# Inheritance of resistance to the deforming pepper mosaic virus, PepDMV, in *Capsicum*

# Herencia de la resistencia al virus del mosaico deformante del pimentón PepDMV en *Capsicum*

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## Abstract

With the aim to determine the mode of inheritance in three resistant materials, crosses were performed towards three susceptible lines. We followed the backcrossing method used by Warner (1952), based on the mathematical model of Fisher Immer & Tedin (1932), described in detail by Mater (1949) and Jenkins (1982, 1984). In this method the genetic variance is partitioned into three components: additive, dominant and epistatic. The backcross method includes the two parents, the F1 hybrid, and the self-pollination of the F1 to form the F2 population, and the backcrosses to both parents. The populations were evaluated for resistance to the pepper mosaic virus PepDMV in greenhouse conditions. The results showed that the model additive-dominant explained the resistance in the hybrids formed between resistant and susceptible material. The genes with heritable action transmit to their offspring the resistance effect. The presence of viral resistance is given by the presence of resistant parents.

**Key words:** Solanaceae, chili, virus, varietal resistance, *Capsicum annuum*, *C. frutescens* and *C. chínense*.

## Resumen

En busca de determinar el modo de herencia de la resistencia en tres materiales resistentes, se hicieron cruzamientos hacia tres líneas susceptibles. Se siguió el método del retrocruzamiento propuesto por Warner (1952) fundamentado en el modelo matemático de Fisher Immer y Tedin (1932) descrito con detalle por Mater (1949) y Jenkins (1982, 1984) en el cual se descompone la varianza genética en tres componentes: aditiva, dominancia y epistática. El modelo del retrocruzamiento incluye los dos parentales, el hibrido de la primera generación y la autofecunfación de la F1 para formar la población F2 y las retrocruzas hacia ambos padres. Las

poblaciones fueron evaluadas a resistencia al virus del mosaico del pimentón PepDMV en condiciones de invernadero. Los resultados mostraron que el modelo aditivodominancia explicó la resistencia en los híbridos formados entre materiales resistentes y susceptibles. Los genes con acción heredable transmiten a la descendencia el efecto de resistencia. La ganancia de la resistencia viral se da por la presencia de parentales resistentes.

**Palabras clave:** Solanaceae, ají, virus, resistencia varietal, *Capsicum annuum*, *C. frutescens* y *C. chínense*.

## Introduction

The genus *Capsicum* includes the species of pepper and chili destined for fresh consumption, and industrial and pharmacological uses. The Research Prgram in Horticultural Improvement at the National University of Colombia, Palmira campus started in 1987, with the collection of material from this genus from the Valle del Cauca department, and, in 1995 the pepper variety UNAPAL Serrano was released (Vallejo *et al.*, 1999).

The *Capsicum* crops are affected by viruses, amongst which those common in Colombia include the Tobacco Mosaic Virus (TMV), the Cuvumber Mosaic Virus (CMV), geminiviruses and Potyviruses (Morales et al., 2005). The most limiting are the potyviruses, which have been found with high frequency in samples collected in the Valle del Cauca (Pardey, 2008). Morales et al. (2005) named this virus as *virus del Mosaico Deformante del Pimentón* –PepDMV [Pepper deforming Mosaic virus]. The Breeding Program of the National University of Colombia (UNAL), Palmira campus has amongst its objectives the evaluation and development of varieties of pepper and chili, with resistance to  PepDMV, derived from the lines Serrano accessions 70 and 24, which have showed resistance to PepDMV (Pardey, 2008). Thus, a requirement is to determine the inheritance mode of the resistance, in order to develop a breeding strategy to improve commercial material that is susceptible in the field.

