Study of inbreeding in tomatillo (Physalis ixocarpa Brot. ex Horm.)

Estudio de la endogamia en tomate de cáscara (Physalis ixocarpa Brot. ex Horm.)

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Abstract

Only intervarietal and interfamilial hybridization can be carried out in tomatillo. Therefore, the objective was to study the effect of inbreeding in families of four varieties of tomatillo obtained through three generations of mating by fraternal and plant-to-plant crosses. The varieties studied were Tecozautla, Diamante, Manzano and Morado, each represented by three maternal half-sib families (Generation 1). In 2018, plant-to-plant and fraternal crosses were made in selected plants within each family, resulting in full-sib (FSF) and maternal half-sib (MHSF) families, respectively (Generation 2). In 2019, the process was repeated in Generation 2 families, and another generation of FSFs and MHSFs (Generation 3) was obtained. Field evaluation was conducted in 2020. A randomized complete block design with four replications was used, and yield per plant was evaluated in two harvests and total yield per plant, as well as fruit weight, volume and bulk density, in each harvest and average of harvests. Inbreeding depression occurred among generations. Fruit yield, size and volume in the first harvest decreased over generations. The Tecozautla and Diamante varieties showed greater inbreeding depression. The type of cross had a different effect depending on the variety. Fruit size was lower in plant-to-plant crosses in Tecozautla, Diamante and Morado; that is, they generated greater inbreeding depression than the fraternal crosses.

Keywords: inbreeding depression, mating systems, half-sib families, full-sib families.

Resumen

En tomate de cáscara sólo se puede hacer hibridación intervarietal e interfamilial. Por ello, el objetivo fue estudiar el efecto de la endogamia en familias de cuatro variedades de tomate de cáscara obtenidas a través de tres generaciones de apareamiento por cruzas fraternales y planta a planta. Las variedades estudiadas fueron Tecozautla, Diamante, Manzano y Morado, cada una representada por tres familias de medios hermanos maternos (Generación 1). En 2018 se realizaron cruzas planta a planta y fraternales en plantas seleccionadas dentro de cada familia, lo que dio origen a familias de hermanos completos (FHC) y medios hermanos maternos (FMHM), respectivamente (Generación 2). En 2019, el proceso se repitió en las familias de la Generación 2, y se obtuvo otra generación de FHC y FMHM (Generación 3). La evaluación en campo se realizó en 2020. Se usó un diseño de bloques completos al azar con cuatro repeticiones, y se evaluó el rendimiento por planta en dos cortes y total, así como el peso, el volumen y la densidad aparente de frutos, en cada corte y promedio de cortes. Se presentó depresión endogámica entre generaciones. El rendimiento, el tamaño y el volumen de fruto en el primer corte disminuyó con el paso de las generaciones. Las variedades Tecozautla y Diamante presentaron mayor depresión endogámica. El tipo de cruza tuvo un efecto diferente en función de la variedad. El tamaño de fruto fue inferior en cruzas planta a planta en Tecozautla, Diamante y Morado; es decir, generaron mayor depresión endogámica que las cruzas fraternales.

Keywords: depresión endogámica, sistemas de apareamiento, familias de medios hermanos, familias de hermanos completos.

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**Introduction**

In 2019, tomatillo was grown in 30 states of the Mexican Republic (Sistema de Información Agroalimentaria y Pesquera [SIAP], 2021), where it is cultivated with everything from the traditional rainfed system with direct sowing to fertigation with mulching and trellising. In the spring-summer and autumn-winter cycles, it is grown in both irrigated and rainfed systems, so the product is available in the market all year round (Peña-Lomelí, Santiaguillo-Hernández, & Magaña-Lira, 2007).

Most farmers use seed that they get from their crops. In some parts of the country, farmers use commercial varieties obtained from the multiplication of outstanding landrace materials, but which have not undergone a robust breeding program (Magaña-Lira, Santiaguillo-Hernández, & Grimaldo-Juárez, 2011), and aspects such as identity, genetic purity, and quality (physical, physiological, sanitary and genetic), among other agronomic attributes, cannot be guaranteed. Therefore, it is important to produce certified seed of improved and registered varieties in order to give certainty to the producer of the quality of the seed and improve crop productivity (Santiaguillo-Hernández et al., 2012).

Tomatillo has gametophytic self-incompatibility determined by two independent genes with multiple alleles (Mulato-Brito, Peña-Lomeli, Sahagún-Castellanos, Villanueva-Verduzco, & Lópe-Reynoso, 2007; Pandey, 1957), which is why it is not possible to form highly inbred lines or hybrids with classical techniques. Consequently, its genetic improvement is based on selection (Peña-Lomelí & Márquez-Sánchez, 1990).

Inbreeding is the mating of individuals that are related to each other by ancestry. The essential consequence of two individuals having a common ancestor is that both of them may carry replicates of one of the genes present in the ancestor and, if they mate, they can inherit it. The most notable effect of inbreeding is loss of vigor or inbreeding depression, characterized by a reduction in the phenotypic value shown by traits related to reproductive ability or physiological efficiency (Falconer & Mackay, 1996).

Heterosis occurs in crosses of inbred lines and in intervarietal crosses, as in the case of tomatillo (Sahagún-Castellanos, Gómez-Ruiz, & Peña-Lomeli, 1999). Peña-Lomeli et al. (1998) worked with eight varieties analyzed in a diallelic and found that the mean heterosis was significant for total yield (17.19 %) and number of fruits per plant (10.42 %), so it would be possible to obtain hybrids with better traits than the varieties. Santiaguillo-Hernández, Cervantes-Santana, Peña-Lomelí et al. (1998) worked with eight varieties analyzed in a diallelic and found that the mean heterosis was significant for total yield (17.19 %) and number of fruits per plant (10.42 %), so it would be possible to obtain hybrids with better traits than the varieties. Santiaguillo-Hernández, Cervantes-Santana, & Peña-Lomelí, 1998).

