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ESTRUCTURA GENÉTICA Y SELECCIÓN DE LA RESISTENCIA A LA MOSQUITA BLANCA (*Bemisia tabaci*) EN POBLACIONES DE TOMATE SILVESTRE (*Solanum lycopersicum* var. *cerasiforme*)

T E S I S

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Por medio de la presente me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 27 de junio del 2005, se acordó poner a su consideración el siguiente jurado para el examen de DOCTOR EN CIENCIAS del alumno **Sánchez Peña Pedro** con número de cuenta **501048879** , con la tesis titulada: **"Estructura genética y selección de la resistencia a la mosquita blanca (Bemisia tabaci) en poblaciones de tomate silvestre (Solanum lycopersicum var. cerasiforme)"**, bajo la dirección del **Dr. Alberto Ken Oyama Nakagawa.**

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A t e n t a m e n t e
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CONTENIDO

RESUMEN

En el presente estudio se analizó la variación genotípica y fenotípica de poblaciones silvestres de tomate (*Solanum lycopersicum* var. *cerasiforme*), el pariente más cercano del tomate cultivado. El análisis fenotípico se hizo sobre caracteres vegetativos, de historia de vida y resistencia a mosquita blanca (*Bemisia tabaci*), una plaga de los cultivos de tomate. El análisis de la variación genética y estructura poblacional se realizó en poblaciones silvestres y cultivadas de tomate usando marcadores genéticos de RAPD's. También, este estudio presenta información sobre la varianza genética aditiva, permitiendo la estimación de la heredabilidad (h^2) y la diferenciación poblacional (*Qst*) para cada caracter analizado. De esta manera, se contrasta el nivel de diferenciación entre poblaciones silvestres utilizando marcadores selectivamente neutros y caracteres cuantitativos. En el Capítulo I, se hace una revisión de los aspectos de mayor importancia del tomate relacionados con este estudio, como lo son el origen, domesticación, genética poblacional y taxonomía. Las evidencias científicas presentadas indican que la domesticación del tomate ocurrió en México y que taxonómicamente debe ubicarese en el género *Solanum* y la especie *lycopersicum.* En el Capítulo II se analiza la variación de ocho poblaciones de tomate silvestre (*Solanum lycopersicum* var. *cerasiforme*) del Noroeste de México, en un experimento de jardín común, respecto a los niveles de infestación de mosquita blanca, la densidad de tricomas como un carácter defensivo en contra de la mosquita blanca, y el efecto negativo de la mosquita blanca en caracteres reproductivos y vegetativos. La densidad de tricomas está correlacionada significativa y negativamente con la incidencia de mosquita blanca, y existen diferencias entre poblaciones silvestres para este carácter. Asimismo, la incidencia de mosquita blanca afectó negativamente el crecimiento y la reproducción de las plantas. En el Capítulo III, se analiza la existencia de variación

genética de 60 poblaciones silvestres de tomate (*Solanum lycopersicum* var. *cerasiforme*) y tres variedades cultivadas (*Solanum lycopersicum*), utilizando marcadores moleculares RAPD's. Los resultados indican niveles mayores de variación en las poblaciones silvestres que en las cultivadas. También, se encontró que gran parte de la variación genética está distribuida entre poblaciones, dando por resultado un alto nivel de diferenciación. En el Capítulo IV, empleando la metodología de la genética cuantitativa, se analizaron las diferencias entre y dentro de poblaciones de tomate respecto a la varianza genética aditiva de la resistencia a *Bemisia sp.*, en la tasa de crecimiento y en caracteres reproductivos con la finalidad de estimar la h^2 y la diferenciación entre poblaciones. Asimismo, se estimó el modo y magnitud de la selección fenotípica y sobre los valores reproductivos ("breeding values") de la resistencia a *Bemisia sp.* y la tasa de crecimiento. Los resultados indicaron la existencia de varianza aditiva en todos los caracteres, aunque no en la misma cantidad, ni en todas las poblaciones. Se detectaron niveles elevados de diferenciación poblacional en todos los caracteres cuantitativos (*Qst*). Se detectó selección natural fenotípica sobre la resistencia a *Bemisia tabaci* en dos poblaciones, mientras que en una poblaciones con niveles elevados de resistencia no hubo efecto de la selección (ausencia de varianza fenotípica). No se detectó seleción sobre los valores reproductivos debido a un bajo poder de la prueba. También se detectó selección positiva sobre la tasa de crecimiento. Finalmente, existen diferencias entre poblaciones en el costo de la infestación por *Bemisia sp.*, lo cual sugiere la existencia de un mosaico geográfico selectivo en la interacción entre tomate y el herbívoro.

ABSTRACT

In this study, the phenotypic and genetic variation of populations of wild tomato, the closest relative of cultivated tomato (*Solanum lycopersicum* var. *cerasiforme*), was analyzed. Phenotypic analysis of phenotypic variability was carried out on vegetative, reproductive, life history characters, and plant resistance to whitefly (*Bemisia spp.*), a herbivore pest of cultivated tomato. The analysis of the genetic variation and population structure of wild and cultivated populations of tomato were analyzed using RAPDs molecular markers. In addition to this analysis, additive genetic variation of quantitative characters within and among populations allowed the estimation of trait heritabilities (h^2) and population differentiation (*Qst*), respectively. In this way, the level of differentiation in neutral markers and quantitative characters among populations of wild tomato can be contrasted. In Chapter I, a review of the major aspects of genetics, systematics, and domestication of wild tomato, related to this study, is presented. The evidence indicated that domestication of cultivated tomato took place in Mexico, and that taxonomically must be placed in the genus *Solanum* (and *lycopersicum* as species). In Chapter II, using a common garden experiment, phenotypic variation in plant's leaf trichome density, a putative defensive character, and the level of infestation by whitefly was analyzed in eight populations of wild tomato in northwestern Mexico. Leaf trichome density was found to be negatively associated with the level of infestation by whiteflies. Differences among natural populations in trichome density were detected. Whitefly infestation affected negatively plant's growth and reproduction. In Chapter III, genetic variation of 60 populations of wild tomato and three cultivated varieties was surveyed using RAPDs markers. Higher levels of genetic variation in wild populations than in cultivated varieties were found. A large fraction of the genetic variation is distributed among populations, resulting in a high level

of differentiation. In Chapter IV, using a quantitative genetic study, the additive genetic variance of growth rate, reproductive characters, and plant resistance to whitefly, was obtained in order to estimate h^2 in four populations of wild tomato. Also, the magnitude of population differentiation (*Qst*) for the same characters was obtained. Additionally, the mode and magnitude of selection upon growth rate and plant resistance to whiteflies was estimated on both phenotypic and breeding values of the two characters, in each population. Additive genetic variance was detected for all characters although no character possessed genetic variance in all populations, and no populations was genetically variable for all characters. High levels of population differentiation (*Qst*) were detected for all characters. Phenotypic natural selection was detected for increasing plant resistance in two populations. The selection gradients of the breeding values of the characters were all non significant due to a lower power of the test. In contrast, positive directional selection was detected on growth rate. Finally, there were differences among populations in the cost of infestation by whitefly, suggesting a selective geographic mosaic in the interaction between wild tomato and whitefly.

PRESENTACIÓN GENERAL

El estudio de los parientes silvestres de las plantas cultivadas es de gran importancia debido a que sus acervos de genes podrían ser de utilidad para dar respuesta a la problemática que enfrenta la agricultura moderna. El tomate (*Solanum lycopersicum* L) es el cultivo hortícola de mayor importancia económica en el mundo (Nuez *et al.*, 2004). La producción de tomate enfrenta una gran diversidad de problemas, siendo el de mayor importancia las enfermedades virales transmitidas por mosquita blanca. La obtención de fuentes de resistencia a mosquita blanca y a las enfermedades virales transmitidas por su principal vector, es un objetivo fundamental en los programas de mejoramiento de tomate. Las poblaciones silvestres de tomate constituyen una fuente natural de variación genética en la resistencia contra factores ambientales adversos y para el mejoramiento de las cualidades de producción de tomate (Rick, 1978; Taylor, 1986; Tanksley y Miller 1990; Sánchez-Peña *et al.*, 1995; Rick y Chetelat, 1995; Nuez *et al.*, 2004). Son pocos los estudios sobre diversidad genética que han analizado al ancestro más cercano del tomate cultivado en la región donde se supone fue domesticado; además, no existe información de la situación en que se encuentran estos recursos genéticos en su lugar de domesticación. Basado en estos antecedentes, el propósito de esta tesis fue el estudiar la diversidad genética del pariente más cercano del tomate cultivado en su lugar de domesticación. En el Capítulo I se presenta una revisión de la taxonomía, domesticación y genética de poblaciones del tomate.

Las interacciones planta-herbívoro (insecto) son de gran importancia, no únicamente por el impacto que los insectos tienen sobre las plantas al consumir el 10% de producción primaria neta anual (Hertley y Jones, 1997), sino por que también este tipo de

interacción, junto con otras interacciones antagónicas que se dan entre las plantas y sus enemigos naturales (virus, hongos, bacterias, nematodos y mamíferos), han producido la mayor parte de la diversidad biológica presente en la tierra (Rausher, 2001). En condiciones naturales se han documentado las interacciones entre poblaciones de planta con sus enemigos naturales (Nuñez-Farfán y Dirzo, 1994; Coley y Barone, 1996), así como los mecanismos de defensas basado en la presencia de tricomas (Valverde *et al.*, 2001). Debido a que la mayoría de los estudios sobre resistencia en tomate se han realizado en sus especies emparentadas, el sitema de estudio elegido en la parte experimental del trabajo fue el ancestro más cercano al tomate cultivado, la variedad o subespecie silvestre *Solanum lycopersicum* var. *cerasiforme*. De esta forma, en el Capítulo II (Sánchez-Peña *et al.*, en prensa) se presenta un estudio experimental que evalúa la variación en la resistencia a mosquita blanca en poblaciones silvestres de tomate del Noroeste de México. En el estudio, se evalúa el papel que tiene la densidad de tricomas foliares como componente defensivo a la mosquita blanca en las poblaciones de tomate silvestre.

Para que un recurso genético sea explotado en los programas de mejoramiento debe mostrar amplia variacion genética. En este sentido, en el Capítulo III se presenta la evidencia molecular de la existencia de variación genética en las poblaciones silvestres de tomate en México. El estudio se realizó empleando la técnica de RAPDs en 60 poblaciones de México, y tuvo como objetivo determinar la variación genética de las poblaciones silvestres de tomate, así como la forma en que se encuentra distribuida esta variación.

Los estudios que evalúen la evolución de la resistencia deben demostrar la existencia de variación genética para la resistencia, que los genotipos de diferentes valores de resistencia difieren en adecuación y que la manipulación y abundancia de herbívoros

naturales genere cambios en los patrones de selección sobre resistencia (Rausher, 1996). Por esta razón el análisis de la resistencia a herbívoros contempla un análisis a nivel genético (Rausher y Simms, 1989; Núñez-Farfán y Dirzo, 1994; Mauricio y Rausher, 1997; Mauricio, 1998; Shonle y Begelson, 2000). En el Capítulo IV se presenta la evidencia de un estudio realizado bajo condiciones experimentales en la zona productora de tomate más importante de México. El objetivo fue evaluar la existencia de variación genética en caracteres reproductivos, vegetativos y de resistencia a *Bemisia*, en cuatro poblaciones de tomate silvestres de Sinaloa. El estudio contempló el análisis de la variación genética aditiva de la resistencia a mosquita blanca y su relación con características reproductivas y de adecuación. Finalmente, se analiza el efecto de la selección impuesta por mosquita blanca en las poblaciones silvestres de tomate.

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CAPÍTULO I

SÍNTESIS DEL CONOCIMIENTO TAXONÓMICO, ORIGEN, DOMESTICACIÓN Y GENETICA DE POBLACIONES DEL TOMATE

Resumen

El tomate es el cultivo hortícola de mayor importancia en términos económicos. Esto hace que sea unos de los cultivos agrícolas más estudiados genéticamente, lo cual ha hecho posible la elaboración de su mapa genético con suficientes marcadores en cada uno de sus doce cromosomas. Existe consenso de que el centro de origen al que pertenece el tomate cultivado se ubica en la región Andina compartida por Perú, Ecuador y Chile en Sudamerica; sin embargo no existe consenso en definir el lugar en donde se realizó la domesticacion, así como la taxonomía del mismo. Las evidencias científicas establecen que el centro de domesticación es México y que el tomate cultivado debe ser ubicado dentro del género *Solanum* y de la especie *lycopersicum*. Trabajos taxonómicos recientes han logrado definir doce especies silvestres de tomate (*S. pinpinellifolium, S. chiesmanii, S. pennellii, S. habrochaites, S. neorickii, S. chiemilewskii, S. chilense, S. peruvianum, S. arcanum, S. corneliomuelleri, S. galapagense, y S. huaylasense*), y una variedad o subespecie, también silvestre (*Solanum lycopersicum* var. *cerasiforme*), dentro del tomate cultivado.

Introducción

En la literatura científica es común referirse al tomate cultivado como tomate, nombre con el que se le conoce en el Noroeste de México; sin embargo en la mayor parte de México generalmente se le conoce como jitomate, y tomate es utilizado para designar a las formas de *Physalis*, conocido en el Noroeste como tomatillo, tomate verde o tomate de cáscara. De acuerdo a la traducción que hace Oliva (1992), en el diccionario de lengua náhuatl, textualmente maneja "tomatl s. Tomate, solanácea que tiene cinco especies principales: _xitomatl_, que es grande; _miltomatl_, muy pequeño; _coatomatl_, que tiene color de serpiente; _izuatomatl_, recubierto de una membrana; _coztomatl_, que crece en la arena (Hern.)". Independientemente de los nombres con los que son designados, éste tiene una forma científica (género y especie en latín) que también se ha venido modificando con el tiempo. El nombre inicial, establecido por Linneo, *Solanum lycopersicon* fue remplazado por Miller en 1768 (Taylor, 1986) quien propuso este nombre y es el preferido para designar al tomate o jitomate cultivado (*Lycopersicon esculentum* Mill), no obstante que en las investigaciones más recientes, se han presentado argumentos para designarlo como *Solanum lycopersicum* (Peralta y Spooner, 2001; Darwin *et al.*, 2003; Spooner *et al.*, 2005; Peralta *et al.*, 2005). El dilema de la clasificación del tomate o jitomate se debe en parte a la ausencia de información científica detallada de su sistemática, además de que se ubica dentro de la familia Solanaceae, una de las más grandes y con mayor importancia económica dentro de las angiospermas, que incluye a géneros como *Solanum* (papa), *Nicotiana* (tabaco) y *Capsicum* (chile).

El cultivo de tomate, además de estar distribuido alrededor del mundo ocupa el segundo lugar en importancia mundial, solamente superado por la papa (*Solanum tuberosum*) (FAOSTAT, 2005); sin embargo, Nuez *et al.* (2004) lo ubican como el cultivo hortícola económicamente más importante en el mundo. Dado que los problemas que enfrenta la producción de cultivos son particulares para cada region, la búsqueda de variedades de cultivos que se adapten a las condiciones de sistemas de producción específicos de cada región es la tendencia de los programas de mejoramiento de plantas. Fitomejoradores, biotecnólogos y científicos en general han venido trabajando en este camino, obteniendo conocimientos referente a la utilidad del germoplasma silvestre y la forma en cómo estos pueden contribuir a incrementar la productividad en los cultivos (Rick, et al., 1995; Sánchez-Peña *et al.*, 1995; Tankley y McCouch, 1997; Lee, 1998; Zamir, 2001; Gur y Zamir, 2004). De esta manera, las

especies silvestres y variedades nativas emparentadas con las plantas cultivadas se han convertido en un recurso genético de gran utilidad, dado que en él encontramos un acervo de genes que puede contribuir en la solución de problemas agrícolas presentes o futuros, tales como la tolerancia o la resistencia a plagas o enfermedades, e incremento de la calidad y cantidad de la producción (Harlan, 1976; Stalker, 1980; Burdon y Jarosz, 1989).

