two blocks and the number of plants per treatment and block were variable. The total number of plants evaluated in each family were 15, 14, 10, 9, 7, and 6 for F₂, BCP₂, F₁, BCP₁, P₂, and P₁, respectively. The growing medium was 1 peat : 1 silica sand : 1 sandy loam soil (by volume). In each pot, 18 g of a slow-release fertilizer (Osmocote 14N-4.2P-11.6K; Scott's-Sierra Horticultural Products) was topdressed at transplanting and again at flowering. Seedlings were watered twice daily to maintain optimum growth. Mature red succulent fruits were harvested from the first four node positions and then bulked per plant for analysis.

FIELD EXPERIMENT. In 1998, F₁, F₂, BCP₁, and BCP₂ populations were evaluated along with their parents under field conditions at the Leyendecker Plant Science Research Center (LPSRC), 12 km south of Las Cruces, New Mexico on glendale loam soil

(Bulloch and Neher, 1980). The average daily maximum temperature of the LPSRC during the growth period was 33 °C and average daily minimum temperature was 14 °C. Seeds of each family were sown in the greenhouse and seedlings were transplanted to the field 7 weeks after sowing. As in the screen house experiment, a randomized complete block design was used and each treatment was planted in two blocks with variable numbers of plants per plot and family. Total number of plants evaluated in each family were, 27, 24, 22, 16, 12, and 6 for F₂, BCP₁, BCP₂, P₂, P₁, and F₁, respectively. Individual plants were spaced 30 cm within rows and 100 cm between rows. Standard growing practices for southern New Mexico were used (Bosland, et al., 1994). The field was furrow irrigated as needed, usually at 7- to 10-d intervals. Mature red succulent fruits were harvested from the first four node positions and then bulked per plant for analysis.

LABORATORY ANALYSIS. The method as described by Collins et al. (1995) to extract, separate, and quantify capsaicinoids using high-performance liquid chromatography (HPLC) was followed. The HPLC data were transformed to parts per million (ppm) or mg·kg⁻¹. Conversion to Scoville Heat Units can be made by multiplying ppm or mg·kg⁻¹ by a factor of 15. The only capsaicinoids detected in the test populations and studied in this investigation were nordihydrocapsaicin, capsaicin, dihydrocapsaicin, isomer of dihydrocapsaicin, and homodihydrocapsaicin. The sum of these capsaicinoids, i.e., total capsaicinoid content, was also evaluated. Because research results (Ahmed et al., 1982; Gill et al., 1973; Ishikawa et al., 1995; Ohta, 1962) have reported only total capsaicinoid content, it was considered also in this analysis for possible comparison.

DATA ANALYSES. Homogeneity of error variance across the two environments, screen house and field, was tested by the F test (Gomez and Gomez, 1983) and none of the error mean squares were significant for any of the capsaicinoids. Combined analyses of variances for families across the two environments were performed to determine family × environment interaction for each capsaicinoid using the GLM procedure of SAS (SAS Inst., Inc., 1996). Families were considered as fixed effects while environments were random effects. Significant levels were determined as suggested by McIntosh (1983) for combined analysis. Because there was not a significant difference among family × environment interactions (Table 1), data of the screen house and field experiments were combined for generation mean analysis. The combined number of plants per family were 42, 36, 33, 23, 18, and 16 for F₂, BCP₂, BCP₁, P₁, P₂, and F₁, respectively. Mean, variance, and standard error of the F₁, F₂, BCP₁, BCP₂, and the parents were determined using procedure means of the SAS program. Calculated means and variances were used to estimate the midparent (m), additive [d], and dominance [h] gene effects as described by Rowe and Alexander (1980) following the method for three-parameter model of Mather and Jinks (1977).

Table 1. Mean squares for total capsaicinoids (CAPSD), capsaicin (CAP), dihydrocapsaicin (DH), nordihydrocapsaicin (NDH), isomer of dihydrocapsaicin (ISO), and homodihydrocapsaicin (HD) from six chile families tested across two environments.

Source of variation	df	CAPSD	CAP	DH	NDH	ISO	HD
Environment (E)	1	4248304 ^{NS}	769436 ^{NS}	909095*	17268 ^{NS}	5650 ^{NS}	573 ^{NS}
Block (environment)	2	418050	222913	21752	302	457	404
Family (F)	5	91695983**	33500768**	14127379**	93457**	12243**	4884**
F × E	5	1162096 ^{NS}	291081 ^{NS}	318149 ^{NS}	6771 ^{NS}	743 ^{NS}	212 ^{NS}
Error	10	1457126	537682	255740	2263	730	114

^{NS},*,** Nonsignificant or significant at $P < 0.05$ or 0.01 , respectively.