**Introducción**

En 2019, el tomate de cáscara se cultivó en 30 estados de la República Mexicana (Sistema de Información Agroalimentaria y Pesquera [SIAP], 2021); en donde se puede encontrar desde el sistema tradicional con siembra directa en temporal, hasta el fertirriego con acolchado y espaldera. En los ciclos primavera-verano y otoño-invierno, se cultiva tanto en riego como en temporal, por lo que el producto está disponible en el mercado todo el año (Peña-Lomelí, Santiaguillo-Hernández, & Magaña-Lira, 2007).

La mayoría de los agricultores utilizan semilla que ellos obtienen de sus cultivos. En algunas partes del país se utilizan variedades comerciales obtenidas de la multiplicación de materiales criollos sobresalientes, pero que no han pasado por un robusto programa de mejoramiento (Magaña-Lira, Santiaguillo-Hernández, & Grimaldo-Juárez, 2011), y no se pueden garantizar aspectos como identidad, pureza genética, calidad (física, fisiológica, sanitaria y genética), entre otros atributos agronómicos. Por lo anterior, es importante producir semilla certificada de variedades mejoradas y registradas, para dar certeza al productor de la calidad de la semilla y mejorar la productividad del cultivo (Santiaguillo-Hernández et al., 2012).

El tomate de cáscara presenta autoincompatibilidad gametofítica determinada por dos genes independientes con alelos múltiples (Mulato-Brito, Peña-Lomeli, Sahagún-Castellanos, Villanueva-Verduzco, & López-Reynoso, 2007; Pandey, 1957), razón por la cual no es posible formar líneas altamente endogámicas ni híbridos con las técnicas clásicas. En consecuencia, su mejoramiento genético está basado en la selección (Peña-Lomelí & Márquez-Sánchez, 1990).

La endogamia es el apareamiento de individuos que están relacionados entre sí por ascendencia. La consecuencia esencial de que dos individuos tengan un ancestro común es que ambos pueden portar réplicas de uno de los genes presentes en el ancestro y, si se aparean, puedan heredarlo. El efecto más notable de la endogamia es la pérdida de vigor o depresión endogámica, caracterizada por la reducción del valor fenotípico que muestran los caracteres relacionados con la capacidad reproductiva o con la eficiencia fisiológica (Falconer & Mackay, 1996).

La heterosis se presenta en cruzas de líneas endogámicas y en cruzas intervarietales, como en tomate de cáscara (Sahagún-Castellanos, Gómez-Ruiz, & Peña-Lomeli, 1999). Peña-Lomeli et al. (1998) trabajaron con ocho variedades analizadas en un dialélico y encontraron que la heterosis media fue significativa para rendimiento total (17.19 %) y número de frutos...
and Peña-Lomelí (2004) found significant positive average heterosis for total yield per plant (21.4 %) in plant-to-plant crosses between Verde Puebla and CHF1 Chapingo varieties, although in fruit quality traits the average heterosis was negative.

Peña-Lomelí et al. (1999) point out that it is possible to obtain hybrids from crosses between maternal half-sib families (MHSF), and Santiaguillo-Hernández et al. (2004) note that they can also be obtained by plant-to-plant crosses. However, maintaining the stability of families through seed-increasing cycles can be a problem due to the small number of individuals, which can generate inbreeding depression. One way to conserve the genotype of families or progenitor plants of hybrids is in vitro multiplication (Andrade-Rodríguez, López-Peralta, González-Hernández, García-Velázquez, & Peña-Lomelí, 2005), although the complete protocol for mass propagation is not yet available.

Therefore, the objective of this work was to study the effect of inbreeding in families of four varieties of tomatillo obtained through three generations of mating by fraternal and plant-to-plant crosses.

**Materials and methods**

The tomatillo varieties evaluated were Tecozautla, Diamante, Manzano and Morado San Miguel (Servicio Nacional de Inspección y Certificación de Semillas [SNICS], 2021). In each one, three MHSFs obtained from six seed-increasing cycles by fraternal crosses (Generation 1) were studied.

In the autumn-winter 2018-2019 cycle, 114 plants of each family (12 in total) were established in a hydroponic greenhouse system. The five best plants of each family were selected using the criteria of height, vigor and number of flowers at 15 days after transplantation (dat). Plant-to-plant and fraternal crosses were made in the selected plants using the controlled pollination technique described by Peña-Lomelí, Magaña-Lira, Gámez-Torres, Mendoza-Celino, and Pérez-Grajales (2018).

The plant-to-plant crosses were made in a chain. The first plant was crossed as a male with the second, this with the third and so on, and the fifth plant was crossed as a male with the first. For the fraternal crosses, pollen from the five plants was placed in a Petri dish and mixed, and then each plant was pollinated. In plant-to-plant and fraternal crosses, each selected plant gave rise to a full-sib family (FSF) and a MHSF, respectively (Generation 2).

In the fall-winter 2019-2020 cycle, families resulting from Generation 2 were established in a hydroponic greenhouse system. The five best plants of each family (12 in total) were established in a hydroponic greenhouse system. The five best plants of each family were selected using the criteria of height, vigor and number of flowers at 15 days after transplantation (dat). Plant-to-plant and fraternal crosses were made in the selected plants using the controlled pollination technique described by Peña-Lomelí, Magaña-Lira, Gámez-Torres, Mendoza-Celino, and Pérez-Grajales (2018).