La fragmentación y destrucción del hábitat en que se encuentran las poblaciones vegetales silvestres constituyen una seria amenaza para los recursos genéticos, y hacen urgente el estudio y la estimación de la cantidad de variabilidad genética presente en las poblaciones silvestres de especies que potencialmente son útiles para la humanidad (Vida, 1994). Dirzo y Raven (2003) con base a los datos de Hilton-Taylor (2002), mencionan que para el caso de plantas se tienen 5714 especies amenazadas que corren el riesgo de su extinción por las actividades directas o indirectas del ser humano.

México, considerado como uno de los mayores centros de domesticación de plantas (Harlan, 1971; Rick, 1979), que además de su riqueza cultural, es también reconocido como uno de los centros de diversidad vegetal más importante del planeta, ya que alberga el 12% de la riqueza biológica mundial en tan solo el 2% de la superficie terrestre (Mesoamérica, informe 2002). La diversidad vegetal presente en México, especialmente aquella contenida en los parientes silvestres de muchas plantas cultivadas, constituye una fuente importante de recursos genéticos para el mejoramiento de los cultivos.

Con base a lo anterior, la presente revisión pretende abordar aspectos sobre el origen, domesticación, taxonomía, y genética del tomate (diversidad).

Origen y domesticación

Con relación al origen del tomate, no existe duda de que su centro de origen es el área Andina compartida por Ecuador, Perú, Bolivia y Chile (Rick, 1976). En esta región, se encuentran todas las especies silvestres de tomate (*L. pinpinellifolium, L. cheesmanii, L. parviflorum, L. chmielewski, L. hirsutum, L. pennellii, L. chilense* y *L. peruvianum)* (Rick, 1978; Taylor, 1986), incluyendo la variedad o subespecie silvestre *cerasiforme* (Dun) A. Gray (Jenkins, 1948; Rick, 1978). Por otro lado, las evidencia genéticas a partir de los estudios con marcadores moleculares isoenzimáticos en poblaciones silvestres, sugieren que el tomate cultivado tienen como posibles ancestro a las especie silvestre *L. pimpinellifolium* y la variedad

o subespecie también silvestre *Lycopersicum esculentum* var. *cerasiforme*, ambas con centro de origen en la región Andina (Rick y Fobes 1975). Esto confirma que este cultivo tuvo su origen en el nuevo mundo ya que este no era conocido en Europa y en el resto del viejo mundo antes del descubrimiento de América (Rick, 1976, 1978).

Con relación al lugar de domesticación del tomate, se ha planteado que tuvo lugar en Perú y Ecuador (Muller, 1940; Luckwill, 1943) o México (Jenkins, 1948; Rick, 1978). De acuerdo con evidencias históricas de distribución y de diversidad fenotípica, Jenkis (1948) postula que en México y particularmente en las áreas de Veracruz y Puebla, el tomate fue domesticado a partir de la variedad o subespecie *cerasiforme*. Asimismo, estudios moleculares izoenzimáticos han demostrado la existencia de mayor similitud entre los tomates cultivados del viejo mundo, con las poblaciones silvestres de México y América Central que las encontradas en la zona andina (Rick, 1978). Por otro lado, también existen evidencias que indican que a la llegada de los españoles a América, el tomate era cultivado, comercializado y consumido por las culturas Mesoamericanas, situación que no sucedió con las culturas de la región Andina; aunado a que el tomate no tiene ningún nombre conocido en los dialectos andinos; mientras que su nombre moderno deriva de *tomatl*, vocablo de la lengua Nahuatl de México (Esquinas-Alcázar y Nuez, 2001).

Otro argumento que sustenta que el origen de la domesticación se realizó en México, lo constituye el hecho de que en los utensilios primitivos de la zona Andina no se ha encontrado ninguna representación de tomates o partes de la planta, ni tampoco se han encontrado restos de esta planta en los yacimientos arqueológicos, situación que contrasta con el hecho de que se han localizado restos para la mayoría de las plantas nativas cultivadas de esta región. Aunado esto al hecho de la existencia de registros de que el tomate se sembraba, aunque poco, en la zona de tierras bajas Mayas de México, y que los tomates silvestres tienen dos loculos en el fruto (característica ancestral) y las formas multiloculadas son derivadas. Tambien, está documentado que en la actualidad existe una variedad domesticada biloculada en el Sur de México y en Guatemala por lo que se supone que los primeros cultivos habrían sido de este tipo (Harlan, 1976).

Consecuentemente, toda las evidencias etnobotánicas, genéticas, lingüísticas e históricas, indican que el tomate fue domesticado en México (Jenkins, 1948; Harlan, 1976; Rick, 1978; Taylor, 1986), a partir del tomate silvestre (*Lycopersicon esculentum* var.

cerasiforme), distribuido en América Latina y los trópicos del nuevo mundo (Harlan, 1976; 1992).

A pesar de que México es considerado el centro de domesticación del tomate, se infiere que ésta se dio en etapas relativamente recientes, dado que no se han encontrados vestigios en los restos arqueológicos de Tehuacán, Puebla, en donde sí se encontraron restos de un pariente del tomate, *Physalis*, que se utilizaba y se sigue utilizando como alimento (Esquinas- Alcázar y Nuez, 2001). Esto sugiere que la domesticación del tomate se dio después de *Physalis* (Harlan, 1992), a partir de selecciones guiadas por los antiguos agricultores indígenas, dando como resultado las variantes conocidas en México, cuyas relaciones evolutivas se presentan en la Figura 1 (Rick, 1976), y las posibles rutas de distribución del tomate en el resto del mundo en la Figura 2 (Esquinas- Alcázar, 1981).

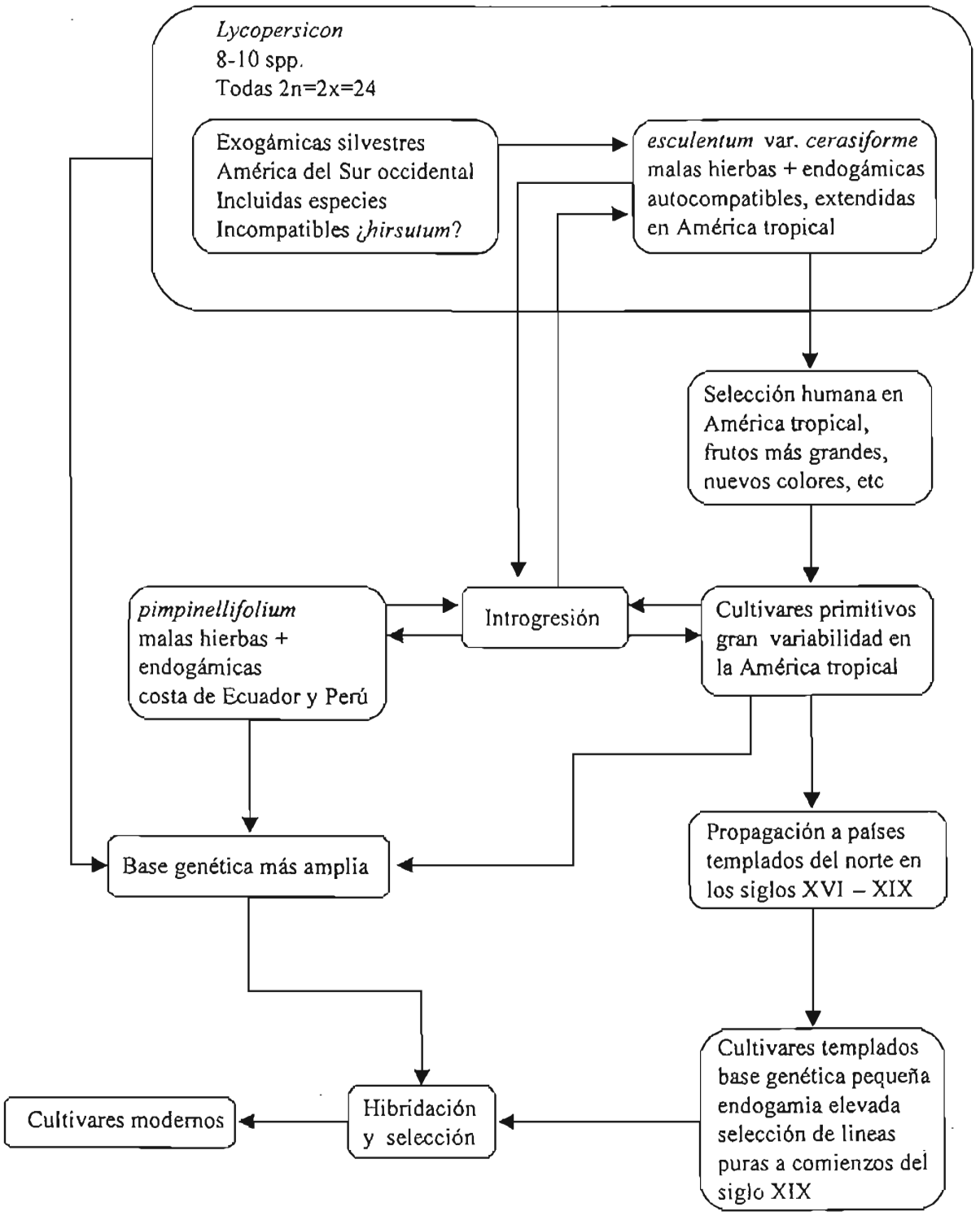


Figura 1. Relaciones evolutivas del tomate (Rick 1976)

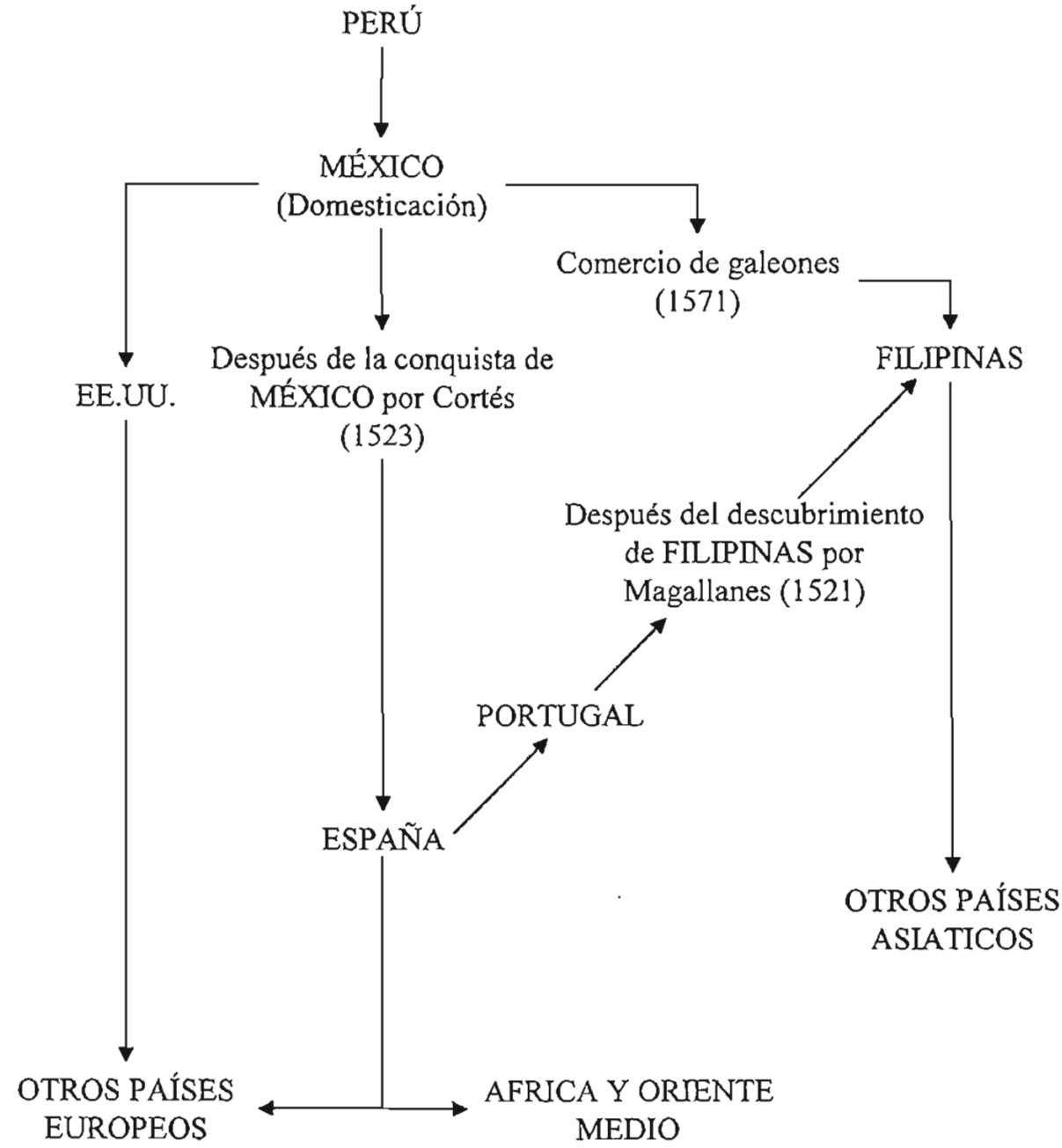


Figura 2. Posibles rutas de propagación del tomate desde el siglo XVI (Esquinas-Alcázar, 1981)

Taxonomía

Existe consenso en ubicar al tomate dentro de la familia Solanaceae; sin embargo la ubicación de este a nivel de género y especie tiene una polémica muy rica en la que dos posiciones generales se debaten. Por un lado aquella que ubica al tomate dentro del género *Lycopersicon* y de la especie *esculentum* (Muller, 1940; Luckwill, 1943; Correll, 1962; D'Arcy, 1972, 1987, 1991; Hunziker, 1979; Rick, 1978, 1979; Symon, 1981, 1985; Taylor, 1986; Warnock, 1988; Hawkes, 1990; Rick *et al.*, 1990); en cambio otros, lo ubican dentro del género *Solanum* y de la especie *lycopersicum* (Fosberg, 1987; Child, 1990, Spooner *et al.*, 1993; Bohs y Olmstead, 1999; Knapp y Spooner, 1999; Olmstead *et al.*, 1999; Peralta y Spooner, 2001; Darwin *et al.*, 2003; Spooner *et al.*, 2005; Peralta *et al.*, 2005; Spooner *et al.*, 2005).

Los trabajos que sintetizan la evolución de la ubicación taxonómica de tomate son cinco (Muller, 1940; Luckwill, 1943; Rick, 1960, 1979; Child, 1990; Spooner *el al.*, 1993; Peralta y Spooner, 2001; Darwin *et al.*, 2003; Spooner *et al.*, 2005; Peralta *et al.*, 2005). Muller (1940) estableció que el tomate tiene seis especies y debe ser ubicado dentro del género *Lycopersicon*, y que éste comprende dos subgéneros. El subgénero *Eulycopersicon*, caracterizado por tener dos especies (*L. esculentum* y *L. pinpinellifolium*) con hojas que no contienen pseudoestípulas y frutos de color que van de naranja a rojo. En cambio, el subgénero *Ericopersicon* incluye a cuatro especies (*L. peruvianum, L. cheesmananiae, L. hirsutum, L. glandulosum*) y se caracteriza por tener hojas con pseudoestípulas y los frutos verdes (Cuadro 1). Años después, Luckwill (1943) adoptó la misma clasificación, con la diferencia de que dentro del subgénero *Euricopersicon* incluyó otra especie más (Cuadro 1).