Table 2. Estimated variance components for total capsaicinoids (CAPSD), capsaicin (CAP), dihydrocapsaicin (DH), nordihydrocapsaicin (NDH), isomer of dihydrocapsaicin (ISO), and homodihydrocapsaicin (HD).

Source of variation	CAPSD	CAP	DH	NDH	ISO	HD
Environment (E)	100919.3	-48520.0	26121.1	494.3	310.0	-13.1
Family (F)	90533886.0	33209687.0	13809230.0	86687.3	11499.5	4672.1
F × E	-147514.8	-123300.5	31204.6	2254.0	6.6	48.8

Adequacy of the additive-dominance model was determined by χ^2 test with three degrees of freedom and was accepted if $P > 0.05$ (nonsignificant χ^2 value). The deviation from zero was tested using the normal deviate table for each parameter as suggested by Mather and Jinks (1977). When the three-parameter model was inadequate (significant χ^2 value), the interaction terms (additive × additive [i], additive × dominance [j], and dominance × dominance [l]) were computed (Mather and Jinks, 1977). The genetic parameters (m, [d], [h], [i], [j], and [l]) were tested for significance using unpaired *t* test. Genetic correlation was determined using the following formula (Burton, 1951): genetic correlation = $(cvXYF_2 - cvXYF_1) / ((\sigma^2XF_2 - \sigma^2XF_1)(\sigma^2YF_2 - \sigma^2YF_1))^{1/2}$, where $cvXYF_2$ = covariance of capsaicinoids X and Y in F_2 generation, $cvXYF_1$ = covariance of capsaicinoids X and Y in F_1 generation, σ^2XF_2 = variance of capsaicinoid X in F_2 generation, σ^2XF_1 = variance of capsaicinoid X in F_1 generation, σ^2YF_2 = variance of capsaicinoid Y in F_2 generation, and σ^2YF_1 = variance of capsaicinoid Y in F_1 generation.

Environmental variance (σ^2E) and broad sense heritability (H_b^2) were estimated using the following formula (Ito and Brewbaker, 1991): $H_b^2 = (\sigma^2F_2 - \sigma^2E) / \sigma^2F_2$, where $\sigma^2E = 1/4(\sigma^2P_1 + \sigma^2P_2 + 2\sigma^2F_1)$, σ^2F_2 = variance of the F_2 population, σ^2P_1 = variance of the high capsaicinoid content parent, σ^2P_2 = variance of the low capsaicinoid content parent, and σ^2F_1 = variance of the F_1 population.

The number of effective factors (k), defined as the number of gene pairs in which two true breeding lines differ (Mather and Jinks, 1977), involved in capsaicinoid inheritance was estimated

by two different methods: $k = 0.25(0.75 - h + h^2)D^2 / (\sigma^2F_2 - \sigma^2F_1)$ (Burton, 1951) and $k = D^2 / 8(\sigma^2F_2 - \sigma^2F_1)$ (Castle, 1921), where $h = F_1 - P_2$; $D = P_1 - P_2 / P_1 - P_2$, k = minimum number of effective factors, P_1 = mean of the highest capsaicinoid content parent, P_2 = mean of the smallest capsaicinoid content parent, F_1 = mean of the F_1 population, F_2 = mean of the F_2 population, σ^2F_1 = variance of the F_1 population, and σ^2F_2 = variance of the F_2 population.

Results

Results of combined analyses of variances for families across the two environments indicated that, except for dihydrocapsaicin, there were no significant differences between environments. The family × environment interactions for each of the capsaicinoids were also nonsignificant (Table 1). When the estimated variance components of family, environment, and family × environment interactions were examined, the proportion of the variances for the families were ≥97% for each of the capsaicinoids (Table 2). Therefore, the influence of environment and the interactions were considered negligible in this study.

The capsaicinoid content of the parents differed significantly, as was expected, with ‘Habanero’ having the highest content (Table 3). For the F_1 progeny, the means of total capsaicinoids, dihydrocapsaicin, nordihydrocapsaicin, and isomer of dihydrocapsaicin were higher than the midparent value, indicating partial dominance toward the highest parent. In contrast, the F_1 means for capsaicin and homodihydrocapsaicin were less than the midparent indicating partial dominance toward the lowest

Table 3. Capsaicinoid content (mean ± SE) for P_1 ‘Habanero’, P_2 (PI 298646), and their F_1 , F_2 , BCP_1 ($F_1 \times P_1$), and BCP_2 ($F_1 \times P_2$).