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greenhouse system. As some crosses did not produce enough seed, plants from families having both FSFs and MHSFs were chosen. Therefore, five plants within each family were selected. In the previous cycle, both types of crosses were made for each plant, and in the new selection cycle only one type of cross was made per plant, which depended on its origin. If the plant came from a FSF, plant-to-plant crosses were made; if it came from a MHSF, fraternal crosses were made. This gave rise to new FSFs and MHSFs (Generation 3). For field evaluation, all the families obtained were used.

In the spring-summer cycle of 2020, the field evaluation was made of those families obtained in both selection-cross cycles in the greenhouse and that had enough seed, plus the original families (that came from the six seed-increasing cycles by fraternal crosses); this gave rise to 82 families (Generations 1, 2 and 3). Sowing was done on February 29, and 200-cavity polystyrene trays with peat moss as substrate were used. One to two seeds were placed per cavity depending on their availability. Seedlings were kept under greenhouse conditions and watered every other day with 50 % Steiner’s nutrient solution for three weeks; thereafter, they were irrigated daily with 100 % Steiner’s nutrient solution (Steiner, 1984). Fifteen days after sowing, one plant per cavity was thinned.

The evaluation was established in lot 10-C (19° 27’ 60” N and 98° 54’ 19” W) of the experimental field of the Colegio de Postgraduados, Montecillo campus, State of Mexico. The land was prepared with fallowing and harrowing; the furrowing was done at 1 m apart. Transplanting was carried out on April 16 with 30 cm spacing between plants. A randomized complete block design with four replications was established. Each experimental unit consisted of a 4.2 m furrow (15 plants). Irrigation was carried out weekly using siphons and fertilization was done with 200 N – 100 P₂O₅ – 50 K₂O. The first fertilization was made one week after transplantation: half the urea and all the diammonium phosphate and potassium chloride were applied. The second fertilization was performed 28 dat and the rest of the urea was applied. In addition to weekly applications of foliar fertilizer (Bayfolan Forte® + surfactant), preventive sprayings for pests and diseases (Confidor® [Imidacloprid] and Lannate® [Methomyl]) were carried out. Weeds were controlled with three hoeing and two weeding operations, and 112.5 g·ha⁻¹ of Provence 75 WG® (Isoxaflutole) were applied after earthing up.

At 40 dat, data were taken on plant height and number of bags formed (set fruits). Height (PH, cm) was taken from ground level to the tip of the highest branch. For the number of bags (NB), calyces with fruit development were counted. For both variables, the mean per experimental unit was obtained.
Harvesting was carried out in two harvests: June 30 and July 10. In both, yield per plant (YP1 and YP2, kg) and total yield per plant (YP, kg) were evaluated; in addition, 10 fruits were weighed at random (W10F1 and W10F2, g) and only in the first harvest was the volume (V1, mL) measured. From the weight and volume of 10 fruits, the bulk density of fruits in the first harvest (D1, g·mL−1) was estimated, which in turn was used to estimate the volume in the second harvest (V2, mL). The average weight and volume of the 10 fruits (AW10F and AV, respectively) were also obtained. The weight of 10 fruits was considered as an estimator of their size (very large, large and medium fruit) (Peña-Lomeli, Ponce-Valerio, Sánchez-del Castillo, & Magaña-Lira, 2014).

The analysis of variance was performed according to the following model: \( Y_{ijl} = \mu + \beta_i + V_j + C_{ik} + GC_{ijk} + \varepsilon_{ijkl} \), where \( Y_{ijl} \) is the observed value of the variable \( Y \), \( \mu \) is the overall mean, \( \beta_i \) is the effect of block \( i \), \( V_j \) is the effect of variety \( j \), \( C_{ik} \) is the effect of generation \( k \) nested in variety \( i \), \( GC_{ijk} \) is the effect of the type of cross \( k \) nested in variety \( i \), \( \varepsilon_{ijkl} \) is the generation \( x \) cross interaction nested in variety \( i \) and \( \varepsilon_{ijkl} \) is the random error. Mean comparison tests (Tukey, \( P \leq 0.05 \)) were performed between varieties, between generations for each variety and between crosses for each variety.

Results and discussion

The analysis of variance (Table 1) shows that Variety had a highly significant effect (\( P \leq 0.01 \)) on all variables. This indicates different behaviors among varieties, which is related to the distinctive traits of each one of them, such as fruit size and yield per plant. The effect of the Generation nested in Variety factor was not significant in YP2 and D1; in PH and V2 the effect was significant (\( P \leq 0.05 \)), and in the rest of the variables it was highly significant (\( P \leq 0.01 \)). This may indicate inbreeding depression across generations in at least one of the varieties studied. The Cross nested in Variety factor had no significant effect on YP2 and D1, but it was significant (\( P \leq 0.05 \)) for PH, W10F2, V1 and V2; the effects were highly significant (\( P \leq 0.01 \)) for the rest of the variables. This implies that, at least for one variety, the type of cross produces a different effect. The Generation \( x \) Cross interaction was not significant.