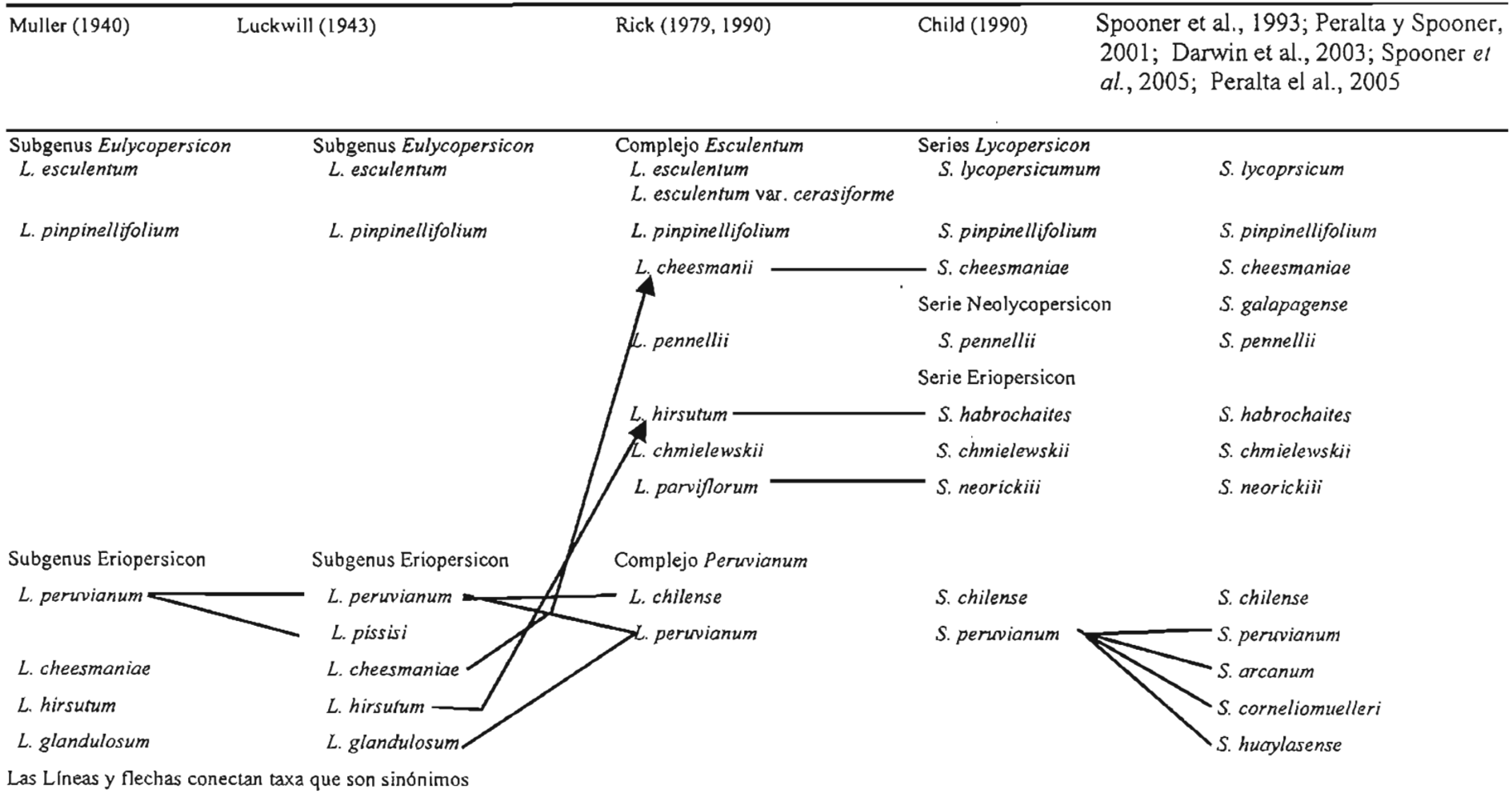
Rick (1960, 1979) planteó que la clasificación del tomate por debajo del género debería de hacerse con base a la capacidad de cruzamiento de las especies, estableciendose dos complejos: el constituido por las especies que tienen la capacidad de cruzarse con tomate (complejo *esculentum*) y el que comprende especies que son incapaces de entrecruzarse (complejo *peruvianum*). En el complejo *esculentum* hay siete especies *(L. esculentum, L. pinpinellifolium, L. cheesmaniaae, L. pennellii, L. hirsutum, L. chmielewskii, y L. parviflorum),* mientras que en el complejo *peruvianum* se encuebtrán dos especies de tomate (*L. chilense y L. Peruvianum*; ver Cuadro 1).

Los estudios más recientes ubican al tomate dentro del genero *Solanum* (Child, 1990; Spooner *et al.*, 1993; Peralta y Spooner, 2001; Darwin *et al.*, 2003; Spooner *et al.*, 2005; Peralta *et al.*, 2005). En el trabajo de Child (1990) ubica al tomate dentro del genero *Solanum*, subgénero *Potatoe*, Sección *Lycopersicon*, subsección *Lycopersicon*, y a todas las especies dentro del mismo las agrupa en tres series (*Lycopersicon, Neolicopersicon y Eriopersicon*). En la serie *Lycopersicon* incluye a todos los especies de tomates que tienen fruto de color (*S. lycopersicon, S. pimpinellifolium*, y *S. cheesmaniae),* mientras que en la serie *Neolycopersicon* sólo incluye a la especie *S. pennellii*. Finalmente en la serie *Ericopersicon* incluye a cinco especies (*S. habrochaites, S. chmielewskii, S. chilense, S. peruvianum* y *S. neorickii*). En esta clasificación es necesario hacer notar que contiene las mismas nueve especies que consideró Rick (1979); sin embargo, a dos especies les ha cambiado el nombre. A la especie *hirsutum*, la llama *habrochaites*, y a la especie *parviflorum* la denomina *neorickii* (Cuadro 1). Los trabajos más reciente sobre la taxonomía del tomate (Darwin *et al.*, 2003; Spooner *et al.*, 2005; Peralta *et al.*, 2005) están en concordancia con el planteado por Child (1990), sin embargo adicionan nuevas especies, especialmente las ubicadas dentro de *peruvianum* (Cuadro 1).

Los argumentos esgrimidos por los estudios que ubican al tomate dentro del género *Lycopersicon* tienen como base general diferencias morfológicas muy marcadas con el género *Solanum*. En el tomate y sus parientes silvestres las anteras tienen características que lo diferencian del género *Solanum*. En *Lycopersicon* el extremo superior de sus cinco anteras se unen formando un cono estaminal característico, además de que la liberación de polen se hace de manera lateral y permanece dentro del cono; en cambio en el género *Solanum* las anteras no se unen y la liberación del polen es por la parte terminal de las anteras; sin embargo, una de las especies (*pennellii*) tiene características del género *Solanum* en cuanto a la liberación del polen (Esquinas-Alcázar y Nuez, 2001).

Por otro lado, Esquinas-Alcázar (1981) describe la distribución y las características de mayor importancia de las especies silvestres de *Lycopersicon* (Cuadro 2), y Rick et al. (1990) a partir de características morfológicas, estableció una clave simplificada para la diferenciación de las especies dentro del género *Lycopersicon* en donde incluye a la var. *cerasiforme* dentro de la especie *esculentun* (Cuadro 3).

Cuadro 1. Comparaciones de la clasificación de tomate y sus parientes silvestres (con base a Muller, 1940; Luckwill, 1943; Rick, 1979, 1990; Child, 1990; Spooner et al., 1993; Peralta y Spooner, 2001; Darwin et al., 2003; Spooner *et al.*, 2005; Peralta el al., 2005).



Las Líneas y flechas conectan taxa que son sinónimos

Cuadro 2. Características reproductivas, distribución, variabilidad genética y algunas características importantes de las especies silvestres de Lycopersicon (Esquinas-Alcázar, 1981)

Especie	Sistema de Fecundación	Capacidad de cruzamiento con tomates	Distribución, variabilidad genética y otras características
L. esculentum var. *ceraciforme (Dun.)* Gray.	Autopolinización, en practicamente todas las regiones.	Muy buena.	Regiones tropicales; zona nativa: Ecuador/Perú. En Perú oriental, variable; en otras regiones monomórfica. Posible origen de formas cultivadas; introgresión de genes de *L. pimpinellifolium* .
L. pimpinellifollium (Jusl.) Mill.	Diferencias regionales de autopolinización.	Buena.	Costa del Perú, interandina, Perú septentrional; Ecuador. Diferencias regionales; correlación con la autopolinización. Es la especie más estrechamente relacionada con *L. esculentum*.
L. cheesmaniee Riley.	Muy autógama.	Posible.	Endémica del archipiélago de Galápagos. Uniformidad dentro de las poblaciones; diferencias entre poblaciones. Varios taxones subespecíficos.
L. chmielewskii Rick, Kebs Fob & Holle.	Autocompatible.	Posible.	Perú central; región interandina. Moderadamente variable. Junto con *L. parviflorum* , se clasificó oficialmente como complejo *L. minutum* .
L. parviflorum Rick, Kes., Fob. & Holle	Muy autógama.	Posible.	Perú septentrional y central; Ecuador meridional; región interandina. Relativamente uniforme. Junto con *L. chmielewskii* , se clasificó oficialmente como complejo *L. minutum* .
L. hirsutum Hum. & Bonpl.	Autoincompatible, con diferencias regionales.	Sólo si se utiliza como macho.	Del Perú central al Ecuador septentrional, 500 - 3300 m. s. n. m. Diferencias regionales. Olor fuerte, abundantes pélos glandulares.
L. peruvianum (L.) Mill.	Autoincompatibilidad estricta.	Sólo mediante cultivo de téjidos	Amplia distribución en el Perú, penetrando en Chile septentrional. La más variable de *Lycopersicon* spp.; numerosas variedades. Complejo subgenérico con L. *chilense* .
L. chilense Dun.	Totalmente autoincompatible.	Mejor que *L. peruvianum* .	Perú meridional y parte más septentrional de Chile. Relativamente variable. Complejo subgenérico con L. *peruvianum* .
L. pennellii (Corr.) D' Arcy.	Autoincompatible; pocas excepciones.	Posible.	Elevaciones medias próximas a la costa de Perú central. Muy variable. Sistema radicular poco desarrollado. Dehiscencia poral.

Cuadro 3. Clave simplificada para identificar especies del género *Lycopersicon* según Rick *et al.* (1990).

1. Interior del fruto maduro rojo: semilla 1.5 mm o más largas.
   1.1 Diámetro del fruto mayor de 1.5 cm; margen del las hojas generalmente serradas.
      1.1.1 Diámetro del fruto 3 cm o más ancho, 2 a muchos lóculos.
      L. esculentum Mill.
      1.1.2 Diámetro del fruto 1.5-2.5 cm; dos lóculos
      ***L. esculentum var.* cerasiforme;**(Dun.) Gray
   1.2 Diámetro del fruto menor que 1.5 cm, usualmente alrededor de 1 cm generalmente ondulado o entero.
      L. pinpinellifolium (JUSL.) Mill.

2. Interior del fruto amarillo o naranja; semillas 1.0 mm o más cortas.
   L. cheesmanii, Riley

3. Interior del fruto maduro verde o blanquecino; semillas de varios tamaños.
   3.1 Simpodio con tres hojas.
      L. hirsutum. Humb. & Bonpl.
   3.2 Simpodio con dos hojas.
      3.2.1 Inflorescencias con bracteas pequeñas o sin ellas (complejo sub. genérico *minutum*).
      a. Flores pequeñas (diámetro de la corola 1.5 cm o menos); semillas mm o más cortas.
      L. parviflorum. Rick, Kesicki , Fobes & Holle.
      b. Flores más anchas (diámetro de la corola 2 cm o mas); semillas 1.5 mm o más largas.
      L. chmielewskii. Rick, Kesicki, Fobes & Holle.
      3.2.2 Inflorescencias con brácteas anchas .
      a. Anteras asociadas en un tubo o cono estaminal, dehiscente por aberturas laterales (complejo subgenérico, *Peruvianum).*
         i. Plantas erectas: pedúnculo más largo de 15 cm, flores amontonadas; cono estaminal recto.
         L. chilese, Dun.
         ii. Plantas rastreras : pedúnculo más corto de 15cm; flores más pobremente agrupadas; cono estaminal generalmente estrangulado distalmente.
         L. peruvianum (L.)Mill.
      b. Antera libre, dehiscencia poral.
      L. pennelli. (Corr.) D' Arcy (anteriormente, *Solanum pennellii*. Corr.)

No obstante las diferencias morfológicas marcadas entre *Solanum* y *Lycopersicon*, los que ubican a los tomates dentro del género *Solanum*, manifiestan argumentos sólidos desde el punto de vista molecular (Peralta y Spooner, 2001; Darwin *et al.*, 2003; Spooner *et al.*, 2005; Peralta *et al.*, 2005), además de que también afirman que los sugéneros de *Potatoe* y *Lycopersicon* tienen similitudes morfológicas, como el hecho de que la mayoría son hierbas, pentámeras, con semillas pubescentes, entre otros (Chield, 1990). Por otro lado, los estudios de Lester (1991) y Spooner *et al.* (1993, 1997) establecen claramente que los tomates, papas y pepinos están muy estrechamente relacionados y son miembros del mismo grupo monofilético. A la luz de las evidencias morfológicas, genéticas y moleculares, no debe de existir duda de excluir al tomate dentro del género *Solanum*, situación que ha llevado a taxónomos y recientemente a mejoradores a adoptar a *Solanum* como nombre genérico y *lycopersicum* como nombre específico del tomate.

La diferenciación a niveles más bajos de especie han continuado y recientemente Nuez *et al.* (2004) estudiaron la variación existente dentro de la especie *cheesmanii* y describe a tres variantes (*short*, *long* y *minor*). En el Apéndice 1 se describen las características más importantes de las especies y variedades o subespecies del tomate descritas hasta la fecha y de sus parientes silvestres, adoptando el nombre genérico de tomate (*Solanum*) y agregadole su equivalente previo.

Genética

A la fecha se reconocen trece especies del género (*Solanum*) en el cual se ubica los tomates: *S. esculentum, S. pinpinellifolium, S. chiesmanii, S. pennellii, S. habrochaites, S. neorickii, S. chiemilewskii, S. chilense, S. peruvianum, S. arcanum, S. corneliomuelleri, S. galapagense,* y *S. huaylasense* (Darwin *et al.*, 2003; Spooner *et al.*, 2005; Peralta *et al.*, 2005). Todas las especies son diploides y con número cromosómico 2n=2x=24. Dada la importancia que tiene el tomate, las investigaciones al nivel genético son muy diversas; sin embargo aquí solo abordaremos aquellos que hicieron posible la elaboración del mapa del ligamiento y las que tienen que ver con el estudio de la estructura genética de las poblaciones.