## Materials and Methods

In order to determine the inheritance mode of resistance in the material Serrano, accessions 70 and 631 and 24 crosses were performed towards the commercial varieties that are susceptible to the PepDMV virus:  Cayenne (*Capsicum annuum*), Tabasco (*Capsicum frutescens*) and Habanero (*Capsicum chinense*). Intra-specific crosses were performed (Box 1) under controlled conditions (for temperature and

insect-free) in greenhouses. The resistant introductions were Serrano (*Capsicum annum*), a commercial variety of pepper released by the UNAL in 1995, the introduction 70 (*Capsicum frutescens*), originating from Ecuador and donated by the US Department for Agriculture (USDA) in 2000, the introduction 631(*Capsicum chínense*) collected in the Department of Guainía by SINCHI and UNAL, in 1998 and the introduction 24 (*Capsicum chínense*) collected in the Valle del Cauca.

Box 1. Crossing scheme between PepDMV resistant material, and commercial varieties of chili.

**Cuadro 1.** Esquema de cruzamientos entre materiales resistentes a virus del mosaico deformante del pimentón -PepDMV y variedades comerciales de ají

| Cayenne | | | Tabasco | | | Habanero | | |
|---------|---|---------|---------|---|---------|----------|---|---------|
| Parental | | Parental | Parental | | Parental | Parental | | Parental |
| Cayenne | x | Serrano | Tabasco | x | 70 | Habanero | x | 24 |
| Serrano | x | Cayenne | 70 | x | Tabasco | 24 | x | Habanero |

The F1 generations were obtained for each species (Photo 1). Direct and reciprocal crosses were performed in order to identify maternal affects and / or incompatibility barriers between parentals. Crosses were performed between the F1 towards each parental in order to obtain the backcrosses RC1 and RC2. The F1 seed was planted in isolation in order to obtain the F2 seed with no cross-pollination (Box 2).
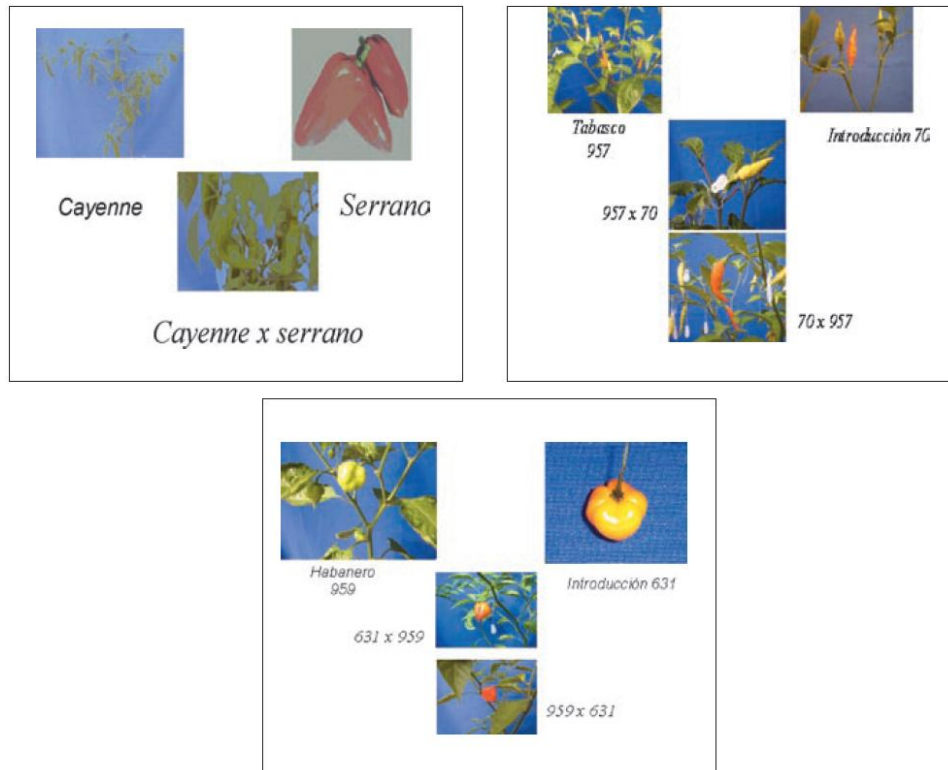
Foto 1. Cruce entre especies de: (a) *C.annuum:* Cayenne y Serrano; (b) *C. frutescens:* Tabasco e Introducción 70; (c) *C. chinense:* Habanero e introducción 631

Photo 1. Crosses between the species: (a) *C. annuum*: Cayenne and Serrano; (b) *C. frutescens*: Tabasco and the Introduction 70; (c) *C. chinense*: Habanero and introduction 631.