The Manzano variety had the greatest PH, while the others did not differ statistically from each other (\( P \geq 0.05 \)). Diamante had the highest NB, followed by Morado, Tecozautla and Manzano. In YP1 and TYP, Diamante was superior, although in the second harvest it was not different from Morado. D1 was no different in Diamante, Manzano and Morado, but all three were superior to Tecozautla. In W10F1 and AW10F, Tecozautla was superior, but in W10F2 it was not different from Diamante. Regarding the volume variables, Tecozautla was superior in all three (Table 2). A to the 40 ddt, se tomaron datos de altura de planta y número de bolsas formadas (frutos amarrados). La altura (ALT, cm) se tomó del nivel del suelo a la punta de la rama más alta. Para el número de bolsas (BOL), se contaron los cálices con desarrollo de fruto. En ambas variables se obtuvo la media por unidad experimental.

La cosecha se efectuó en dos cortes: 30 de junio y 10 de julio. En ambos se evaluó el rendimiento por planta (RPC1 y RPC2, kg) y el rendimiento total por planta (RTP, kg); además, se pesaron 10 frutos al azar (P10FC1 y P10FC2, g) y solamente en el primer corte se midió el volumen (V1, mL). A partir del peso y el volumen de 10 frutos se estimó la densidad aparente de frutos en el primer corte (D1, g·mL−1), que a su vez sirvió para estimar el volumen en el segundo corte (V2, mL). También se obtuvo el peso y el volumen promedio de los 10 frutos (PP10F y VP, respectivamente). El peso de 10 frutos se consideró como un estimador de su tamaño (fruto muy grande, grande y mediano) (Peña-Lomeli, Ponce-Valerio, Sánchez-del Castillo, & Magaña-Lira, 2014).

El análisis de varianza se realizó según el siguiente modelo: \( Y_{ijl} = \mu + \beta_i + V_j + C_{ik} + GC_{ijk} + \varepsilon_{ijkl} \), donde \( Y_{ijl} \) es el valor observado de la variable \( Y \), \( \mu \) es la media general, \( \beta_i \) es el efecto del bloque \( i \), \( V_j \) es el efecto de la variedad \( j \), \( C_{ik} \) es el efecto de la generación \( k \) anidado en la variedad \( i \), \( GC_{ijk} \) es el efecto del tipo de cruza \( k \) anidado en la variedad \( i \), \( \varepsilon_{ijkl} \) es la interacción generación \( x \) cruzan anidada en la variedad \( i \) y \( \varepsilon_{ijkl} \) es el error aleatorio. Se hicieron pruebas de comparación de medias (Tukey, \( P \leq 0.05 \)) entre variedades, entre generaciones para cada variedad y entre cruzas para cada variedad.

Resultados y discusión

El análisis de varianza (Cuadro 1) muestra que Variedad tuvo un efecto altamente significativo (\( P \leq 0.01 \)) sobre todas las variables. Esto indica comportamientos diferentes entre variedades, lo cual está relacionado con las características distintivas de cada una de ellas, como el tamaño de fruto y el rendimiento por planta. El efecto del factor Generación anidado en Variedad no fue significativo en RPC2 y D1; en ALT y V2 el efecto fue significativo (\( P \leq 0.05 \)), y en el resto de las variables fue altamente significativo (\( P \leq 0.01 \)). Lo anterior puede indicar depresión endogámica a través de generaciones en al menos una de las variedades estudiadas. El factor Cruza anidado en Variedad no tuvo efecto significativo sobre RPC2 y D1, pero lo tuvo (\( P \leq 0.05 \)) para ALT, P10FC2, V1 y V2; los efectos fueron altamente significativos (\( P \leq 0.01 \)) para el resto de las variables. Esto implica que, al menos para una variedad, el tipo de cruz produce un efecto diferente. La interacción Generación \( x \) Cruza no fue significativa.

La variedad Manzano fue la de mayor ALT, mientras que las otras no difirieron estadísticamente entre sí
### Table 1. Mean squares of the analysis of variance for twelve variables evaluated in four varieties of tomatillo (Physalis ixocarpa Brot. ex Horgm.).

| Source / Fuente | DF/GL | PH / ALT | NB / BOL | YP1 / RPC1 | YP2 / RPC2 | TYP / RTP | D1 |
|-----------------|-------|----------|----------|------------|------------|------------|-----|
| Block / Bloque  |       | 12.10**  | 25.60**  | 11.67**    | 10.20**    | 1.926      | 1.97* |
| V               | 3     | 0.90**   | 0.91**   | 0.92**     | 0.91**     | 1.168      | 1.16**|
| G(V)            | 7     | 0.90**   | 0.91**   | 0.92**     | 0.91**     | 1.168      | 1.16**|
| C(V)            | 4     | 0.90**   | 0.91**   | 0.92**     | 0.91**     | 1.168      | 1.16**|
| GxG(V)          | 2     | 0.90**   | 0.91**   | 0.92**     | 0.91**     | 1.168      | 1.16**|
| Error           | 327   | 0.90**   | 0.91**   | 0.92**     | 0.91**     | 1.168      | 1.16**|
| Total           | 330   | 0.90**   | 0.91**   | 0.92**     | 0.91**     | 1.168      | 1.16**|

### Table 2. Comparison of means among four varieties of tomatillo (Physalis ixocarpa Brot. ex Horgm.).

| Variety / Variedad | PH / ALT | NB / BOL | YP1 / RPC1 | YP2 / RPC2 | TYP / RTP | D1 |
|--------------------|----------|----------|------------|------------|------------|-----|
| Tecozautla         | 25.63 b  | 6.65 c   | 0.610 b    | 0.137 b    | 0.747 bc   | 0.832 b  |
| Diamante           | 24.38 b  | 11.11 a  | 0.841 a    | 0.227 a    | 1.068 a    | 0.964 a  |
| Manzano            | 30.46 a  | 5.08 d   | 0.598 b    | 0.125 b    | 0.723 c    | 0.935 a  |
| Morado             | 23.77 b  | 7.92 b   | 0.658 b    | 0.210 a    | 0.868 b    | 0.949 a  |