Mapas de ligamiento

Los mapas de ligamiento genético son de gran importancia en las investigaciones básicas y aplicadas por tres razones principales. En primer lugar, son la clave para caminar a lo largo de los cromosomas, lo que nos permite localizar a genes de interés. Una vez identificado un gen que está fuertemente ligado a un marcador molecular, es posible llevar acabo su clonación. Un mapa de ligamiento con suficiente cantidad de marcadores genéticos, posibilita definir el punto de inicio para caminar a lo largo del cromosoma en cualquier gene de importancia del genoma (Tanksley *et al.*, 1992). En segundo lugar, los mapas de ligamiento con suficientes marcadores moleculares tienen una aplicación práctica en el mejoramiento genético de plantas y animales, dado que se asegura que cualquier carácter de importancia económica estará fuertemente ligado a cuando menos a un marcador molecular en el genoma de referencia . Esto, es de vital importancia, ya que podría ser explotado en los programas de mejoramiento genéticos, como marcadores que asisten a la selección (Burr *et al.*, 1983; Tankley *et al.*, 1989). Finalmente, los mapas de ligamiento que contengan muchos marcadores, nos dan la posibilidad de que el genoma en su totalidad estará completamente cubierto por marcadores moleculares definidos, y por lo tanto, se podrian detectar y caracterizar loci que definen los caracteres de mayor importancia económica (cuantitativos), los cuales pueden estar ubicados en cualquier parte del genoma (Paterson *et al.*, 1988; Lernder y Bolstein, 1989).

La idea de la construcción de los mapas de ligamiento fue propuesta a partir del análisis de los polimorfismo en la longitud del fragmento de restricción (RFLPs), inicialmente usado para humanos (Bolstein *et al.*, 1980); sin embargo, los mapas se han construido para una gran diversidad de organismos, entre los que se encuentra el tomate. Para esta especie, la primer aproximación fue dada por Bernatzky y Tanksley (1986), que desarrollaron este mapa usado isoenzimas y clonas aleatorias de ADN (cADN) derivadas de ARN mitocondrial (mARN). En este mapa se presenta la ubicación de todos los marcadores moleculares en cada uno de los cromosomas; sin embargo es de hacer notar que los cromosomas 9 y 11 no contienen ningún marcador molecular y las distancias entre marcadores es muy amplia. Estas desventajas fueron cubiertas en el trabajo que realizó Tanksley y colaboradores (1992), que elaboraron el mapa de ligamiento más completo de tomate. En este mapa se incluyen más de 1030 marcadores

moleculares con una distancia aproximada entre ellos de 1.2 cM (ca. 900 kb) y en la que en cada cromosoma seencontran al menos 50 marcadores.

Genética de poblaciones

La genética de poblaciones es el estudio de cómo las leyes Mendelianas y otros principios genéticos son aplicados a toda la población (Hartl y Clark, 1989). Este estudio es fundamental para el entendimiento de la evolución y de los procesos que la producen; desde el punto de vista poblacional, la evolución es el resultado de los cambio progresivos en la composición genética de las proporciones de las diferentes variantes de los alelos en las poblaciones (Nei, 1987; Hartl y Clarck, 1989; Suzuki *et al.*, 1996; Futuyma, 2005).

La genética de poblaciones, nos ayuda a conocer cuál es la composición genética de las poblaciones y cómo ésta puede ser modificada por los factores genéticos, ecológicos y evolutivos. Además, nos permite entender cómo es la estructuras genéticas de las poblaciones y como se distribuye esta en las mismas. La estructura genética de las poblaciones se ha podido evaluar más eficientemente a partir de la década de los 1990's gracias a la utilización de marcadores moleculares; sin embargo, la pregunta acerca de cuál es la base genética de la adaptación no se ha podido contestar del todo con marcadores moleculares (Hartl y Clark, 1988; Allard, 1999; Nybom y Bartish, 2000; van Tienderen *et al.*, 2002).

Para estudiar la estructura genética de las poblaciones del tomate se han utilizado isoenzimas, RFLPs, RAPDs y microsatelites como marcadores genéticos. Los primeros estudios de la variación genética del tomate y de sus parientes silvestres fueron realizados con isoenzimas. Rick y Fobes (1975), analizaron la variación de dos especies silvestres (*L. cheesmanii* y *L. pimpinellifolium)* en comparación con el tomate cultivado (*L. esculentum*), utilizando isoenzimas como marcadores moleculares en 400 materiales, encontrando que existe una diversidad genética tanto entre como dentro de poblaciones. Asimismo, confirmaron que las especies silvestres son más variables genéticamente que las cultivadas, al encontrar que *L. pimpinellifolium* es la especie más variable, y que contiene todos los alelos de las especies analizadas, así como algunos alelos únicos. Utilizando el mismo tipo de marcadores moleculares, Rick y Holle (1990), realizaron un ensayo de variación aloenzimática en la forma silvestre del tomate cultivado (*L. esculentum* var. *cerasiforme*) y en sus parientes silvestres Andinos más cercanos, encontrando una variación genética relativamente baja pero suficiente

para proveer indicios de hibridación, filogenia y posibles interacciones con los tomates cultivados. En estos estudios se analizó la variación genética de 246 colecciones del ancestro más cercano del tomate cultivado (*L. esculentum* var. *cerasiforme*) provenientes de las zonas montañosas de Perú, Ecuador y Bolivia. La variación genética fue analizada a partir de 20 loci enzimáticos y 5 loci morfológicos monogénicos. También observaron niveles de variación y frecuencia de alelos diferente en las regiones, siendo la parte central de Perú donde existe la mayor variación en cuanto a tamaño, forma y color de fruto. Además, mencionan que la variación medida en términos de proporción de alelos variantes fue de 0-20%. Finalmente, concluyen que el este Andino puede ser un centro de diversidad secundaria, pero no un probable sitio de domesticación del tomate cultivado.

Los marcadores moleculares RFLPs han sido también utilizados para definir la diversidad de las poblaciones de tomate y de sus parientes silvestres. Tanksley y Miller (1990) investigaron la diferenciación genética en las poblaciones de tomate y determinaron que la cantidad de variación genética existente tanto dentro como entre poblaciones difiere de manera significativa entre las diferentes especies. También confirmaron que la menor diversidad se encuentra en la especie cultivada (*L. esculentum)*, en donde reportan que menos del 10% de la variación está dentro de poblaciones, lo que significa que la mayoría de la variación genética está entre poblaciones. Por otro lado, confirman que las poblaciones silvestres de tomate (*L. peruvianum, L. hirsutum* y *L. pennelii*) incluyendo la variedad o subespecie del mismo (*L. esculentum* var. *cerasiforme*) tenían niveles de variación más altos que los calculados en los cultivos modernos. Dentro de las poblaciones silvestres obtieenen los niveles más altos de variación genética en las poblaciones que son autoincompatibles; se observó que 75% de los RFLP's son exclusivos en relación a los encontrados en las poblaciones compatibles, confirmando que el sistema de apareamiento es fundamental en la definición de la constitución genética de las poblaciones

Usando RFLPs y RAPDs Williams y St. Clair (1993), evaluaron los niveles de diversidad en las variedades clásicas (liberadas en 1960 o antes), modernas (liberadas después de 1960), variedades regionales de Sudamérica (introducidas en los últimos 200 años y mantenidas y mejoradas con germoplasma de *L. pimpinellifolium* (Rick, *et al.*, 1974), la forma silvestre del tomate cultivado (*L. esculentum* var. *cerasiforme*) y otra especie silvestre pariente del tomate cultivado (*L. cheesmanii*). Encontraron que la frecuencia de polimorfismo dentro de

los grupos es similar, independientemente del marcador utilizado. Sin embargo cuando utilizan los RAPDs como marcadores moleculares y se hace la comparación entre grupos, observan que el polimorfismo es menor en las variedades clásicas (2.8%) seguido especie silvestre *Solanum cheesmanii* (4.65%), las variedades modernas (11.6%), las variedades regionales (20.3 %) y el máximo polimorfismo fue encontrado en *L. esculentum* var. *cerasiforme* (24.5%). Explican que la basja diversidad en las variedades clásicas ha sido causada por los cuellos de botella (bottlenecks) impuestos por la endogamia de los materiales que introdujeron los españoles a Europa y que fueron la base para la formación de estas variedades. Por otro lado, el incremento de casi cuatro veces de variación en las variedades modernas se debe en éstas se han incorporado genes de otras especies, fundamentalmente los genes de resistencia, ampliando de esta manera la base genética y por consecuencia la diversidad. Finalmente, reportan que los RAPDs fueron los marcadores más sensible para detectar polimorfismos.

Rus-Kortekaas *et al.* (1994), compararon los niveles de variación genética entre poblaciones cultivadas (*L. esculentum*) y materiales silvestres (*L. pennellii, L. parviflorum, L. hisurtum, peruvianum*) utilizando RAPDs y microsatélites. Encuentran que los microsatélites detectan mayor cantidad de variación; además de que confirman la existencia de mayor variación genética en las especies silvestres respecto a las cultivadas. En sus estudios obtuvieron 66 bandas polimórficas en las poblaciones silvestres y 55 bandas en las cultivadas cuando se utilizan microsatélites como marcadores genéticos. Los niveles de polimorfismo fueron menores en ambas poblaciones cuando se utilizan los RAPDs como marcadores. Asimismo, reportan que el porcentaje de bandas compartidas en las poblaciones cultivadas y silvestres difieren cuando se utilizan los dos tipos de marcadores. De esta manera, las poblaciones cultivadas comparten 50.8% de bandas cuando se utilizan microsatélites en comparación con un 82.2% cuando se utilizan RAPDs. En cambio encuentran un 13.1% de bandas compartidas en las poblaciones silvestres cuando se utilizan microsatélites y 47.8% cuando se utilizan RAPDs. Estos resultados confirman la importancia del mantenimiento y conservación de las poblaciones silvestres de tomate, debido a que representan una fuente inagotable de genes de importancia para la agricultura moderna.

A partir de la clasificación de Rick (1979), en la que dividió la diversidad del tomate en dos grupos (complejo *esculentum* y complejo *peruvianum*), Egashira *et al.* (2000) analizaron la diversidad genética de las especies incluidas en cada complejo utilizando los RAPDs como

marcadores moleculares y demostraron que las especies incluidas en el complejo *peruvianum* (*L. peruvianum* y *L. chilense*) presentaron la mayor diversidad genética. Este resultado está en concordancia con el sistema de polinización ya que son autoincompatibles e incapaces de cruzarse con el tomate cultivado. Se detectaron 27 RAPDs (loci) con diez primers (oligos) en las dos colecciones de *L. esculentum* var. *cerasiforme*. El rango estuvo entre 0-7 (OPK3 y OPK7 respectivamente). Esto significa que detectaron un promedio de 2.7 locus por primer. También, encontraron que las poblaciones de *Solanum lycopersicum* var. *cerasiforme* se asocian con *L. pinpinelifolium*. Por otro lado, recientemente Primieri *et al.* (en prensa) utilizando el mismo marcador para analizar la diversidad genética en poblaciones cultivadas y locales de tomate del Brazil, encuentran que existen diferencias significativas entre ambos grupos, indicando que las poblaciones locales de tomate pueden ser una fuente importante de variación en los programas de mejoramiento de este cultivo.

Apéndice 1.

Descripción de las especies, variedades o subeespecies silvestres emparentadas con tomate

***Solanum lycopersicum* L. , [*Lycopersicon esculentum* Mill.]**

Este es el tomate cultivado que se ha distribuido alrededor del mundo. El lugar de domesticación del tomate cultivado es polémico; sin embargo la mayoría de las evidencias sugieren que es México. Todas las formas de *Solanum lycopersicum* son autocompatibles (Esquinas-Alcázar, 1981).

***Solanum lycopersicum* var. *cerasiforme*, [*Lycopersicon esculentum* var. *cerasiforme (Dun) Gray*.]**

Es la forma, variedad o subespecie silvestre del tomate cultivado, y se distribuye en todas las regiones tropicales y sub tropicales del mundo. Se comporta como maleza de los cultivos. Se considera a la región de Ecuador y Perú su centro de origen y distribución. En las costas Peruanas sobrevive en condiciones pobres en tierras montañosas donde se ha adaptado y sobrevive, gracias a la maduración temprana y a la produción abundante frutos, a pesar de la muerte temprana de cultivos. Se le considera como el más probable ancestro inmediato del tomate cultivado dado que es la forma silvestre común, abundante en América tropical y subtropical (Jenkins, 1948; Rick, 1978).

***Solanum pimpinellifolium* L. [*Lycopersicon pimpinellifolium* (L.) Mill.]**

Es una especie de frutos rojos originaria de Perú y Ecuador, se desarrolla tanto en hábitats mesofíticos como en condiciones de sequía. Esta especie pueden ser autógama, presentando grados variables de alogamia en los lugares de origen, sobretodo en la zona costera norte del Perú (Rick *et al.*, 1977). Esta especie se encuentra a altitudes menores a 1000 m.s.n.m. (Taylor, 1986); todas las poblaciones de *pimpinellifolium* son autocompatibles y con frutos coloreados similares a los del tomate cultivado; sin embargo, son muchos más pequeños ya que miden aproximadamente 1 cm de diámetro. Uno de los caracteres que se puede utilizar para distinguirla de especie *lycopersicum* es el margen de las hojas que no es aserrado como el tomate cultivado y produce una mayor cantidad de flores por inflorescencia (Muller, 1940;

Taylor, 1986). Se cruza fácilmente con el tomate cultivado, con el que muestra introgresión, lo que permite inferir que junto con la var. *cerasiforme* puede estar involucrado de manera directa como ancestro del tomate cultivado (Rick, 1976). Es la especie de tomate que más ha sido utilizada como fuente de germoplasma en los programas de mejoramiento genético para incorporar características de resistencia de plagas y enfermedades a las variedades cultivadas de tomate (Rick,1978).

***Solanum cheesmaniae* (L. Riley), [*Lycopersicon cheesmaniae* (L. Riley)]**

Es la especie con el hábitat más restringido, prefiriendo lugares de poca altura de la zona litoral salina del archipiélago de las Galápagos, lo que la hace ser es una especie tolerante a la sal. Todas las formas de *cheesmaniae* son compatibles, autofecundables, e hibridiza fácilmente con el tomate cultivado (Muller, 1940; Taylor, 1986; Esquinas-Alcázar, 1981). Esta forma silvestre representa un recurso genético de vital importancia en los programas de mejoramiento genético. Nuez, *et al.* (2004) describe tres variedades o subespecies (*short*, *long* y *minor*).

Solanum cheesmaniae* var. *short

Esta variante es encontrada solamente sobre los acantilados y áreas abiertas que no se encuentran perturbadas. La germinación es muy lenta y en muchas ocasiones la testa debe de ser removida para permitir la germinación. Las plantas tienen un follaje verde pálido y entrenudos cortos (2-4 cm), característica que persiste a pesar de encontrarse en suelos buenos y condiciones uniformes. Las hojas y tallos son muy quebradizos y los frutos son de color rojo naranja (Nuez, *et al.*, 2004).

Solanum cheesmaniae* var. *long

Esta variante es encontrada a campo abierto en las Islas Galápagos. Su follaje es más oscuro que el de la forma *short;* en cambio, los entrenudos son más largos (5-8 cm) que en la forma *short* . La germinación es buena y rápida. Las hojas y tallos no tienen la característica de ser tan quebradizos como la forma *short* y los frutos varían de amarillo paja al amarillo naranja gris (Nuez, *et al.*, 2004).