Cuadro 2. Cantidad de semillas evaluada en cada cruzamiento para determinar el modo de herencia de la resistencia en *Capsicum*

| | Parental comercial | Introducción resistente | F1 | F2 | RC1 | RC2 |
|---|---|---|---|---|---|---|
| Cayenne x Serrano | 20 | 20 | 50 | 250 | 50 | 50 |
| Serrano x Cayenne | 20 | 20 | 50 | 250 | 50 | 50 |
| Tabasco x Introducción 70 | 20 | 20 | 50 | 250 | 50 | 50 |
| Introducción 70 x Tabasco | 20 | 20 | 50 | 250 | 50 | 50 |
| IHabanero x Introducción 24 | 20 | 20 | 50 | 250 | 50 | 50 |
| Introducción 24 x Habanero | 20 | 20 | 50 | 250 | 50 | 50 |

Box 2. Quantity of seed evaluated in each cross in order to determine the inheritance mode for resistance in *Capsicum*.

The evaluation of resistance to PepDMV was carried out in the populations F1, F2, RC1, RC2 and the parentals of each one of the species. The populations of each cross were planted in trays. Seed resulting from direct and reciprocal crosses was differentiated. Two replicas were performed for each cross. Inoculations were

carried out twice during the seedling stage, at an interval of 8 days between the first and subsequent inoculation with isolates of PepDMV maintained on plants of *Nicothiana benthamiana*; inoculation was achieved by gently rubbing the leaves with humid gauze. The evaluation was initiated after 15 days, when the plant presented new leaves. Asymptomatic plants were evaluated using the immuno-enzymatic technique ELISA. The incidence in the plant of the mosaic virus (absence of presence) was evaluated.

With the incidence data obtained frequency tables were constructed to test for Mendelian inheritance through one or two genes, and for epistatic effects. The validity of the models was confirmed with the Chi-square test ($X^2$). When the crosses did not fit to the simple inheritance models, generation means analyses were performed.

The components included in the generation means analysis were the mean (*m*) as the average of the phenotypes of the parentals. From this, the parameters [a] and [d] were derived, where [a] is the distance from each parent (homozygote lines) to the mean, and [d] the distance from the F1 (heterozygote line) to the mean. [a] is the heritable value for a trait; [d] is the non-heritable value for the trait; as the components of genetic variation of a trait are given by additive variance, the dominance variance, and the interaction genetic variance.

The expected components for the means of the distinct generations as a function of *m*, [a] and [d], and assuming the absence of epistasis between loci were the following:

| Generación | Fenotipo promedio esperado | | |
|---|---|---|---|
| | M | [a] | [d] |
| P1 | 1 | -1 | 0 |
| P2 | 1 | 1 | 0 |
| F1 | 1 | 0 | 1 |
| F2 | 1 | 0 | 1/2 |
| RC1 | 1 | -1/2 | 1/2 |
| RC2 | 1 | 1/2 | 1/2 |

From the components for each generation the expected mean was calculates for each one. The validity of the model was determined with the weight of the variance of each population by the number of data and the inverse was calculated 1/ [d $^2$/n] consisting of the weight of the weighting; with greater mean variance of a given generation, with less precision will be determined the actual value of the measure, and thus, the lower must be the weight that contains relevant information in the group scale test (Ceballos, 2008).