### Notes:

Source = source of variation; V = variety; G(V) = generation nested in variety; C(V) = type of cross nested in variety; GxG(V) = generation x type of cross interaction, nested in variety; CV = coefficient of variation; DF = degrees of freedom; PH = plant height (cm); NB = number of bags; YP1 and YP2 = yield per plant in harvest 1 and 2, respectively (kg); TYP = total yield per plant (kg); D1 = density of 10 fruits in harvest 1 (g mL⁻¹); W10F1 and W10F2 = weight of 10 fruits in harvest 1 and 2, respectively (g); AV10F = average weight of 10 fruits (g); V1 and V2 = volume of 10 fruits in harvest 1 and 2, respectively (mL); AV = average volume of 10 fruits (mL); "*" y "**" = significant with P ≤ 0.01 and P ≤ 0.05, respectively.

Fuentes = Fuente de variación; V = variedad; G(V) = generación anidada en variedad; C(V) = tipo de cruz anidado en variedad; GxG(V) = interacción generación x tipo de cruz, anidada en variedad; CV = coeficiente de variación; GL = grados de libertad; ALT = altura de planta (cm); BOL = número de bolsas; RPC1 y RPC2 = rendimiento por planta en el corte 1 y 2, respectivamente (kg); RTP = rendimiento total por planta (kg); D1 = densidad de 10 frutos en el corte 1 (g mL⁻¹); P10FC1 y P10FC2 = peso de 10 frutos en el corte 1 y 2, respectivamente (g); PP10F = peso promedio de 10 frutos (g); V1 y V2 = volumen de 10 frutos en el corte 1 y 2, respectivamente (mL); VP = volumen promedio de 10 frutos (mL); "*" y "**" = significativo con P ≤ 0.01 y P ≤ 0.05, respectivamente.

Means with the same letter within each column do not differ statistically (Tukey, P ≤ 0.05).

ALT = altura de planta (cm); BOL = número de bolsas; RPC1 y RPC2 = rendimiento por planta en el corte 1 y 2, respectivamente (kg); RTP = rendimiento total por planta (kg); D1 = densidad de 10 frutos en el corte 1 (g mL⁻¹); W10F1 y W10F2 = peso de 10 frutos en el corte 1 y 2, respectivamente (g); AV10F = peso promedio del 10 frutos (g); V1 y V2 = volumen de 10 frutos en el corte 1 y 2, respectivamente (mL); VP = volumen promedio de 10 frutos (mL); "*" y "**" = significativo con P ≤ 0.01 y P ≤ 0.05, respectivamente.

Means with the same letter within each column do not differ statistically (Tukey, P ≤ 0.05).

ALT = altura de planta (cm); BOL = número de bolsas; RPC1 y RPC2 = rendimiento por planta en el corte 1 y 2, respectivamente (kg); RTP = rendimiento total por planta (kg); D1 = densidad de 10 frutos en el corte 1 (g mL⁻¹); W10F1 y W10F2 = peso de 10 frutos en el corte 1 y 2, respectivamente (g); PP10F = peso promedio del 10 frutos (g); V1 y V2 = volumen de 10 frutos en el corte 1 y 2, respectivamente (mL); VP = volumen promedio de 10 frutos (mL); "*" y "**" = significativo con P ≤ 0.01 y P ≤ 0.05, respectivamente.

Means with the same letter within each column do not differ statistically (Tukey, P ≤ 0.05).

ALT = altura de planta (cm); BOL = número de bolsas; RPC1 y RPC2 = rendimiento por planta en el corte 1 y 2, respectivamente (kg); RTP = rendimiento total por planta (kg); D1 = densidad de 10 frutos en el corte 1 (g mL⁻¹); W10F1 y W10F2 = peso de 10 frutos en el corte 1 y 2, respectivamente (g); PP10F = peso promedio del 10 frutos (g); V1 y V2 = volumen de 10 frutos en el corte 1 y 2, respectivamente (mL); VP = volumen promedio de 10 frutos (mL); "*" y "**" = significativo con P ≤ 0.01 y P ≤ 0.05, respectivamente.

Means with the same letter within each column do not differ statistically (Tukey, P ≤ 0.05).
Tecozautla was the variety with the largest fruit, but with the lowest density. Diamante had the highest earliness and yield. The growth habit in Manzano was more erect than in the others. Morado was the variety with the smallest fruits. The foregoing coincides with what was reported by Sánchez-Martínez and Peña-Lomelí (2015) regarding the distinguishing traits of these varieties.

**PH** was only different among generations for the Manzano variety, where Generation 2 had the highest value (Figure 1a). Generation 1 of the Diamante variety had fewer bags than Generations 2 and 3, which were not different from each other. In the rest of the varieties, no differences in NB were found (Figure 1b). YP1 and YP2 were not different between Generations 1 and 2 in all varieties, but in Tecozautla and Diamante a significantly lower yield was obtained in Generation 3 (Figures 1c and 1e). According to Márquez-Sánchez (2007), decreased yield is a measurable indicator of inbreeding depression. YP2 and D1 were not different among generations for any variety (Figures 1d and 1f).

In Tecozautla and Diamante, Generation 1 was superior in W10F1, W10F2, AW10F, V1, V2 and AV. Similarly, Generations 2 and 3 were not different from each other in Diamante (Figure 2). It should be remembered that there was not enough seed from Tecozautla’s Generation 2 for field evaluation. In Manzano, a decrease was only observed in W10F1 and V1 (Figures 2a and 2d), where Generation 1 was significantly superior to Generations 2 and 3, between which there were no significant differences. For the rest of the variables, no differences were found among generations. The Morado variety did not show significant differences among generations for any variable (Figures 1d and 1f).