Solanum cheesmaniae* var. *minor

Esta forma sólo es encontrada en las áreas no perturbadas de la costa y las semillas tiene una alta latencia. Tienen un follaje verde pálido, con entrenudos que van de 2-4 cm, y la

morfología de la planta es muy distintiva ya que las hojas son erectas y más pinadas, además de que toda las partes de la planta son extremadamente quebradizas. El fruto es similar a la forma *short* (Nuez, *et al.*, 2004).

***Solanum chmielewskii* (Rick, Kesicki Fobes y Holle), [*Lycopersicon chmielewskii* (Rick y Kesicki)]**

Esta especie se caracteriza por tener tallos delgados; la hoja es simple al igual que su inflorescencia, frutos maduros en color verde-blanco. Es nativo de una zona restringida a la Cordillera de los departamentos de Aporimar y Ayacucho, Perú, y prefiere las condiciones de medianas altitudes. De acuerdo a los estudios realizados, su variación de aloenzimas es moderadamente variable, autocompatible y es sujeta a la polinización cruzada (Rick,1979). La característica más sobresaliente del taxón es su alto contenido de sólidos solubles, aspecto de gran importancia para tomates industriales (Lobo y Medina, 1998).

***Solanum neorickii* (Spooner, Anderson y Jansen), [*Lycopersicon parviflorum* (Rick, Kesicki, Fobes y Holle)]**

Es similar a *chmielewskii* en la mayoría de las características morfológica y autoecológicas, excepto por su tamaño de flor y tendencias a crecer a menores altitudes. Esta entidad es una especie descendiente de *chmielewskii*, ocupa el mismo territorio pero se extiende hacia el norte a la frontera de Ecuador. Es altamente autógama y genéticamente uniforme (Rick, 1978). Posiblemente se originó de *chmielewskii*, aislándose de éste por adquisiciones de autogamia (Rick, 1977).

***Solanum habrochaites* (Knapp y Spooner), [*Lycopersicon hirsutum* (Dunal)]**

Las plantas de esta especie se caracterizan por ser robustas, pubescentes, frutos verdes y con olor desagradable, distinguiéndola por este último carácter con el resto de las especies. Es nativa del oeste del Perú y Ecuador, pero también extiende su distribución al este de la división continental en Ecuador y parte norte del Perú (Rick,1978). Esta planta puede hibridizarse con *Solanum lycopersicum* pero solo si esta última funciona como progenitor femenino (Rick,1978). No es capaz de soportar las heladas y las bajas temperaturas; sin embargo, los biotipos de las elevaciones más altas (3200 m.s.n.m.) son más resistentes al daño por frío que

aquellas de elevaciones más bajas. Esta especie es utilizada como fuente de resistencia a insectos en los programas de mejoramiento genético (Rick,1978).

***Solanum pennellii* (Correll), [*Lycopersicon pennellii* (Correll) D'Arcy]**

Es una especie que contiene frutos verdes e hibridiza fácilmente pero unilateralmente con *lycopersicum*. Su distribución se limita a elevaciones medias del centro de Perú. *Solanum pennelli* ocupa las elevaciones más altas. La habilidad de tener la capacidad de soportar condiciones secas, parece que le confiere la capacidad a las hojas de *pennellii* de resistir la pérdida del agua (Rick,1979).

***Solanum peruvianum* (L), [*Lycopersicon peruvianun* (L) Mill.]**

Esta especie y *chilense* forman un complejo subgenérico que se separa del resto de las especies. La cruza con *lycopersicum* puede hacerse sólo con gran esfuerzo y la aplicación de cultivo de tejidos. La especie se distribuye ampliamente en Perú a lo largo de las costas y al oeste. Se extiende en la parte norte de Chile y hacia el noroeste, y regularmente en el río Marañon. *Solanum peruvianum* es la especie más variable de los tomates (Rick, 1978).

***Solanum chilense* (Dunal) Reiche, [*Lycopersicon chilense* (Dunal)]**

Además de formar un complejo subgenérico con *chilense*, se distigue de éste por que se desarrolla bajo condiciones más secas (Rick,1978), además de tener un sistema radicular más profundo, lo que le permite ser un recurso genético en programas de mejoramiento para incorporar tolerancia a sequía en el tomate cultivado (Sánchez-Peña *et al.*, 1995).

Solanum arcanum (Peralta) [parte de *Lycopersicon peruvianum* (L.) Miller]

Es una especie descrita recientemente (Peralta *et al.*, 2005). Anteriormente fue parte de la especie *peruvianum*. Es una especie extremadamente variable que de acuerdo a datos moleculares y morfológicos está muy relacionada con las especies *neorickii* y *chmielewskii*. Se distribuye en el norte de Perú a elevaciones que van de 100 a 2800 m (Peralta *et al.*, 2005).

Solanum corneliomuelleri (J. F. Macbr.) [parte de *Lycopersicon peruvianum* (L.) Miller, también conocida como *Lycopersicon glandulosum* C. F. Mull.]

Es una especie que anteriormente fue parte de *peruvianum*. Se distribuye del centro al sur de Perú y al oeste de las cordillera de los Andes a elevaciones que van de 200 a 3300 m. s. n. m. (Peralta *et al.*, 2005).

Solanum galapagense (Darwin and Peralta) [parte de *Lycopersicon cheesmaniae* (L.) Riley, previamente conocida como var. *minor*]

Es una especie que anteriormente fue parte de *cheesmaniae*. Es endémica de las Islas Galápagos en la parte costera, frecuentemente a elevaciones de 1 m. s. n. m., pero ocasionalmente puede encontrarse a 50 m. s. n. m. (Peralta *et al.*, 2005).

Solanum huaylansense (Peralta) [parte de *L. peruvianum* (L.) Miller]

Es una especie descrita recientemente (Peralta, *et al.* 2005). Anteriormente fue parte de la especie *peruvianum*. Es una especie que se distribuye en el norte de Perú a lo largo del río Santa, a elevaciones que van de 200 a 3300 m. s. n. m. (Peralta *et al.*, 2005).

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CAPÍTULO II

SOURCES OF RESISTANCE TO WHITEFLY IN WILD POPULATIONS OF *SOLANUM LYCOPERSICUM* VAR. *CERASIFORME* IN NORTHWESTERN MEXICO

FUENTES DE RESISTENCIA A MOSQUITA BLANCA EN POBLACIONES SILVESTRES DE *SOLANUM LYCOPERSICUM* VAR. *CERASIFORME* EN EL NOROESTE DE MÉXICO

Resumen

La variación genética que albergan poblaciones silvestres de especies estrechamente emparentadas a plantas cultivadas, constituyen un importante recurso genético potencialmente útil en los programas de mejoramiento. En este artículo, se analiza la variación de ocho poblaciones silvestres de tomate (*Solanum lycopersicum* var. *cerasiforme*) en un experimento de jardín común, respecto a sus niveles de infestación por mosquita blanca, la densidad de tricomas foliares, como un carácter defensivo que evita la infestación de mosquita blanca, y el efecto que tiene la incidencia de la mosquita blanca sobre caracteres vegetativos y reproductivos de la planta. Se cuantificó el número de adultos de mosquita blanca en ocho poblaciones silvestres de *Solanum lycopersicum* var. *cerasiforme*, en la especie silvestre *Solanum habrochaites* (C-360 = *L. hirsutum*), y una variedad cultivada de *S. lycopersicum* (variedad Río Grande). Se detectaron diferencias significativas entre las poblaciones de *S. lycopersicum* var. *cerasiforme* para el porcentaje de incidencia de mosquita blanca y densidad de tricomas. El tomate cultivado presentó los niveles *más* altos de incidencia de mosquita blanca ($\bar{x}$ = 7.50 ± 0.14), seguido de *S. lycopersicum* var. *cerasiforme* ($\bar{x}$ = 2.02 ± 0.92), mientras que las plantas de *S. habrochaites* presentaron los niveles más bajos de incidencia ($\bar{x}$ = 0.36 ± 0.35). La incidencia de mosquita blanca se correlacionó negativamente con la densidad de tricomas (r = -0.38, $P < 0.0001$), sugiriendo que los tricomas limitan el establecimiento de la mosquita blanca, y fue un componente defensivo. Asimismo, se detectó un efecto significativo y negativo de la incidencia de mosquita blanca a lo largo del desarrollo de la planta, con respecto a la tasa de crecimiento (número de ramas y altura) y la producción de frutos.

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Sources of resistance to whitefly in wild populations of *Solanum lycopersicum* var. *cerasiforme* in Northwestern Mexico

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Abstract

Genetic variability of wild populations, closely related to domesticated species, constitute important genetic resources for plant breeding programs. In this paper, we analysed the variation of eight wild populations of *S. lycopersicum* var. *cerasiforme* in a common garden experiment for levels of plant infestation by whitefly, leaf trichome density as a defensive character preventing infestation by whitefly, and the effect of whitefly incidence into vegetative and reproductive plant characters. Number of adults of whitefly was recorded in the eight wild populations of *S. lycopersicum* var. *cerasiforme*, one population of the wild species *S. habrochaites* (C-360), and one of a cultivated variety of *S. lycopersicum* (Rio Grande). There were significant differences among the wild populations of *S. lycopersicum* var. *cerasiforme* in the average level of whitefly incidence and trichome density. Cultivated tomatoes had the higher incidence of whiteflies ($\bar{x} = 7.50 \pm 0.14$) followed by plants of *S. lycopersicum* var. *cerasiforme* ($\bar{x} = 2.02 \pm 0.92$) and plants of *S. habrochaites* with the lowest incidence ($\bar{x} = 0.36 \pm 0.35$). Whitefly incidence was negatively correlated with trichome density ($r = -0.38, p < 0.0001$), suggesting that trichomes deter or limit the establishment of whiteflies. Additionally, a significant negative effect of whitefly incidence along the growing season upon plant growth rate (number of branches and height) and fruit production was detected.

Introduction

After insecticides started to be applied for the control of insect pest populations, the number of pest species that acquired resistance against these chemicals has increased exponentially (Georghiou 1972; Metcalf 1994). The recognition that the evolutionary response of insect pests against

insecticides is economically unsustainable, pointed out the need for the development of long-term strategies of pest management programs (Rausher 2001; Stuiver and Custers 2001). During the last decades the tomato leaf curl geminivirus, transmitted by the whitefly, has increased its levels of incidence upon horticulture crops (Brown and Nelson 1988; Idris and Brown 1998; Idris et al. 2001; Narasegowda et al. 2003). Cultivated tomato (*Solanum lycopersicum* L.) (Spooner et al. 1993) is one of the main crops affected by whitefly, which has repeatedly overcome the toxic effects of insecticides. Only in the southern region of the United States the disease transmitted by whitefly resulted in 500 million dollar losses between 1991–1993 (Ramírez 1996). In tropical and subtropical areas, yield losses can reach levels around 50–90% of total production (Pico et al. 1996; Ramírez 1996; Torres-Pacheco et al. 1996). During the same period, cost increment of insecticides for the control of whitefly populations rendered this practice less profitable, particularly for small farmers. The introduction of resistance genes into cultivated lines from wild relatives using traditional crop improvement methods, is one alternative to reduce losses by insect pests (Allard 1978). This technique has been used to introduce resistance genes in (*S. lycopersicum*) from wild relatives (Rick 1973, 1987; Kasrawi et al. 1988; ■ Please add this reference in list■ Zakay et al. 1991; Freitas et al. 2002). However, the current low levels of tomato resistance to whitefly (Freitas et al. 2002), make necessary the screening of additional sources of genetic resistance.

Plant diversity of tropical and subtropical Mexico constitutes an important source of genetic resources for future crop improvement, and it is considered one of the major centres of domestication in the world (Harlan 1971; Rick 1979). Sinaloa state is the most important region of Mexico for the production of tomato *S. lycopersicum* (SAGARPA 2004). In this region the negative effects of whitefly have been observed since 1960 (Ramírez 1996). Similarly, wild populations of *S. lycopersicum* var. *cerasiforme* (Dunal) Spooner, Anderson and Jansen, closely related to cultivated tomato, occurs in abandoned fields, formerly tropical dry forest within coastal sites and in the Pacific slopes (ca. 300–1100 m) of The Sierra Madre Occidental of Sinaloa state. These populations constitute a natural source of potential resistance genes against whitefly. *S. lycopersicum* var. *cerasiforme* has scarcely studied as a source of genetic resistance for cultivated tomato. Hence, in this study we describe the natural variation in levels of infestation by whitefly, leaf trichome density, vegetative and reproductive characters in plants of *S. lycopersicum* var. *cerasiforme* collected from eight wild populations and transplanted into a common garden. Additionally, we examined the association between whitefly infestation and leaf trichome density, a putative defensive character. For the analysis of whitefly incidence and leaf trichome density we also analysed the resistant wild species *S. habrochaites* Knapp and Spooner, and one susceptible commercial variety (Rio Grande) of *S. lycopersicum*.

Materials and methods

Study system

The genus *Solanum* (Solanaceae) includes the cultivated species *S. lycopersicum* L. (tomato) and several wild relatives (*pinpinellifolium*, *cheesmaniae*, *chmielewskii*, *pennellii*, *chilense* and *peruvianum*; Taylor 1986; Spooner et al. 1993). The domesticated *S. lycopersicum* has a wild relative, *S. lycopersicum* var. *cerasiforme* (Esquinas-Alcazar 1981; Spooner et al. 1993), distributed in tropical and subtropical areas (Esquinas-Alcazar and Nuez 2001). In Mexico, *S. lycopersicum* var. *cerasiforme* is a widely distributed ruderal plant, associated to cultivated fields of tomato and behaves as a weed of vegetable crops (Sánchez-Peña 2000).

Plant material

Eight populations of *S. lycopersicum* var. *cerasiforme* were collected along a latitudinal North-South transect of 700 km in the states of Sinaloa and Nayarit in northwestern Mexico. In 2000, ten mature fruits were collected from each of 35 randomly selected individual plants in the localities of Jahuara, Mocorito, Limonba, Ensenada, Urraca, Potrerillo, Isla del Bosque and Quimichi (Table 1). These sites are separated by an average distance of 90 km. Seeds of one cultivated variety of *S. lycopersicum* (Rio Grande) and of the wild species *S. habrochaites* (C-360) (Knapp and Spooner 1999)

Table 1. Geographic location of eight populations of *Solanum lycopersicum* var. *cerasiforme* in Northwestern Mexico.

Population	Location (Lat. N-Long. W)		Altitude m a.s.l.	Mean number of white flies ± SD	Mean number of leaf trichomes ± SD
Jahuara	26°00′	108°55′	45	1.15^{dc} ± 0.50	26.79^{cd} ± 7.69
Mocorito	25°28′	107°55′	80	1.59^{cd} ± 0.61	48.17^{ab} ± 16.98
Limonba	25°35′	107°20′	1104	1.97^{bcd} ± 0.67	28.48^{cd} ± 5.79
Ensenada	24°00′	106°40′	84	1.56^{cd} ± 0.49	26.06^{cd} ± 7.89
Urraca	23°04′	106°17′	20	2.64^{b} ± 1.00	38.56^{bc} ± 7.53
Potrerillo	23°27′	105°52′	900	2.82^{b} ± 0.93	24.22^{d} ± 5.41
I. Bosque	22°43′	105°52′	12	2.27^{bc} ± 0.93	27.05^{cd} ± 10.38
Quimichi	22°24′	105°29′	50	2.36^{bc} ± 0.86	25.96^{cc} ± 7.60
S. habrochaites				0.36^{e} ± 0.35	52.81^{a} ± 10.46
'Saladette'				7.50^{a} ± 0.14	14.00^{dc} ± 10.66
Mean				1.89 ± 1.19	33.01 ± 13.96

Mean number of white flies per plant and of leaf trichomes (0.025 mm^2) in each population. Means of *Solanum habrochaites* and the cultivated variety 'Saladette' are provided. Mean with same letters did not differ significantly after the Bonferroni correction ($p > 0.001$).

were obtained from the germplasm bank of INIFAP (Instituto Nacional de Investigaciones Forestales y Pecuarias, Km 16.5, Carretera Culiacán-El Dorado, Culiacán, Sinaloa.). Among the six species of whitefly recorded in the State of Sinaloa, two species are the most abundant at the site where the experiment was carried out, *Bemisia argentifolii* and *Bemisia tabaci* (Ramírez 1996).