Family	Content (mg·kg ⁻¹)						No. of plants
	CAPSD ²	CAP	DH	NDH	ISO	HD	
P_1	13032 ± 555	7819 ± 414	4574 ± 175	377 ± 30	163 ± 13	99 ± 7	18
BCP_1	9336 ± 427	4828 ± 323	3971 ± 194	384 ± 42	85 ± 17	67 ± 9	33
F_1	7116 ± 460	2437 ± 190	4168 ± 260	359 ± 27	114 ± 7	37 ± 3	16
F_2	4554 ± 511	1528 ± 210	2606 ± 304	311 ± 40	66 ± 11	44 ± 7	42
BCP_2	1490 ± 333	426 ± 99	880 ± 200	138 ± 32	32 ± 7	14 ± 3	36
P_2	24 ± 4	6 ± 2	9 ± 3	3 ± 0	3 ± 0	3 ± 0	23
Midparent	6528	3913	2292	190	83	51	

²CAPSD = total capsaicinoids, CAP = capsaicin, DH = dihydrocapsaicin, NDH = nordihydrocapsaicin, ISO = isomer of dihydrocapsaicin, and HD = homodihydrocapsaicin.

Table 4. The range of total capsaicinoids (CAPSD), capsaicin (CAP), dihydrocapsaicin (DH), nordihydrocapsaicin (NDH), isomer of dihydrocapsaicin (ISO), and homodihydrocapsaicin (HD) in the parents (P_1 and P_2) and segregating families (BCP_1 , BCP_2 , and F_2).

Family	Content (mg·kg ⁻¹)					
	CAPSD	CAP	DH	NDH	ISO	HD
P_2	15–107	3–36	3–62	3–3	3–3	3–3
BCP_2	15–5878	3–2069	3–3651	3–660	3–163	3–57
F_2	15–10091	3–5637	3–6784	3–904	3–291	3–208
BCP_1	4187–14902	2200–9121	1630–6327	77–925	3–379	3–220
P_1	9375–17792	5325–10907	3261–6149	240–782	71–268	44–190

Table 5. Joint scaling test and estimates (\pm SE) with three-parameter model using six families mean for total capsaicinoids (CAPSD), capsaicin (CAP), dihydrocapsaicin (DH), nordihydrocapsaicin (NDH), isomer of dihydrocapsaicin (ISO), and homodihydrocapsaicin (HD) content in PI 298646 x 'Habanero' hybridization.

Parameter ^z	CAPSD	CAP	DH	NDH	ISO	HD
m	6410** \pm 236	3608** \pm 165	2282** \pm 81	194** \pm 14	75** \pm 6	51** \pm 3
[d]	6386** \pm 236	3602** \pm 165	2272** \pm 81	191** \pm 14	72** \pm 6	48** \pm 3
[h]	-939* \pm 465	-2109** \pm 232	1111** \pm 220	161** \pm 29	23** \pm 9	-16** \pm 4
χ^2	34.8	63.4	26.3	2.6	21.2	3.3
P	<0.005	<0.005	<0.005	0.50-0.25	<0.005	0.50-0.25

^zm = midparent, [d] = additive, and [h] = dominance.

***Significant from zero at $P < 0.05$ or 0.01 , respectively, based on normal deviates table.

Table 6. Joint scaling test and estimates (\pm SE) with six-parameter model using six families mean for total capsaicinoids (CAPSD), capsaicin (CAP), dihydrocapsaicin (DH), and isomer of dihydrocapsaicin (ISO) content in PI 298646 x 'Habanero' hybridization.

Parameter ^z	CAPSD	CAP	DH	ISO
m	3090 \pm 2330	-486 \pm 1097	3012* \pm 1339	113* \pm 56
[d]	6504** \pm 278	3907** \pm 207	2282** \pm 87	80** \pm 6
[h]	1829 \pm 5308	5130* \pm 2710	-2782 \pm 2972	-188 \pm 141
[i]	3438 \pm 2314	4398** \pm 1077	-721 \pm 1336	-30 \pm 56
[j]	2685* \pm 1217	991 \pm 792	1617** \pm 584	-52 \pm 39
[l]	2197 \pm 3166	-2207 \pm 1686	3938** \pm 1737	189* \pm 87

^zm = midparent, [d] = additive, [h] = dominance, [i] = additive \times additive, [j] = additive \times dominance, and [l] = dominance \times dominance.