In summary, the comparison of means indicates that fruit yield, size and volume decreased in Tecozautla and Diamante across generations. Yield decreased after the second generation, while size and volume did so after the first generation. In Manzano only fruit size and volume in the first harvest were affected, in both cases after Generation 1. This is an indicator of inbreeding depression, as pointed out by Márquez-Sánchez (2007). Based on the above, it can be said that inbreeding depression had a greater effect on the Tecozautla and Diamante varieties, which may be due to their initial level of inbreeding. Both have more selection cycles than Manzano and Morado (Peña-Lomelí et al., 2018; Sánchez-Martínez & Peña-Lomelí, 2015), so it is inferred that there is more inbreeding in Tecozautla and Diamante.

**PH** was only different between cross types in Manzano, where families obtained by plant-to-plant crosses were superior (Figure 3a). NB and YPC1 were different in Morado, with families obtained from fraternal crosses (\( P \geq 0.05 \)). Diamante tuvo el mayor número de BOL, seguida de Morado, Tecozautla y Manzano. En el RPC1 y el RTP Diamante fue superior, aunque en el segundo corte no fue diferente de Morado. La D1 no fue diferente entre Diamante, Manzano y Morado, pero las tres fueron superiores a Tecozautla. En el P10FC1 y el PP10F Tecozautla fue superior, pero en el P10FC2 no fue diferente de Diamante. Con respecto a las variables de volumen, Tecozautla fue superior en las tres (Cuadro 2).

Tecozautla fue la variedad con frutos más grandes, pero con menor densidad. Diamante fue la de mayor precocidad y rendimiento. El hábito de crecimiento en Manzano fue más erecto que en las otras. Morado fue la variedad con los frutos de menor tamaño. Lo anterior coincide con lo reportado por Sánchez-Martínez y Peña-Lomelí (2015) respecto a las características distintivas de dichas variedades.

La ALT sólo fue diferente entre generaciones para la variedad Manzano, donde la Generación 2 presentó el valor más alto (Figura 1a). La Generación 1 de la variedad Diamante presentó menor número de BOL que las Generaciones 2 y 3, las cuales no fueron diferentes entre sí. En el resto de las variedades, no se encontraron diferencias en BOL (Figura 1b). El RPC1 y el RTP no fueron diferentes entre las Generaciones 1 y 2 en todas las variedades, pero en Tecozautla y Diamante se obtuvo un rendimiento significativamente menor en la Generación 3 (Figuras 1c y 1e). De acuerdo con Márquez-Sánchez (2007), la disminución en el rendimiento es un indicador medible de la depresión endogámica. El RPC2 y la D1 no fueron diferentes entre generaciones para ninguna variedad (Figuras 1d y 1f).

En Tecozautla y Diamante, la Generación 1 fue superior en P10FC1, P10FC2, PP10F, V1, V2 y VP. De igual manera, las Generaciones 2 y 3 no fueron diferentes entre sí en Diamante (Figura 2). Cabe recordar que no se contó con semilla suficiente de la Generación 2 de Tecozautla para la evaluación en campo. En Manzano, únicamente se observó disminución en el P10FC1 y el V1 (Figuras 2a y 2d), donde la Generación 1 fue significativamente superior a las Generaciones 2 y 3, entre las cuales no hubo diferencias significativas. En el resto de las variables, no se encontraron diferencias entre generaciones. La variedad Morado no presentó diferencias significativas entre generaciones para ninguna variable (Figuras 1 y 2).

En resumen, la comparación de medias indica que el rendimiento, el tamaño y el volumen de fruto disminuyeron en Tecozautla y Diamante con el paso de las generaciones. El rendimiento disminuyó después de la segunda generación, mientras que el tamaño y el volumen lo hicieron después de la primera. En Manzano solamente el tamaño y el volumen de fruto en el primer corte se vio afectado, en ambos casos después
Figure 1. Comparison of means in three generations of crosses for four varieties of tomatillo (*Physalis ixocarpa* Brot. ex Horm.): a) plant height (PH, cm), b) number of bags (NB), c) yield per plant in harvest 1 (YP1, kg), d) yield per plant in harvest 2 (YP2, kg), e) total yield per plant (TYP, kg) and f) density of 10 fruits in harvest 1 (D1, g·mL⁻¹). HSD = honestly significant difference. Means with the same letter in each variety do not differ statistically (Tukey, *P* ≤ 0.05).

Figura 1. Comparación de medias en tres generaciones de cruzas para cuatro variedades de tomate de cáscara (*Physalis ixocarpa* Brot. ex Horm.): a) altura de planta (ALT, cm), b) número de bolsas (BOL), c) rendimiento por planta en el corte 1 (RPC1, kg), d) rendimiento por planta en el corte 2 (RPC2, kg), e) rendimiento total por planta (RTP, kg) y f) densidad de 10 frutos en el corte 1 (D1, g·mL⁻¹). DMSH = diferencia mínima significativa honesta. Medias con la misma letra en cada variedad no difieren estadísticamente (Tukey, *P* ≤ 0.05).
Figure 2. Comparison of means in three generations of crosses for four varieties of tomatillo (*Physalis ixocarpa* Brot. ex Horm.): a) weight of 10 fruits in harvest 1 (W10F1, g), b) weight of 10 fruits in harvest 2 (W10F2, g), c) average weight of 10 fruits (AW10F, g), d) volume of 10 fruits in harvest 1 (V1, mL), e) volume of 10 fruits in harvest 2 (V2, mL) and f) average volume of 10 fruits (AV, mL). HSD = honestly significant difference. Means with the same letter in each variety do not differ statistically (Tukey, $P \leq 0.05$).