When the model was not satisfactory, due to the differences between the calculated values and the observed values being too big to be considered random, a more complete model was tested including interaction parameters. The analysis performed was a regression using the program SAS 2006.

| Parámetro | | Modelo matemático |
|---|---|---|
| $m$ | = | 1/2P2+1/2P1+4F2-2RC1-2RC2 |
| $[a]$ | = | 1/2P2-1/2P1 |
| $[d]$ | = | 6RC1+6RC2-8F2-F1-1.5P1-1.5P2 |
| $[aa]$ | = | 2RC1+2RC2-4F2 |
| $[ad]$ | = | 2RC2-P2-2RC1+P1 |
| $[dd]$ | = | P1+P2+2F1+4F2-4RC1-4RC2 |

In order to observe the individual effect of the different parameters, including the different combinations of the six parameters, a stepwise regression analysis was performed. The best fit model was that whose parameter contributed significantly to the total sum of squares.

## Results and discussion

The analysis to determine the inheritance mode for resistance in each of the commercial varieties is presented species by species as each species showed a different model.

### *Capsicum annuum.*

The commercial chili variety Cayenne and Serrano belong to the species *C. annuum*. In the analysis of variance differences were detected between populations  (Parental 1, Parental 2, F1 direct, F1 reciprocal, F2 direct, F2 reciprocal, RC1 direct RC1 reciprocal, RC2 direct, RC2 reciprocal), and not between repeats (Box 3). This shows consistence over time in the behavior of the populations. No maternal effects were seen (Box 4). Differences between the means of the populations showed plants resistant to the PepDMV in the variety Cayenne. The F1 generation showed resistance, indicating that the resistance genes possessed by both varieties dominate over the susceptibility.   The populations formed by the parentals Cayenne and Serrano increase resistance to PepDMV (Box 5).

**Cuadro 3.** Cuadrados medios del análisis de varianza para el porcentaje de plantas resistentes a PepDMV en cruces directos y recíprocos de las especies *Capsicum annuum, C. frutescens* y *C. chinense*. (P < para incidencia).

| FV | g.l. | *C. annuum* | g1 | *C. frutescens* | g1 | *C. chinense** | G1 | *C. chinense*** |
|---|---|---|---|---|---|---|---|---|
| Poblaciones | 9 | 0.040 | 9 | <0.0001 | 4 | <0.0001 | 9 | <0.0001 |
| Repeticiones | 2 | 0.571 | 3 | 0.0871 | 1 | 0.002 | 2 | 0.977 |

\* parentales Habanero e introducción 631.

\*\* parentales Habanero e introducción 24.

Box 3. Squared means of the analysis of variance for the percentage of plants resistant to PepDMV in direct and reciprocal crosses in the species, *Capsicum annuum, C. frutescens,* and *C. chinense* (P< for incidence).

**Cuadro 4** Comparación de medias del porcentaje de plantas resistentes a PepDMV entre poblaciones formados por las variedades Cayenne y Serrano.

| Introducción | Mosaico Media | Desv. estándar | Incidencia Media | Desv. estándar |
|---|---|---|---|---|
| Serrano | 1.07 b* | 0.48 | 0.02 b | 0.16 |
| 958 | 1.54 a | 1.15 | 0.18 a | 0.39 |
| F1 (serranox958) | 1.00 b | 0.00 | 0.00 b | 0.00 |
| F1 (958xserrano) | 1.05 b | 0.33 | 0.02 b | 0.16 |
| F2 (serranox958) | 1.23 b | 0.73 | 0.10 ab | 0.30 |
| F2 (958xserrano) | 1.29 ba | 0.86 | 0.10 ab | 0.31 |
| RC1 (serranox958) | 1.08 b | 0.44 | 0.04 b | 0.19 |
| RC1 (958xserrano) | 1.23 b | 0.76 | 0.09 ab | 0.29 |
| RC2 (serranox958) | 1.30 ba | 0.86 | 0.12 ab | 0.32 |
| RC2 (958xserrano) | 1.05 b | 0.22 | 0.05 b | 0.22 |
| Media general | 1.54 | 1.15 | 0.18 | 0.39 |

\* Medias con la misma letra dentro de una misma columna no son significativamente diferentes según la prueba de Duncan al nivel de 5%.

Box 4. Comparison of means of the percentage of plants resistant to PepDMV between populations formed by the varieties Cayenne and Serrano.