**Deviation from zero is significant at $P < 0.05$ and 0.01 , respectively, according to unpaired t test.

parent (Table 3). The values of both backcross families shifted toward the recurrent parents, except for dihydrocapsaicin and isomer of dihydrocapsaicin in the BCP₁ family.

The ranges of the capsaicinoid content for the five families are presented in Table 4. When the capsaicinoid amounts of individual plants were examined in segregating families, they showed a continuous variation. Thus, it was not possible to classify them into distinct classes. Furthermore, the frequency distribution graph of the backcross families was skewed toward the respective recurrent parents (data not presented). Some plants with higher nordihydrocapsaicin, dihydrocapsaicin, isomer of dihydrocapsaicin, and homodihydrocapsaicin content than the high parent were observed in BCP₁ and F₂ families.

The joint three-parameter scaling test indicated that an additive-dominance model was adequate to explain the variation for only nordihydrocapsaicin and homodihydrocapsaicin, but not adequate for estimating the genetic parameters for total capsaicinoids, capsaicin, dihydrocapsaicin, nor for an isomer of dihydrocapsaicin based on estimates of χ^2 (Table 5). The additive and dominance components of the genetic parameter were significantly different from zero. Further analyses using a joint six-parameter model found that most of the genetic parameters for total capsaicinoids, capsaicin, dihydrocapsaicin, and isomer of dihydrocapsaicin deviated from zero (Table 6). The capsaicin content showed significant additive [d], dominance [h], and additive \times additive [i] effects. Dihydrocapsaicin had significant additive [d], additive \times dominance [j], and dominance \times dominance [l] gene action. For total capsaicinoids, significant additive [d] and additive \times dominance [j] and for isomer of dihydrocapsaicin significant additive [d], and dominance \times dominance [l] effects were observed (Table 6).

Results of the Burton (1951) and the Castle (1921) methods in estimating the number of effective factors are reasonably close in agreement for each capsaicinoid (Table 7). The number of effective factors controlling the individual capsaicinoids was variable. For example, the two methods estimated consistently that capsaicin had more than six effective factors, while for nordi-

hydrocapsaicin the minimum number of effective factor was estimated as 0.4.

The broad sense heritability estimates for the capsaicinoids ranged from 43% for capsaicin (the lowest) to 85% for nordihydrocapsaicin and homodihydrocapsaicin (the highest). The heritability estimate was 72% for total capsaicinoids (Table 7).

Genetic correlation coefficient values for each pair of capsaicinoids are presented in Table 8. High genetic correlation

Table 7. Estimate of the minimum number of effective factors involved in total capsaicinoids (CAPSD), capsaicin (CAP), dihydrocapsaicin (DH), nordihydrocapsaicin (NDH), isomer of dihydrocapsaicin (ISO), and homodihydrocapsaicin (HD) inheritance and broad-sense heritability in PI 298646 x 'Habanero' hybridization.

Capsaicinoids	Effective factors			Heritability (%)
	Burton (1951)	Castle (1921)	Avg ^z	
CAPSD	2.8	2.8	2.8	72
CAP	6.5	6.0	6.3	43
DH	1.3	0.9	1.1	82
NDH	0.4	0.3	0.4	85
ISO	0.9	0.8	0.9	76
HD	0.6	0.6	0.6	85

^zMean of the two methods.

Table 8. Genetic correlation coefficients for pairs of capsaicinoids from hybridization of PI 298646 x 'Habanero'.

	NDH	CAP	DH	ISO	HD
NDH ^z	1				
CAP	0.4	1			
DH	0.8	0.6	1		
ISO	0.5	0.4	0.6	1	
HD	0.8	0.6	0.6	0.4	1

^zNDH = nordihydrocapsaicin, CAP = capsaicin, DH = dihydrocapsaicin, ISO = isomer of dihydrocapsaicin, and HD = homodihydrocapsaicin.

values (0.8) were observed between nordihydrocapsaicin and dihydrocapsaicin; and between homodihydrocapsaicin and nordihydrocapsaicin. The lowest genetic correlation value, 0.4, was observed between capsaicin and nordihydrocapsaicin; between isomer of dihydrocapsaicin and capsaicin; and between homodihydrocapsaicin and isomer of dihydrocapsaicin.