Experiment

Seeds from each plant collected were germinated in the greenhouse of INIFAP, and transplanted to an experimental plot after the first two true leaves were fully expanded (November 2001). Plants were arranged following a completely randomised design in a plot of 2520 m^2. Within a row, plants were 1 m apart, and rows were separated by 1.8 m. Plants were first monitored at day 60 after transplanting and then every 30 days until the end of the experiment (150 days; May 2002). A total of 24 plants of *S. lycopersicum* var. *cerasiforme* of each population were monitored for plant height, number of branches, fruit production and fruit weight. Relative growth rate was calculated as the relative increment in plant height and number of branches between the first $_{(1)}$ and fourth $_{(4)}$ censuses [$(ln\ height_4 - ln\ height_1)/ln height_1$] and [$(ln$ number of $branches_4 - ln$ number of $branches_1)/ln$number of $branches_1$], respectively. Fruit production was estimated in the last census by counting the total number of fruits per plant in the main branch. Fruit weight was estimated as the average fruit weight for each plant in the main branch.

The number of adults of the whitefly (hereafter whitefly incidence) was also recorded in each of 20 plants for the eight wild populations of *S. lycopersicum* var. *cerasiforme*, the wild species *S. habrochaites* (C-360), and the cultivated variety (Rio Grande). The total number of individual whiteflies was recorded in the adaxial side of the leaves. Records were taken early in the morning (from 0600 to 0800 h), when the insects are inactive. A total of ten censuses were taken along the growing season. Previous studies indicate that sampling the leaf immediately below the most recently matured inflorescence is a reliable estimator of whitefly incidence (Aviles 1997). In the last census, four leaves of each plant were collected randomly to estimate leaf trichome density on the abaxial and adaxial surfaces of the leaf at three positions: apical, middle and basal. Because the studied *Solanum* spp. has a compound leaf, trichome density was estimated for the largest leaflet within a leaf. Trichomes were counted within each position within the leaf, using a stereoscopic microscope (100×) in an area of 0.025 mm^2 following Valverde et al. (2001). To assess differences in both trichome density and trichome morphology among populations, the second leaflet was fixed in FAA, dehydrated through ethanol series (30–100%), and finally in absolute acetone. The material was subjected to critical point drying with CO_2 in a pressure chamber (CPA II, Jeol JFC

1100) and coated with gold to obtain images of leaf trichomes under a scanning electron microscope (JEOL JMS-35).

Data analysis

Number of whiteflies on individual plants during the experiment was analysed using repeated measure analyses of variance (Scheiner and Gurevitch 1993). Number of whiteflies was log-transformed to improve normality before running the final analysis.

Nested analysis of variance was used to explore possible sources of variation associated with trichome density (e.g., population, plant, leaf, and position within the leaf). Leaf was nested within plants, and plants nested within populations (Sokal and Rolhf 1995). All these sources of variation were considered random. Position in the leaf (apical, middle and basal) was considered a fixed factor. Separate analyses were performed for the adaxial and abaxial surfaces of leaves. Further analyses of variance were performed to examine variation among plants within a population (i.e., genetic variation) using 20 plants per population. Individual values of leaf trichome density and whitefly incidence were correlated using the Pearson correlation coefficient. A phenotypic correlation matrix was estimated for trichome density, whitefly incidence (cumulative number of whiteflies/plant), relative growth rate (height), relative growth rate (number of branches), fruit production at the end of the experiment (150 days), and average fruit weight (150 days). All analyses were performed using the JMP statistical package (SAS 1995).

Results

Plants of the cultivated tomato had the highest mean incidence of whiteflies during the experiment ($\bar{x} = 7.50 \pm 0.14$) (Figure 1). Wild resistant plants of *S. habrochaites* had the lowest ($\bar{x} = 0.36 \pm 0.35$), whereas the wild plants of *S. lycopersicum* var. *cerasiforme* had intermediate values of whitefly incidence ($\bar{x} = 2.02 \pm 0.92$).

Whitefly incidence differed significantly among populations of *S. lycopersicum* var. *cerasiforme* during the growing season (Table 1, 2). Regarding whitefly incidence, plants of *S. lycopersicum* var. *cerasiforme* had values ranging from 1.15 to 2.82 (Table 1). The Urraca (2.64) and Potrerillo (2.82) populations were the most susceptible with a one-fold increase in whitefly incidence compared to Jahuara (1.15) and Mocorito (1.59) populations that were the most resistant to whitefly incidence (Table 1). A significant time (i.e., census) effect was detected indicating that whitefly incidence was higher at the end of the growing season. Finally, the interaction time × population was also significant (Table 2).

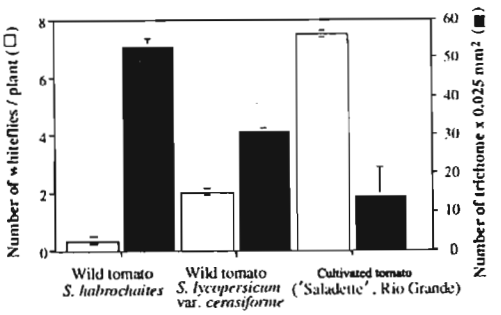

Figure 1. Mean whitefly incidence (±SE) and leaf trichome density for wild and cultivated populations of tomato, *Solanum* spp.

Table 2. Repeated measures analysis of variance of whitefly incidence in wild populations of *Solanum lycopersicum* var. *cerasiforme* in Northwestern Mexico.

Source of variation	d.f.	Wilk's Lambda	*F*	*p*
Population	9, 178	0.1726	94.74	< <0.0001
Time	9, 170	0.3455	35.77	<0.0001
Time × Population	81, 1107	0.0813	6.48	<0.0001

Plants of *S. lycopersicum* var. *cerasiforme* displayed a wide range of variation in mean values of trichome density from 24.22 to 48.17 (Table 1). The Mocorito population (48.17) had the highest mean value of trichome density, while Potrerillo (24.22) and Limonba (24.48) presented 50% less of trichome density (Table 1). Trichome density was higher on the adaxial ($\bar{x} = 30.31 \pm 16.30$) rather than on the abaxial side of the leaf ($\bar{x} = 14.29 \pm 10.29$) (paired *t*-test: $t_{2063} = -64.84$, $p < 0.0001$). Trichome density on both sides of the leaf was highly correlated ($r_{Pearson} = 0.73$, $p < 0.0001$, n = 2064). Because

whitefly is mainly present in the adaxial side of the leaf, and because the same analysis for the abaxial side of the leaf revealed qualitatively similar results, only the results of trichome density for the adaxial side are presented (Table 3). Significant within-plant variation was detected as well as differences between the positions in the leaf (apical, middle and basal). Scanning electron microscope photomicrographs of leaf epidermis from *S. lycopersicum* var. *cerasiforme* showed marked differences in trichome density between populations (Figure 2a, b). In addition, *S. habrochaites* presented higher proportion of glandular trichomes (Figure 2c) compared to *S. lycopersicum* var. *cerasiforme* (Figure 2a, b).

Trichome density in the adaxial side of the leaf showed significant differences among populations (Table 3, Figure 1). The population of *S. habrochaites* had highest number of trichomes 0.025 mm^{-2} ($\bar{x} = 52.81 \pm 10.46$), followed by the wild populations of *S. lycopersicum* var. *cerasiforme* ($\bar{x} = 30.62 \pm 12.07$), and the cultivated tomato ($\bar{x} = 14.00 \pm 10.60$) (Table 1).

The hierarchical analysis of variation in leaf trichome density indicated that the highest proportion of explained variance is accounted at the population level (35.3%). Yet, variation among individual plants within population and leaves within plants, explained a significant amount of variance also (17.7% and 29.3%, respectively; Table 3). Position in the leaf was significant although it explained the lowest percentage of variation in leaf trichome density (2.4%). Univariate analysis in each population of *S. lycopersicum* var. *cerasiforme* indicates significant differences among plants in trichome density suggesting the existence of genetic variation within populations (for all the ANOVA's, minimum $F = 3.83$, all $p < 0.0001$).

A significant negative correlation between leaf trichome density and whitefly incidence indicated that plants with higher number of trichomes were less infected by whiteflies ($r = -0.38$,

Table 3. Nested analysis of variance of trichome density in the adaxial side of the leaves in *Solanum lycopersicum* populations in Northwestern Mexico.

Source of variation	d.f.	MS	*F*	*p*	% Variance
Population	9	20.4427	24.94	<0.0001	35.28
Plant (Pop.)	162	0.8634	3.03	<0.0001	17.72
Leaf (Plant, Pop.)	515	0.2816	6.76	<0.0001	29.32
Position in the leaf	2	4.5245	108.61	<<0.0001	2.39
Error	1375	0.0416			15.28

Similar results were obtained in a separate analysis for trichome density in the abaxial side of the leaves (see text).

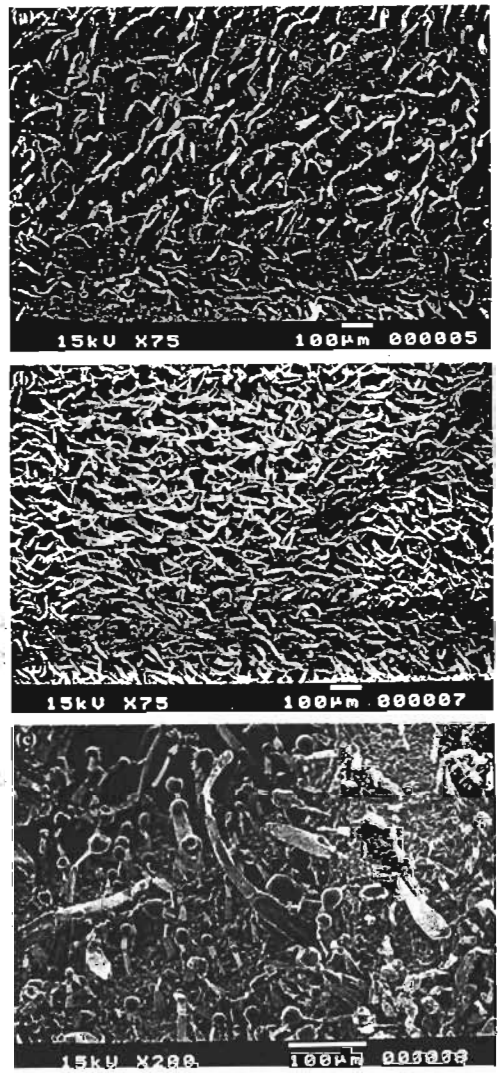

Figure 2. Scanning electron microscope photomicrographs of the leaf epidermis (adaxial) *Solanum lycopersicum* var. *cerasiforme*: (a) Ensenada population (75×), and (b) Mocorito population (75×), and (c) *Solanum habrochaites* (200×). Bar = 100 µm.

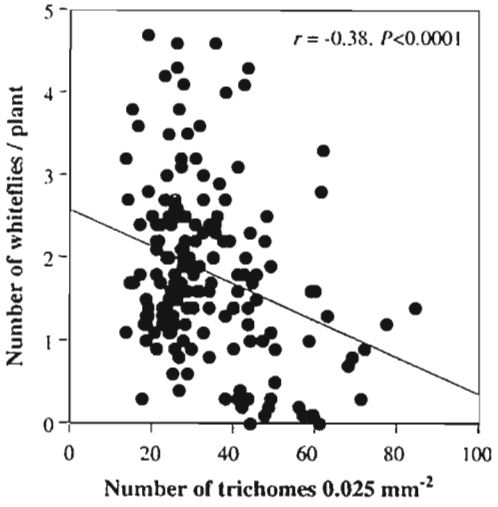

Figure 3. Relationship between whitefly incidence and trichome density in Solanum lycopersicum spp.

$p < 0.0001$, Figure 3). The analysis of the relationship between whitefly incidence with both growth rate (height increment and branch number) and reproductive output revealed a significant negative association between mean whiteflies/plant and mean relative growth rate and reproduction (Figure 4a–c). No relationship was detected between number of whiteflies/plant and average fruit weight ($r = -0.08$, $p = 0.3704$). The amount of trichomes per unit area showed a significant positive correlation with the number of fruits (Figure 5), and no association with relative growth rate.

Discussion

The results of the present study indicate that populations of *S. lycopersicum* differ in their level of whitefly incidence and leaf trichome density when grown in a common garden. Variation across species in whitefly incidence levels (*S. lycopersicum* > *S. lycopersicum* var. *cerasiforme* > *S. habrochaites*) supports previous studies indicating that cultivated species are less resistant against herbivores than wild populations (Martins et al. 2001; Freitas et al. 2002; Tripathi and Varma 2002). Variation in populations of *S. lycopersicum* var. *cerasiforme* from northwest-

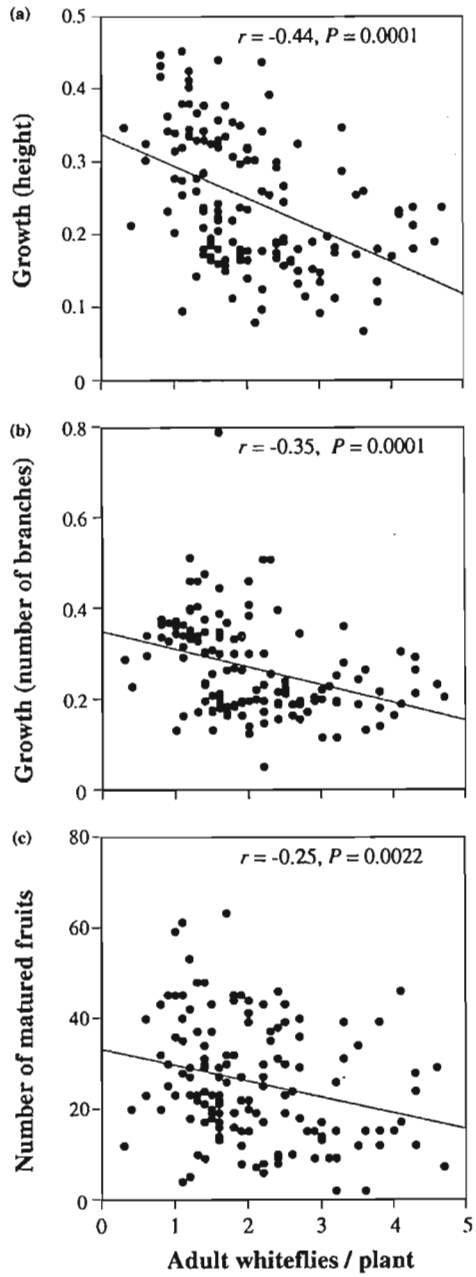

Figure 4. Correlations between whitefly incidence (number of adult whiteflies per plant) and relative growth rate in height, number of branches, and fruit production in *Solanum lycopersicum* var. *cerasiforme*.