Figura 2. Comparación de medias en tres generaciones de cruzas para cuatro variedades de tomate de cáscara (*Physalis ixocarpa* Brot. ex Horm.): a) peso de 10 frutos en el corte 1 (P10FC1, g), b) peso de 10 frutos en el corte 2 (P10FC2, g), c) peso promedio de 10 frutos (PP10F, g), d) volumen de 10 frutos en el corte 1 (V1, mL), e) volumen de 10 frutos en el corte 2 (V2, mL) y f) volumen promedio de 10 frutos (VP, mL). DMSH = diferencia mínima significativa honesta. Medias con la misma letra en cada variedad no diferen estadísticamente (Tukey, $P \leq 0.05$).
Study of inbreeding in tomatillo...

being superior (Figures 3b and 3c). The type of cross had an effect on yield variables in Diamante, since, in both harvests and total yield, families from plant-to-plant crosses had lower yields (Figures 3c, 3d and 3e). In the Tecozautila variety, no effect of the type of cross was found on PH, NB or yield variables (Figure 3). Density was not affected by the type of cross.

Due to the type of family generated by each cross, it was expected that the variables evaluated would have lower expression in the families derived from plant-to-plant crosses, since mating between full siblings generates greater inbreeding than between half-siblings (Falconer & Mackay, 1996). This may be because the crosses were made between selected plants in both cases and possibly still have high heterozygosity. Hallauer, Carena, and Miranda (2010) note that the change in vigor is directly proportional to the change in heterozygosity in the population, i.e., the higher the heterozygosity, the higher the yield.

Fruit size (weight and volume) in the first harvest was different between the type of crosses in Tecozautila and Morado. In both cases, a significant decrease was observed in plant-to-plant crosses with respect to fraternal crosses (Figures 4a and 4d). In Tecozautila and Diamante, differences were found between the type of crosses for W10F2 and V2 (Figures 4b and 4e). The families obtained by plant-to-plant crosses had lower values than those of the fraternal crosses. In the average fruit size of Tecozautila, Diamante and Morado, it was also found that the families of plant-to-plant crosses were inferior to those of fraternal crosses (Figures 4c and 4f). In general, no differences were found between the type of crosses for Manzano (Figures 3 and 4).

Tecozautila performed differently in the variables related to fruit size and volume. Diamante was different in TYP, AW10F and AV. Manzano was different only in PH. Morado had different behavior in YP1, W10F1, V1 and AV. In Tecozautila, Diamante and Morado, the fraternal cross was superior, whereas in Manzano the plant-to-plant cross was better. In general, this indicates that plant-to-plant crosses generated a greater inbreeding depression than fraternal crosses, except in Manzano.

The greater inbreeding depression in the plant-to-plant cross is due to the fact that only two individuals come into play during pollination, while five are involved in the fraternal cross. With fewer individuals, the probability of close relatives mating increases and thus homozygosity as well, so the frequency of dominant phenotypes decreases, and the deleterious effects of recessive alleles increase. Inbreeding is greater in FSFs than in MHSFs (Falconer & Mackay, 1996; Hallauer et al., 2010).

La ALT solamente fue diferente entre tipos de cruzas en Manzano, donde las familias obtenidas por cruzas planta a planta fueron superiores (Figura 3a). El BOL y el RPC1 fueron diferentes en Morado, siendo superiores las familias obtenidas de cruzas fraternales (Figuras 3b y 3c). El tipo de cruzas tuvo efecto sobre las variables de rendimiento en Diamante, ya que, en ambos cortes y en el rendimiento total, las familias provenientes de cruzas planta a planta presentaron menor rendimiento (Figuras 3c, 3d y 3e). En la variedad Tecozautila, no se encontró efecto del tipo de cruzas sobre la ALT, el BOL ni en variables de rendimiento (Figura 3). La densidad no fue afectada por el tipo de cruzas.

Por el tipo de familia que genera cada cruzada, se esperaba que las variables evaluadas tuvieran menor expresión en las familias derivadas de las cruzas planta a planta, pues el apareamiento entre hermanos completos genera mayor endogamia que entre medios hermanos (Falconer & Mackay, 1996). Lo anterior se puede deber a que las cruzas se hicieron entre plantas selectas en ambos casos y posiblemente aún presentan alta heterocigosidad. Hallauer, Carena, y Miranda (2010) mencionan que el cambio de vigor es directamente proporcional a la modificación en la heterocigosidad en la población, es decir, a mayor heterocigosidad mayor rendimiento.

El tamaño de fruto (peso y volumen) en el primer corte fue diferente entre tipo de cruzas en Tecozautila y Morado. En ambos casos, se observó una disminución significativa en las cruzas planta a planta respecto de las fraternales (Figuras 4a y 4d). En Tecozautila y Diamante se encontraron diferencias entre tipo de cruzas para P10FC2 y V2 (Figuras 4b y 4e). Las familias obtenidas mediante cruzas planta a planta presentaron valores inferiores a los de las fraternales. En el tamaño promedio de fruto de Tecozautila, Diamante y Morado también se encontró que las familias de cruzas planta a planta fueron inferiores a las de cruzas fraternales (Figuras 4c y 4f). En general, no se encontraron diferencias entre tipos de cruzas para Manzano (Figuras 3 y 4).