**Cuadro 5.** Incidencia de virus PepDMV en cruzamiento de Serrano x Cayenne.

| Población | Frecuencia (n) | Media x | Varianza $D^2$ | Varianza promedio$D^2$/n | Peso $1/(D^2/n)$ |
|---|---|---|---|---|---|
| Cayenne | 53 | 0.188 | 0.156 | 0.0029 | 339.69 |
| Serrano | 39 | 0.025 | 0.025 | 0.0006 | 1521.00 |
| F1 | 58 | 0.017 | 0.017 | 0.0002 | 3363.99 |
| F2 | 487 | 0.108 | 0.097 | 0.0001 | 5011.04 |
| RC958 | 205 | 0.112 | 0.100 | – | 2050.00 |
| RCSerrano | 145 | 0.048 | 0.046 | 0.0003 | 3134.15 |

Box 5. Incidence of the virus PepDMV in the cross Serrano x Cayenne.

It was not possible to determine the number of genes involved in the resistance to PepDMV in the varieties Cayenne and Serrano because the variety Cayenne did not present complete susceptibility in the greenhouse trials. The variety Cayenne is considered by growers as susceptible to the virus. The generational mean analysis showed that in the varieties Serrano and Cayenne the additive effects

were more important compared to dominance (Box 6), and resistance was obtained through the sum of the resistance genes possessed by both varieties.

**Cuadro 6.** Importancia relativa de cada coeficiente para el cruce entre las variedades Cayenne y Serrano.

| Coeficiente | SC secuencial | %total | $R^2$ acumulado |
|---|---|---|---|
| a | 0.01600 | 72.48 | 72.48 |
| d | 0.00417 | 21.28 | 91.36 |
| aa | 0.00172 | 7.78 | 99.16 |

Box 6. Relative importance of each coefficient for the cross Cayenne x Serrano.

The susceptibility of plants produced by the cross Serrano x Cayenne revealed weak plants, with deformed fruits, loss of size and weight, and non-homogeneous red fruit coloration when mature (streaks exist where the coloration is not as intense).

The Serrano variety released by the UNAL in 1997 shows resistance to mites. The resistance shown by this variety to the virus seen in this study, now increases its value as a genotype to be included in improvement programs, as well as a continuing to be a variety in the pepper market.

### *Capsicum frutescens*

The analysis of variance found significant differences between populations and not between repeats (Box 3), nor was the presence of a maternal effect detected (Box 7).

**Cuadro 7.** Comparación de medias del porcentaje de plantas resistentes a PepDMV entre poblaciones formadas por Tabasco e introducción 70.

| introducción | Mosaico | | | Incidencia | | |
|---|---|---|---|---|---|---|
| | Media | Desv. estándar | varianza | Media | Desv. estándar | varianza |
| Tabasco | 4.00 a* | 0 | 0 | 1.00 a | 0.00 | 0 |
| F1 (Tabascox70) | 1.71 b | 1.14 | 1.24 | 0.33 bc | 0.47 | 0.22 |
| F1 (70xTabasco) | 1.27 dc | 0.84 | 0.71 | 0.10 de | 0.30 | 0.09 |
| F2 (Tabascox70) | 1.81 b | 1.20 | 1.44 | 0.34 b | 0.47 | 0.22 |
| F2 (70xTabasco) | 1.78 b | 1.29 | 1.67 | 0.27 bc | 0.44 | 0.20 |
| RC1 (Tabascox70) | 1.18 d | 0.64 | 0.41 | 0.08 de | 0.27 | 0.07 |
| RC1 (70xTabasco) | 1.1 d | 0.59 | 0.35 | 0.04 e | 0.19 | 0.03 |
| RC2 (Tabascox70) | 1.54 cb | 1.11 | 1.23 | 0.20 cd | 0.40 | 0.16 |
| RC2 (70xTabasco) | 1.75 b | 1.19 | 1.41 | 0.32 bc | 0.46 | 0.22 |
| 70 | 1.00 d | 0 | 0 | 0.00 e | 0.00 | 0 |

\* Medias con la misma letra dentro de una misma columna no son significativamente diferentes según la prueba de Duncan al nivel de 5%.