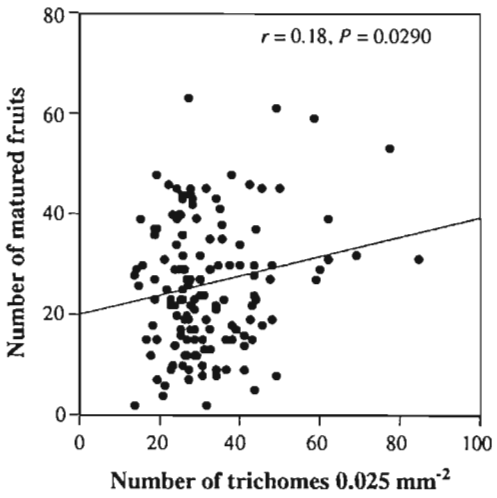

Figure 5. Correlations between number of leaf trichomes 0.025 mm^{-2} and fruit production in *Solanum lycopersicum* var. *cerasiforme*.

ern Mexico suggests that they differ in their level of resistance against whiteflies and trichome density. Moreover, the negative relationship between whitefly incidence and leaf trichome density indicates that trichomes may constitute a component of plant resistance against whiteflies.

Given that wild populations of *S. lycopersicum* var. *cerasiforme* inhabit, at least during the last 50 years, the same geographic area as cultivated tomato in northwestern Mexico, it is likely that wild populations might have been exposed to the selective pressure imposed by whiteflies. This constitutes a plausible explanation for the higher level of resistance against whitefly detected in wild populations. At the same time, wild populations of tomato (*S. lycopersicum* var. *cerasiforme*) have not been sufficiently explored as a source of genetic resistance against whitefly. For this reason, it must be incorporated in future breeding programs to increase pest resistance in tomato. Previous studies indicated that *S. lycopersicum* var. *cerasiforme* may also represent an important source of resistance against fungal diseases and drought stress (Rick 1973).

The experiment carried out attempted to mimic the conditions of cultivation of tomato in the northwestern Mexico both in timing and cultural practices. Three aspects of it merit to be highlighted. First, by using a common garden experiment the phenotypic differences among populations of *S. lycopersicum* var. *cerasiforme* produced by climatic/biotic conditions were eliminated. Second, by randomising individual plants of each population within the experimental plot equivalent probabilities of being found by whiteflies were provided. Finally, the prevalence of phenotypic differences among populations in some plants traits but especially in relation to resistance to whiteflies suggest the existence of genetic differences among populations. The finding of differences in the level of infestation by whiteflies among wild populations of *S. lycopersicum* var. *cerasiforme*, is relevant to pest management and potential use of wild relatives of *S. lycopersicum* to improve resistance to pests like *Bemisia* spp. On the other hand, the analysis of a putative defensive plant character, trichome density, demonstrated the existence of differences among populations. Similarly, although there is intra-plant variation in trichome density, the high and significant component of variance explained by plants within population suggest genetic differences for this character. Moreover, the negative relationship between whitefly abundance on a plant with trichome density is consistent with the interpretation that trichomes, or a correlated character, limit or prevent the establishment of whiteflies. Previous studies also found evidence of the defensive role of leaf trichomes in *S. lycopersicum*. (Freitas et al. 2002; Kennedy 2003). Thus, it is justified to assume trichomes as a defensive character in *S. lycopersicum* var. *cerasiforme*.

Herbivorous insects are detrimental to plant fitness and crop yield in cultivated species. Herbivores can kill a whole plant or can act as a parasite by reducing plant growth and its ability to survive and reproduce (Crawley 1997). Our results also indicated that levels of incidence of whiteflies were correlated with a reduction in plant growth and fruit production. This evidence is indicative of the fitness costs of pest infection to individual plants. Thus, besides the potential detrimental effects of whitefly as a vector of the tomato leaf curl virus it may reduce yield in tomato plants at moderate levels of infestation. This result has not been previously pointed out. In contrast, a fitness benefit of trichome density may be present provided the positive correlation between fruit production and trichome density. These results in turn indicate

that trichome density is a profitable target trait for future studies of plant resistance in tomato.

Resistance to whitefly in tomato via the fixation of defensive plant characters (i.e., high density of leaf trichomes) might reduce the incidence of the tomato leaf curl virus, and hence points the importance of survey and preserve genetic variation of wild populations. However, the analysis of additive genetic variation (i.e., relevant to selection) in both plant resistance to whitefly and leaf trichome density is a necessary step to determine their potential in tomato improvement.

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CAPÍTULO III

GENETIC VARIATION AND DIFERENTIATION AMONG MEXICAN WILD AND CULTIVATED POPULATIONS OF TOMATO (SOLANACEAE) ANALYZED BY RAPDS MARKERS

VARIACIÓN GENÉTICA Y DIFERENCIACIÓN ENTRE POBLACIONES SILVESTRES Y CULTIVADAS DE TOMATE (SOLANACEAE) ANALIZADAS CON MARCADORES RAPDs

RESUMEN

En este estudio se analizó la variación genética y la diferenciación poblacional del tomate silvestre en México (considerado como el centro de domesticación del tomate), y su relación genética con variedades cultivadas. Se estimó la magnitud de la variación genética y estructura poblacional en 60 poblaciones silvestres y tres variedades cultivadas de tomate (N = 860 individuos), usando marcadores moleculares RAPDs. Los cinco oligonucleótidos utilizados produjeron 60 bandas polimórficas tanto dentro como entre poblaciones. El porcentaje de loci polimórficos dentro de las poblaciones silvestres de *cerasiforme* varió de 5.97 a 25.37% ($\bar{x}$ = 15.22%; SE = 0.620). El índice de diversidad de Shannon (S_S) estuvo entre 0.028 y 0.136 ($\bar{x}$ = 0.075; SE = 0.003). Las tres poblaciones de tomate cultivado presentaron valores de diversidad genética dentro del rango de valores observados en las poblaciones de *cerasiforme*. Un análisis molecular de varianza (AMOVA) indicó que las diferencias entre poblaciones explican la mayor proporción de la diversidad genética tanto en las poblaciones silvestres como en las cultivadas de tomate (69.97 y 86.64 %, respectivamente). El análisis de los grupos de las 63 poblaciones reveló un patrón parcialmente relacionado con las distancias (km) que separan las poblaciones dentro de las cuatro regiones geográficas analizadas. Se discute que la historia de las poblaciones, su sistema de apareamiento y el manejo humano probablemente sea la explicación de la desviaciones en las relaciones genéticas de las poblaciones dentro de las regiones.

GENETIC VARIATION AND DIFFERENTIATION AMONG MEXICAN WILD AND CULTIVATED POPULATIONS OF TOMATO (SOLANACEAE) ANALYZED BY RAPDS MARKERS[1]

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ABSTRACT

This study assessed the genetic variation and population differentiation among populations of wild tomato in Mexico, considered the center of domestication of tomato, and their relationship to cultivated varieties. The magnitude of both genetic variation and population structure in 60 wild and three cultivated populations of tomato (N = 860 individuals) were estimated by using RAPD markers. Five oligonucleotides produced 60 scoreable bands, which were polymorphic either within or among populations. The percentage of polymorphic loci within the wild *cerasiforme* populations ranged from 5.97 to 25.37% (mean = 15.22%; SE = 0.620). The Shannon diversity index (S_S) ranged from 0.028 to 0.136 (mean = 0.075; SE = 0.003). The three cultivated tomato populations had values of genetic diversity within the range observed in the *cerasiforme* populations. Differences among populations accounted for a large fraction of the total genetic diversity in both, wild and cultivated varieties (69.97 and 86.64 %, respectively). Cluster analysis of the 63 populations reveled a pattern of genetic distances partially related to the geographic distance separating populations within four different geographic regions. We argue that the history of populations and management by humans may explain deviations in the genetic relatedness of populations within regions.

Key words: cultivated tomato; genetic conservation; genetic variation; RAPD markers; Solanaceae; wild tomato.

INTRODUCTION

Tomato has its primary center of diversity in the Andean area of Ecuador, Peru, Bolivia and Chile (Rick, 1976). This area is a narrow belt that extends from the equator up to 30° latitude S, and from the Andes up to the Galápagos Islands (Zeven and de Wet, 1982). In this region all wild species of tomato (*pinpinellifolium, cheesmanii, parviflorum, chmielewski, hirsutum, pennellii, chilense* and *peruvianum)* are found (Rick, 1978; Taylor, 1986), including the putative progenitor of cultivated tomato *Lycopersicon esculentum* var. *cerasiforme* (Dun) A. Gray (Jenkins, 1948; Rick, 1978). The wild relative of cultivated tomato (the variety or subspecies *cerasiforme*) has been generally placed in the genus *Lycopersicon* (*L. esculentum*) (Muller, 1940; Luckwill, 1943; Rick, 1979; Taylor, 1986; Warnock, 1988; Rick et al., 1990), but recently it has been included in the genus *Solanum* (Child, 1990, Spooner et al., 1993; Bohs and Olmstead, 1999; Knapp and Spooner, 1999; Peralta and Spooner, 2001; Spooner et al., 2005).

Mexico is considered one of the major centers of plant domestication in the world (Harlan, 1971; Rick, 1979). Tomato and many other crops have been domesticated by the Mexican ancient cultures. A commonly accepted hypothesis for the origin of domesticated tomato is that an aggressive colonizer form (*esculentum* var. *cerasiforme*) migrated from Peru to Mexico where it spreaded as a weed and was later domesticated (Jenkins, 1948; Rick, 1976). Domesticated tomato was introduced into Europe by the Spaniards in the sixteenth century and disseminated to many tropical and temperate areas of the world (Rick, 1973, 1976).

Today, cultivated tomato is the world´s most important vegetable crop in economic terms (Nuez et al., 2004). However, tomato cultivation faces problems related to pest control (Sánchez-Peña et al., in press), and the knowledge and preservation of wild populations of tomato are important to maintain and use natural genetic variability for future programs of crop

improvement (e.g., pests, adverse environmental factors, increase quality and quantity of production) (Rick, 1976; Burdon and Jarosz, 1989; Sánchez-Peña et al., 1995).

The wild form of cultivated tomato tolerates a wide range of environmental conditions. It has been collected in arid and humid areas around its center of origin at altitudes ranging from 0 up to 2400 m (Cuatero et al., 1985). In these places, plants are found isolated as groups of relatively few plants (Rick and Holle, 1990). Wild tomato can survive under the extreme drought conditions of the western desert of Peru or at the high humidity of the tropical rainforests of the eastern Andes in the Ecuador (Rick, 1973). In Mexico, it occurs in abandoned fields, derived from the removal of tropical dry forest, in coastal sites of the Pacific slopes (ca. 300-1100 m) of the Sierra Madre Occidental in the state of Sinaloa (Sánchez-Peña et al., in press). In this area, it is considered as a weed of many crops, whereas in other places such as Veracruz, Oaxaca, Chiapas and Yucatan, its presence is promoted in the field, and the fruit is commercialized in the local markets. Due to its wide distribution and to the different ecological, cultural, and technological conditions at which it has been subjected, Mexican populations of the var. *cerasiforme* display a great variation in many morphological and reproductive characteristics (Chaidez, 2003; Medina, 2003; Sánchez, 2003). Population genetics of cultivated tomato and its wild relatives has been analyzed by using different molecular markers, like isozymes (Rick and Fobes, 1975; Rick and Holle, 1990), seed proteins (Wang et al., 2000), RFLPs (William and St. Clair, 1993; Rus-Kortekaas et al., 1994), RAPDs (William and St. Clair, 1993; Paran et al., 1995; Villand et al., 1998; Noli et al., 1999; Egashira, et al., 2000) and microsatellites (Rus-Kortekaas et al., 1994). However, the patterns of genetic variation and population differentiation have not been examined in the closest wild relative of cultivated tomato within the area of domestication. In this study, we conducted a characterization of genetic variation and relationships among

populations of wild tomato growing in many localities of Mexico, and their relationship to cultivated varieties of tomato.

MATERIALS AND METHODS

Plant material—Samples from natural populations of var. *cerasiforme* were collected in 60 localities of ten different states of Mexico corresponding to four main geographic regions (Table 1; Figure 1). The geographic regions were defined on the basis of the geographic proximity among populations. The four regions are: 1) Northwestern (populations 1-16), located between 25° 07′ and 28° 58′ of latitude N and 104° 53′ and 109° 18′ of longitude W; 2) Central-Western (populations 17-38) located between 18° 44′ and 21° 07′ of latitude N and 102° 31′ and 105° 20′ of longitude W; 3), Southeastern (populations 39-57) located between 15° 55′ and 18° 59′ of latitude N and 95° 09′ and 98° 05′ of longitude W, and 4) Northeastern (populations 58-60), located between 21° 26′ and 22° 56′ of latitude N and 99° 02′ and 99° 41′ of longitude W. Populations in region 1 occur in abandoned fields, formerly tropical dry forest, within coastal sites and in the Pacific slopes (ca. 300-1100 m) of the Sierra Madre Occidental of Sinaloa state (Sánchez-Peña et al., in press). Additionally, some populations were found as weeds of vegetable and bean crops in the Sinaloa and Nayarit states. Populations in regions 2 and 4 (Jalisco, Michoacán, Queretaro, and San Luis Potosi states) were found mostly in abandoned fields, whereas populations in region 3 (Veracruz and Oaxaca states) were found in humid environmental conditions; in many sites within this latter region the fruits are commercialized in the local markets.

Between four and 18 plants (mean = 13.35 ± 4.18 SD) were sampled at each site (860 individuals in total). Five to ten intact leaves were taken from each plant and immediately frozen

in liquid nitrogen, and then stored in the laboratory at –80 °C until DNA isolation. Samples from three cultivated varieties (Rio Grande, Comala, and Dorintia) were sampled in commercial fields in the Valley of Culiacan in the State of Sinaloa in Northwestern Mexico.

DNA isolation and RAPD markers—Total genomic DNA was isolated from approximately 100 mg of frozen leaf tissue by using a CTAB method (Doyle, 1991). The concentration of DNA in solution was determined with a Hoefer fluorometer and then standardized to a final concentration of 10 ng/µl for all samples. DNA amplification reactions were carried out in a 25 µl mixture containing 10 ng of template DNA, 1X PCR buffer (Invitrogen), 2mM $MgCl_2$, 0.1 mM each dNTP (Fermentas), 0.2 µM of a single arbitrary 10-mer primer, 5 µg of bovine serum albumin (BSA), and 1 unit of Taq polymerase (Invitrogen). A MJ Research thermal cycler (Watertown, Massachusetts) was used with a program of 45 cycles, each cycle of 94 °C for 1 minute, annealing at 38 °C for 1 minute, and extension at 72 °C for 2 minutes. A final extension step at 72 °C for 15 minutes was included.

Amplification products were electrophoresed at 200 V for 2 h in 1.5% (w/v) agarose gels with 0.5 X TBE buffer, and stained with ethidium bromide. Molecular weight of the bands was estimated by comparison with a 123-pb marker (Gibco BRL). Initially, 60 10-bp random oligonucleotides (series A–C, Operon Technologies, Alameda, California) were tested in a subsample of 19 randomly chosen individuals from different populations. Repeatability of the bands was done by assaying each primer twice. Five oligonucleotides (OPA-2, OPA-4, OPA-7, OPA-8, and OPA-9) gave the best results and, thus, were used to screen the whole sample set. Negative controls were used to prevent amplification of bands from contaminant DNA.