Discussion

All types of digenic epistasis were shown to be important in affecting inheritance of capsaicin, dihydrocapsaicin, and isomer of dihydrocapsaicin. However, a generalization could not be made, because the type of gene action varied among capsaicinoids. The results suggest that the digenic model with no epistasis describes accurately the quantitative inheritance for nordihydrocapsaicin and homodihydrocapsaicin, but the other capsaicinoids require a model with interactions. The positive additive \times additive [i] estimate for capsaicin suggests that gene pairs are in associated forms (Mather and Jinks, 1977), i.e., only 'Habanero' contributes the genes for increasing the capsaicin content.

The transgressive segregates observed for nordihydrocapsaicin, dihydrocapsaicin, isomer of dihydrocapsaicin, and homodihydrocapsaicin contents implied both parents, 'Habanero' and PI 298646, have an allele contributing for increasing these traits. This is also shown by having negative additive \times additive [i] estimates for these capsaicinoids, i.e., the gene pairs are in dispersive form (Mather and Jinks, 1977).

Because of the significant additive gene effect and the tendency of the capsaicinoid values at backcross generations to shift toward the recurrent parents, implied that repeated backcrossing and selection will increase and decrease (depending on the recurrent parent) the capsaicinoid content. Because industrial needs for chile pungency vary, from low or nonpungent paprika for color to very pungent for pharmaceutical purposes, developing high and low pungent chiles is possible either by repeated backcrossing or recurrent selection.

A lack of distinct classes for the capsaicinoids studied in the segregating families implies quantitative inheritance may explain the variation in capsaicinoid content. Therefore, to better understand the quantitative nature of capsaicinoid inheritance, the effective factors (minimum number of genes) were estimated. The effective factor estimates can be used as a guideline in breeding programs (Kondra and Thomas, 1975). If the effect of different genes in the system are not equal, alleles for increasing the trait are not all concentrated in one parent, and the alleles for decreasing the trait are in another parent, the number of effective factors estimated will be low (Mather, 1979). Therefore, the estimates will be unbiased when the following conditions are met: absence of linkage, gene effects for one parent is plus and for the other parent is minus, all genes are equally important, degree of dominance of all plus factors are the same, and an absence of nonallelic interactions (Burton, 1951). Because of the presence of interallelic interactions and dispersive form of the genes for nordihydrocapsaicin, dihydrocapsaicin, isomer of dihydrocapsaicin, and homodihydrocapsaicin in this study, the estimated effective factors were much lower than could be expected. However, the number of effective factors estimated for capsaicin and total capsaicinoids supports the idea that the capsaicinoids are quantitatively inherited traits. The number of effective factors for total capsaicinoids was lower than that for capsaicin. This could be due to different gene effects observed for individual

capsaicinoids, i.e., neutralizations of the effective factors.

The broad-sense heritability of 72% estimated for total capsaicinoids in this study was lower than an earlier report of 98% (Gill et al., 1973). Heritability estimates could vary depending on the methods used to calculate the estimate, variation in the genetic material tested, and the environment. When individual capsaicinoids were examined, except for capsaicin, the heritability values were high. A high heritability value indicates a high efficiency of selection for improving the trait.

Martinez and Foster (1998) reported that although the small correlation coefficients are statistically significant, the values below 0.4 have little practical significance because only a small portion of the total variation is accounted. Therefore, the genetic correlation values observed between capsaicin and nordihydrocapsaicin; isomer of dihydrocapsaicin and capsaicin; and homodihydrocapsaicin and isomer of dihydrocapsaicin were small and may be negligible. The high genetic correlation values between nordihydrocapsaicin and dihydrocapsaicin; and between homodihydrocapsaicin and nordihydrocapsaicin, indicates a close genetic relationship between these capsaicinoids. These capsaicinoids have similar chemical structure, except for number of carbons in the chain. The association of the traits in the population have significant impact on selection. For example, the positive genetic correlation of nordihydrocapsaicin and dihydrocapsaicin imply that selection for high dihydrocapsaicin content results also in selection for high nordihydrocapsaicin content or vice versa.

In conclusion, differences in gene action and effective factors may imply that synthesis of each of the capsaicinoids is controlled by different genes. Furthermore, a lack of distinct classes in the segregating families indicates quantitative inheritance explain the variation in capsaicinoid content. Because of the significant additive gene effect, improvement through repeated backcrossing and selection of desirable recombinants from segregating populations could be an effective way to increase or decrease the capsaicinoid content in chile.

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