Box 7. Means comparisons of the percentage of plants resistant to PepDMV between populations formed by Tabasco and introduction 70.

The separation of means by the Duncan test (Box 7) shows that the introduction 70 carries genes for resistance that mask the effect of the susceptibility genes , populations crossed with introduction 70 considerably increase the number of resistant plants (Box 8). The additive effects are important in increasing the resistance towards the commercial variety Tabasco (Box 9).

**Cuadro 8.** Incidencia de virus PepDMV en cruzamiento de Tabasco e Introducción 70.

| Población | Frecuencia (n) | Media | Varianza $D^2$ | Varianza promedio ($D^2/n$) | Peso $1/(D^2/n)$ |
|---|---|---|---|---|---|
| Introducción70 | 85 | 0 | 0 | 0 | 0 |
| Tabasco | 111 | 1 | 0 | 0 | 0 |
| F1 | 105 | 0.2285 | 0.178 | 0.0016 | 589.81 |
| F2 | 752 | 0.3138 | 0.215 | 0.0002 | 3487.49 |
| RCTabasco | 158 | 0.0632 | 0.059 | 0.0003 | 2648.20 |
| RC70 | 169 | 0.2662 | 0.196 | 0.0016 | 859.90 |

Box 8. Incidence of the virus PepDMV in crosses between Tabasco and the Introduction 70.

**Cuadro 9.** Importancia relativa de cada coeficiente para el cruce entre las variedades Tabasco e introducción 70@

| Coeficiente | SC secuencial | % SC total | $R^2$ acumulado |
|---|---|---|---|
| a | 53.031 | 48.95 | 48.95 |
| d | 0.187 | 0.17 | 49.12 |
| aa | 55.12 | 50.88 | 100 |

Box 9. Relative importance of each coefficient for the cross between the varieties Tabasco and the introduction 70.

The importance of the additive effects for increasing resistance was greater than that of dominance. The model that best explained the expression of resistance is based on additive effects (Box 9). This indicates that the selection to increase resistance levels in PepDMV could be predicted based on the behavior of the parental lines involved in the cross.

*Capsicum chinense*

**Cross Habanero - Introduction 631**

The cross between the commercial chili variety habanero with the introduction 631 presented difficulties at the point of obtaining the seed product in the cross between the F1 and the parental 631.  Thus the backcrosses towards the resistant

parent were not included in the study, and so the estimation od the additive and dominance effects through the regression method were not calculated.

The cross between habanero and the introduction 631 showed differences between populations (Box 3). A maternal effect is suggested, when the resistant introduction 631 acts as the mother, the generation F1 of the direct cross is different to the reciprocal f1 cross. The resistance increases when the introduction 631 acts as a mother (Box 10).

**Cuadro 10** Comparación de medias del porcentaje de plantas resistentes a PepDMV entre poblaciones formadas por Habanero e Introducción 631.

| Introducción | Incidencia | |
|---|---|---|
| | Media | Desv. estándar |
| RC1 (Habanerox631) | 0.82 a* | 0.39 |
| Habanero | 0.60 b | 0.49 |
| F1 (Habanerox631) | 0.60 b | 0.49 |
| F2 (Habanerox631) | 0.53 bc | 0.49 |
| F2 (631xHabanero) | 0.48 bc | 0.50 |
| F1 (631xHabanero) | 0.39 c | 0.49 |
| 631 | 0.00 d | 0.00 |

\* Medias con la misma letra dentro de una misma columna no son significativamente diferentes según la prueba de Duncan al nivel de 5%

Box 10. Means comparison of the percentage of plants resistant to PepDMV between populations formed from Habanero and the introduction 631.

## Cross Habanero - Introduction 24

The cross between material of *C. chinense* showed significant differences between populations, but not between repeats (Box 3). This shows that in the direct and reciprocal crosses there are no maternal effects (Box 11). The analysis of variance showed that the segregating populations tended towards susceptibility. The displacement of the F1 population towards the susceptible material shows that the resistance genes are not dominant over those for susceptibility (Box 12). The additive effects are important, but the dominance effects affect the expression of resistance (Box 13).