Tecozautila tuvo un comportamiento diferente en las variables relacionadas con el tamaño y el volumen de fruto. Diamante fue diferente en el KTP, el PP10F y el
Figure 3. Comparison of means in two types of crosses for four varieties of tomatillo (*Physalis ixocarpa* Brot. ex Horm.): a) plant height (PH, cm); b) number of bags (NB), c) yield per plant in harvest 1 (YP1, kg), d) yield per plant in harvest 2 (YP2, kg), e) total yield per plant (TYP, kg) and f) density of 10 fruits in harvest 1 (D1, g·mL⁻¹). HSD = honestly significant difference. Means with the same letter in each variety do not differ statistically (Tukey, *P* ≤ 0.05).

Figura 3. Comparación de medias en dos tipos de cruza para cuatro variedades de tomate de cáscara (*Physalis ixocarpa* Brot. ex Horm.): a) altura de planta (ALT, cm); b) número de bolsas (BOL), c) rendimiento por planta en el corte 1 (RPC1, kg), d) rendimiento por planta en el corte 2 (RPC2, kg), e) rendimiento total por planta (RTP, kg) y f) densidad de 10 frutos en el corte 1 (D1, g·mL⁻¹). DMSH = diferencia mínima significativa honesta. Medias con la misma letra en cada variedad no difieren estadísticamente (Tukey, *P* ≤ 0.05).
Figure 4. Comparison of means of two types of crosses for four varieties of tomatillo (Physalis ixocarpa Brot. ex Horm.): a) weight of 10 fruits in harvest 1 (W10F1, g), b) weight of 10 fruits in harvest 2 (W10F2, g), c) average weight of 10 fruits (AW10F, g), d) volume of 10 fruits in harvest 1 (V1, mL), e) volume of 10 fruits in harvest 2 (V2, mL) and f) average volume of 10 fruits (AV, mL). HSD = honestly significant difference. Means with the same letter in each variety do not differ statistically (Tukey, $P \leq 0.05$).

Figura 4. Comparación de medias de dos tipos de cruza para cuatro variedades de tomate de cáscara (Physalis ixocarpa Brot. ex Horm.): a) peso de 10 frutos en el corte 1 (P10FC1, g), b) peso de 10 frutos en el corte 2 (P10FC2, g), c) peso promedio de 10 frutos (PP10F, g), d) volumen de 10 frutos en el corte 1 (V1, mL), e) volumen de 10 frutos en el corte 2 (V2, mL) y f) volumen promedio de 10 frutos (VP, mL). DMSH = diferencia mínima significativa honesta. Medias con la misma letra en cada variedad no difieren estadísticamente (Tukey, $P \leq 0.05$).
Results show that it is possible to develop a genetic improvement program by hybridization in tomatillo, despite the self-incompatibility, since it has been demonstrated that plant-to-plant crosses do indeed generate inbreeding. However, it is necessary to consider that to generate a level of inbreeding similar to that of a selfing cycle, several cycles of plant-to-plant crosses are required (Falconer & Mackay, 1996); therefore, the time needed to obtain highly inbred FSFs would be much longer.

Conclusions

Inbreeding depression occurred between generations in fruit yield, size and volume, which decreased across generations.

The Tecozautla and Diamante varieties showed a greater inbreeding depression than Manzano and Morado, as they had a decreasing trend in the variables evaluated across generations.

The type of cross had a different effect depending on the variety. In the variables related to fruit size, the plants originated by plant-to-plant crosses had lower values in Tecozautla, Diamante and Morado, which indicates that a greater inbreeding depression is generated with this type of cross.

It is possible to obtain highly inbred full-sib families for a tomatillo hybridization breeding program.

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La mayor depresión endogámica en la cruz plant a planta se debe a que durante la polinización entran en juego sólo dos individuos, y en la fraternal intervienen cinco. Con menos individuos aumenta la probabilidad de que parientes cercanos se apareen y que la homocigosis aumente, por lo que la frecuencia de los fenotipos dominantes disminuye y los efectos deletéreos de los alelos recesivos incrementan. En las FHC, la endogamia es mayor que en las FMHM (Falconer & Mackay, 1996; Hallauer et al., 2010).

Los resultados muestran que es posible desarrollar un programa de mejoramiento genético por hibridación en tomate de cáscara, a pesar de la autoincompatibilidad, ya que se ha demostrado que, efectivamente, las cruzas planta a planta generan endogamia. Sin embargo, es necesario considerar que para generar un nivel de endogamia similar al de un ciclo de autofecundación se requieren varios ciclos de cruzas planta a planta (Falconer & Mackay, 1996), por lo que el tiempo requerido para la obtención de FHC altamente endógámicas sería mucho mayor.

Conclusiones

Se presentó depresión endogámica entre generaciones en el rendimiento, el tamaño y el volumen de fruto, la cual disminuyó a través de éstas.

Las variedades Tecozautla y Diamante presentaron mayor depresión endogámica que Manzano y Morado, pues tuvieron una tendencia decreciente en las variables evaluadas a través de las generaciones.

El tipo de cruzar tuvo efecto diferente en función de la variedad. En las variables relacionadas con el tamaño de fruto, el comportamiento de las plantas originadas por cruzas planta a planta fue inferior en Tecozautla, Diamante y Morado, lo cual indica que se genera mayor depresión endogámica con este tipo de cruzar.

Es posible obtener familias de hermanos completos altamente endógámicas para un programa de mejoramiento genético por hibridación en tomate de cáscara.
Study of inbreeding in tomatillo...

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