**Cuadro 11.** Comparación de medias del porcentaje de plantas resistentes a PepDMV entre poblaciones formados por Habanero e Introducción 24.

| introducción | Incidencia | |
|---|---|---|
| | Media | Desv. estándar |
| RC959 | 0.9625 a[*] | 0.19 |
| F1 | 0.9062 a | 0.23 |
| 959 | 0.9062 a | 0.29 |
| RC24 | 0.6419 b | 0.48 |
| F2 | 0.8314 b | 0.37 |
| 24 | 0.0000 c | 0.00 |

* Medias con la misma letra dentro de una misma columna no son significativamente diferentes según la prueba de Duncan al nivel de 5%

Box 11. Means comparison of the percentage of plants resistant to PepDMV between populations formed by Habanero and Introduction 24.

**Cuadro 12.** Incidencia de virus PepDMV en cruzamiento de Habanero e introducción 24.

| Población | Frecuencia (n) | Media | Varianza $(D^2)$ | Varianza prom. $(D^2/n)$ | Peso $(1/(D^2/n))$ |
|---|---|---|---|---|---|
| 24 | 33 | 0 | 0 | 0 | 0 |
| Habanero | 32 | 0.906 | 0.087 | 0.0027 | 370.37 |
| F1 | 36 | 0.944 | 0.053 | 0.0014 | 714.28 |
| F2 | 439 | 0.831 | 0.140 | 0.0003 | 3333.33 |
| RC24 | 81 | 0.641 | 0.232 | 0.0028 | 357.14 |
| RC Habanero | 80 | 0.962 | 0.036 | 0.0004 | 2500.00 |

Box 12. Incidence of the PepDMV virus in the cross Habanero x Introduction 24.

**Cuadro 13.** Importancia relativa de cada coeficiente para el cruce entre las variedades Habanero e Introducción 24.

| Coeficiente | SC secuencial | % SC total | R2 acumulado |
|---|---|---|---|
| a | 26.59 | 58.8 | 58.87 |
| d | 16.56 | 36.6 | 95.53 |
| aa | 1.99 | 4.4 | 99.95 |

Box 13. Relative importance of each coefficient for the cross between the varieties Habanero and Introduction 24.

According to this, we can say that the resistance to PepDMV is only given by certain genotypes that express resistance under a certain number of genes that have an additive effect, highly heritable from generation to generation. There are genotypes were the effect of dominance is seen together with additive effects. In

the introductions Cayenne and Serrano, and the introduction 70, the resistance is given by genes with additive effects, in contrast to the introductions 24 and 631, where the genes for resistance in both materials result from dominance effects, possibly given by the Habanero variety. The commercial material, Cayenne, Tabasco and Habanero are not completely susceptible to PepDMV. The lines must be purified in order to increase the levels of resistance.

The result that the variation observed in the generational means in the evaluated crosses was explained by the additive-dominance model, with the additive effect being the most important, suggests that in a breeding program for resistance to PepDMV, methods that accumulate these genes should be used: using resistant parentals in order to obtain the populations subjected to selection, as selection to increase resistance can be predicted on the basis of behavior in the parental lines, as they show a significant additive effect.

## Conclusions

- The resistance of *Capsicum* to the virus PepDMV was seen only in some genotypes that expressed resistance in a number of genes with additive effect, being highly heritable across generations. The dominance effects act together with the additive effects.
- In the varieties Cayenne, Serrano and the accession 70 the resistance was given by genes with additive effect, in contrast to the accessions 24 and 631, where the resistance is given by dominance effects with the variety Habanero.
- The commercial varieties of chili Cayenne, Tabasco and Habanero are not completely susceptible to PepDMV. The lines should be purified in order to increase observed levels of resistance.
- By explaining resistance to PepDMV with an additive-dominance model, with significant additive effects, the prediction of viral resistance gain can be based on the behavior of the parental lines involved in the improvement method.

## Acknowledgements

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