Data analysis—A binary data matrix was generated by recording amplified fragments of the same molecular weight as absent (0) or present (1) for each individual. Molecular diversity within each population was estimated by means of the percentage of polymorphic bands (%*P*), and by obtaining the Shannon diversity index (S_S) using the POPGENE program (version 1.31) (Yeh et al., 1999). In order to identify regions/populations with high genetic diversity, we analyzed the geographic differences in the level of molecular diversity among the wild populations, by estimating the product-moment correlation (Sokal and Rohlf, 1995) of both %*P* and S_S with the latitude and longitude of the geographic location of populations. Additionally, both measures of genetic diversity were compared among the above defined four main geographic regions using a Kruskal-Wallis non parametric test (Zar, 1999).

Genetic relationships among populations were analyzed using a matrix of pairwise Manhattan distances, calculated with the RAPDDIST program (Black, 1995). This distance measure is based on the presence/absence of bands and does not assume allelic frequencies (Swofford et al., 1996). From the matrix of Manhattan distances a dendrogram was constructed to depict the relationships among populations, using the unweighted pair-group method with arithmetic averaging (UPGMA), as implemented in the NEIGHBOR procedure of the PHYLIP 3.5C package (Felsestein, 1993). A Mantel permutation test (Matel, 1967) was preformed to investigate the correlation between the matrix of genetic distances and the corresponding matrix of pairwise geographical distance among populations

Analyses of Molecular Variance (AMOVA) were performed using the ARLEQUIN software (version 2000; Schneider et al., 2000), to estimate the variance components of the RAPD phenotypes associated to the genetic structure of populations. The fractions of genetic variation accounted for individuals within populations, populations within groups, and among

groups were obtained from the AMOVA. Distributions generated from 1000 random permutations were used to estimate the significance of the different variance components (Schneider et al., 2000). To obtain a more detailed insight into the patterns of genetic differences among the various population groups, comparisons of the frequency of each RAPD marker were performed with two-way cross tabulation using the JMP statistical package (SAS Institute, 1995). Due to the low frequency of a great proportion of the RAPD markers, *P*-values for these tests were derived from a likelihood ratio test (Sokal and Rohlf, 1995).

RESULTS

The five oligonucleotides used produced a total of 60 scoreable RAPD markers in the 63 screened populations of tomato. All the markers were polymorphic within or among populations. Most bands occurred in low frequencies in the whole sample. The number of markers amplified in each population varied between 4 and 21, with an average of 15 (SE = 4). Only 7 bands had frequencies greater than 50% in the total sample, and 26 bands had a frequency lower than 5% in all populations. In general, rare bands were shared by at least two populations, and only four markers were restricted to a single population.

The percentage of polymorphic loci (%*P*) within the wild *cerasiforme* populations varied from 5.97% (ISB and CHI) to 25.37% (VIR), with an average of 15.22% (SE = 0.620) (Table 1). The Shannon diversity index (S_S) ranged from 0.028 (MUR) to 0.136 (CAM), with an average of 0.075 (SE = 0.003) (Table 1). In the three cultivated tomato varieties, both measures of genetic diversity had values within the range observed in the wild populations (Table 1).

There was no evidence of a significant geographic pattern of variation in the genetic diversity level. The correlations of %*P* and S_S with latitude ($r = -0.108$, $P = 0.41$; $r = -0.021$, P

= 0.87, respectively) and longitude ($r = -0.149$, $P = 0.25$; $r = -0.120$, $P = 0.36$, respectively) were non significant, neither the two measures of genetic diversity differed among the four main geographic regions according to the Kruskal-Wallis test ($P = 0.83$ for $\%P$ and $P = 0.46$ for S_S).

The genetic structure among populations was assessed by means of analysis of molecular variance (AMOVA) performed at different hierarchical levels. High genetic differentiation among wild *cerasiforme* populations was found (69.97%, $P < 0.0001$, Table 2c). Similarly significant genetic differentiation among cultivated varieties accounted for 86.64 % ($P < 0.0001$) of the total variance (Table 2b). The subdivision of wild populations according to their geographic origin was found to correspond to significant genetic subdivisions, because 18.86% ($P < 0.0001$) of the variation was accounted by differences among the four main geographic regions. Forty-nine markers had significant differences in frequency among the regions and few markers were exclusive of a single region. Three markers were found only in region 3, two markers were exclusive of region 2, and one marker restricted to region 1. None of the markers was exclusive for region 4. Separate AMOVAs for population differentiation within each region indicated similar degrees of genetic structuring as in the whole set of sampled populations. The variance accounted by differences among populations within regions were: 66.65%, $P < 0.0001$ (region 1), 66.61%, $P < 0.0001$ (region 2), and 60.82%, $P < 0.0001$ (region 3), and a lower degree of subdivision within region 4 (32.91%, $P < 0.0001$) (Table 2e-h).

The results also indicated that genetic differentiation between wild and cultivated populations was significant and accounted for 15.68% ($P = 0.005$) of the total genetic variation (Table 2a). All the bands present in the cultivated populations were also present in at least some of the *cerasiforme* populations (i. e., unique bands were not found in any of the cultivated populations) and thus, differentiation between the two groups is due only to marker frequency

differences. The comparison of the three cultivated varieties among themselves revealed a high degree of differentiation (84.64%, $P < 0.0001$, Table 2b). This high dissimilarity resulted from the fact that only three bands were shared without significant frequency differences among these populations.

The UPGMA dendrogram generated from the matrix of pairwise genetic distances (Manhattan distances) is shown in Figure 2. The distances among the 63 populations of tomato ranged from 0.037 to 0.339, with a mean distance of 0.164 ± 0.054. Tomato populations were clustered in four main groups. The cultivated variety SAL (Rio Grande) was the most genetically distinct of all populations. The two other cultivated samples (DOR, "Dorintia", and COM, "Comala") clustered within the next outer group together with seven *cerasiforme* populations. The three populations from region 4 (TEN, SLP and OCA) also formed a subcluster within this group. The clustering pattern of the rest of the *cerasiforme* populations was moderately congruent with their geographic origin. The mantel test indicated a low but significant global correlation ($r = 0.07$; $P = 0.04$) between the genetic distance among populations and the geographical distances separating them.

The two other inner groups included 53 wild populations. One of the two main inner groups in the dendrogram included 18 wild populations, 13 from the central-western region (region 2), intermixed with 3 populations from Southeastern region (region 3), and 2 populations from Northwestern region (region 1). The biggest inner group cluster intermixed 35 wild populations from regions 1, 2 and 3, although showing some congruency with geographic origin, since 16 out of 19 populations from Southeastern region (region 3) and 12 of 16 populations of Northwestern region (region 1) were clustered in this group. Additionally, seven populations from central-western region (region 2) were clustered in this group.

DISCUSSION

The present study demonstrated the existence of genetic variation among wild populations of *cerasiforme* in Mexico, a region considered its center of domestication. Also, extensive genetic differentiation among wild populations, and among regions was found.

Populations of *cerasiforme* from Mexico are differentiated genetically. The apportioning of genetic variation indicates that most variation is accounted by differences among populations. This pattern of great population differentiation agrees with the empirical genetic data gathered for many annual plant species that practice self-fertilization (Hamrick and Godt, 1996). Nearly, 70% of the total variation is contained in the differences among populations whereas the remaining variation is shared. The four different regions of Mexico to which the wild populations of *cerasiforme* belong also account for nearly 19% of genetic variation. The arrangement of genetic variation among populations of *cerasiforme* suggest a hierarchical pattern of gene flow. To date, there is not an extensive survey of genetic variation within wild tomato populations as the one reported here, despite its relevance for germoplasm conservation in relation to crop improvement.

In contrast, the three cultivated varieties of tomato studied showed significantly lower variation than wild relatives. This is in agreement with the general hypothesis that plant evolution under domestication has lead to increased productivity, but at the same time to a reduction of genetic variation (Ladzinsky, 1998).

The levels of genetic polymorphism that we found in Mexican wild and cultivated tomato were slightly lower than those previously reported in samples from other parts of the world (Williams and St. Clair, 1993; Rus-Kortekaas et al., 1994). Williams and St. Clair (1993) found levels of polymorphism ranging from 2.8 to 20.3% in cultivated varieties, while our results showed polymorphism values ranging from 4.97 to 13.43%.

The levels of polymorphism in cultivated tomato can vary widely depending on the varieties analyzed. For instance, the cultivated tomato samples of Williams and St. Clair (1993) were subdivided as vitage (8 samples), regional (11 samples) and modern (16 samples) varieties, which had 2.8, 11.6 and 20.3% of average polymorphism, respectively (Williams and St. Clair, 1993). Since only three cultivated varieties were included in this study, a more complete assessment of the patterns of genetic variation in cultivated tomato from Mexico is still necessary. Regarding wild populations (*cerasiforme*), Williams and St. Clair (1993) found an average polymorphism of 24.5% for 11 populations, while in the present study the average for 60 populations was 15.22%. It is necessary to consider that in the former study sampling was performed in populations from the center of origin of tomato, whereas our samples came from an area that was later colonized by this plant species. It is possible that these populations suffered genetic bottlenecks in the past, particularly during the process of migration, that might explain these differences in the amount of genetic diversity.

Similarly, Rus-Kortekaas et al. (1994) found 44% of polymorphism in fifteen cultivated varieties of tomato highly differentiated in growth habit, fruit size and shape, and disease resistance response. This is consistent with the expectation of high genetic differentiation among populations of selfing annuals and highly differentiated domestic varieties, where most genetic diversity lies in differences among populations (see Hamrick and Godt, 1996). Thus, the wealth of varieties of tomato selected for disease resistance genes and others desirable characteristics maintains the germplasm of tomato base for breeding programs (Rick,1973, 1987).

The relationships among populations as derived from genetic distances showed a general pattern partly explained by the geographic distance separating them. For each region, there is a group of populations clustering together and the three populations from region four formed a

single group. However, populations from three regions are scattered throughout the dendogram except in the subcluster that contains populations from region four and two cultivated populations (Comala and Dorintia). The variety Saladette is the most distant from all populations. We do not know, as yet, if humans have funded populations of *cerasiforme* moving seeds from distant localities, or if particular cases of genetic drift and inbreeding are responsible for the non-congruent pattern of genetic distance among geographically related populations. These aspects deserve further analysis, particularly the history of local populations and the management by humans.

Finally, the finding of differences in genetic variation in Mexican population of wild tomato is relevant in the face of both natural and artificial selection, as long as the variation found in neutral markers correlates with genetic variation in fitness-related traits, adaptability, and yield (Sánchez-Peña et al.; Gur and Zamir, 2004).

Summary of conclusions— The wild and cultivated populations of tomato studied maintain significant genetic variation within and among populations which is consistent with the high variation in morphological characters and defensive traits observed in some wild populations of *cerasiforme* analyzed here (Carrasco, 2003; Chaidez, 2003; Sánchez, 2003; Sánchez-Peña et al., in press). The significant amount of variation accounted at the regional level suggests the need the further sampling in remote regions of Mexico in order to better assess the wild tomato genetic diversity.

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Table 1. Population number and name, abbreviation, origin, status, geographic location, percentage of polymorphism (% P) and Shanon diversity index (Ss) in wild and domesticated tomato in Mexico.

Population number and name	Abbre-viation	Origin	Status	Latitude (N)	Longitude (W)	..... % P	..... Ss
1 Kilómetro 20	K20	Sinaloa	Wild	25°54.398"	108°50.936"	13.43	0.0608
2 Ejidal	EJI	Sinaloa	Wild	25°58.320"	109°18.192"	17.91	0.0997
3 Mocorito	MOC	Sinaloa	Wild	25° 28'56"	107°55'12"	17.91	0.0813
4 Limoncito	LIB	Sinaloa	Wild	25°35.794	107°20.835"	16.42	0.0860
5 Saucito	SAU	Sinaloa	Wild	25°40.416"	107°22.958"	13.43	0.0633
6 Ensenada	ENS	Sinaloa	Wild	24°00"	106°40"	11.94	0.0658
7 Barras	BAR	Sinaloa	Wild	23°38'834"	106°47'566"	13.43	0.0760
8 Limoncito SI	LIS	Sinaloa	Wild	23°37'53"	106°20'32"	17.91	0.1082
9 Potrerillos	POT	Sinaloa	Wild	22°27"	105°52"	8.96	0.0436
10 Urraca	URR	Sinaloa	Wild	23°04"	106°17"	14.93	0.0822
11 Otates	OTA	Sinaloa	Wild	23°01.371"	105°55.282"	14.93	0.0656
12 Isla del Bosque	ISB	Sinaloa	Wild	22°43.233"	105°59.981"	5.97	0.0352
13 Puerta Ventana	PVE	Durango	Wild	25°00.354"	106°45.030"	11.94	0.0626
14 Bejuco	BEJ	Nayarit	Wild	22°01.034"	105°11.230"	14.93	0.0641
15 Acaponeta	ACA	Nayarit	Wild	22°29.814"	105°20.923"	20.90	0.0770
16 Uña de Gato	UGA	Nayarit	Wild	21°07.420"	104°53.524"	14.93	0.0729
17 Ajijic	AJI	Jalisco	Wild	20°17.233"	103°18.356"	8.96	0.0443
18 Molino	MOL	Jalisco	Wild	20°23.295"	103°31.631"	19.40	0.1059
19 San Diego	DIE	Jalisco	Wild	20°20.818"	103°48.673"	8.96	0.045
20 Santa María	MAR	Jalisco	Wild	20°22.922"	103°51.639"	13.43	0.0723
21 La Virgen	VIR	Jalisco	Wild	20°12.102"	104°10.172"	25.37	0.1119
22 Don Pancho	PAN	Jalisco	Wild	21°07.420"	104°53.524"	13.43	0.0843
23 Mezquitán	MEZ	Jalisco	Wild	19°49.116"	104°19.894"	14.93	0.0756
24 Mascuala	MAS	Jalisco	Wild	20°46.646"	102°32.816"	22.39	0.1158
25 Carretera	CAR	Jalisco	Wild	19°41.722"	104°24.8412"	16.42	0.0647
26 Aguacaliente	AGU	Jalisco	Wild	19°21.596"	104°52.877"	11.94	0.0777
27 La Pintada	PIN	Jalisco	Wild	19°54.832"	105°19.048"	13.43	0.0322
28 Zapote	ZAP	Jalisco	Wild	19°53.471"	105°20.142"	20.90	0.1009
29 El Tigre	TIG	Jalisco	Wild	20°07.670"	105°16.152"	14.93	0.0730
30 Las Palmas	PAL	Jalisco	Wild	20°49.485"	105°05.843"	13.43	0.0740
31 Los Espinos	ESP	Jalisco	Wild	20°18.385"	104°48.102"	8.96	0.0332
32 Morillo	MOR	Jalisco	Wild	20°23.295"	103°31.631"	13.43	0.0460
33 Ayotlan	AYO	Jalisco	Wild	20°51.646"	102°32.816"	14.93	0.0645
34 Copetiro	COP	Michoacán	Wild	19°28'687"	102°31'085"	19.40	0.1035
35 Tepalcatepec	TEP	Michoacán	Wild	19°42.515"	102°49.589"	10.45	0.0539
36 Coalcoman	COA	Michoacán	Wild	18°46.156"	103°14.533"	22.39	0.1106
37 Rasca Viejo	RAS	Michoacán	Wild	18°44'581"	103°23'715"	11.94	0.0650
38 Ticla	TIC	Michoacán	Wild	18°58.981"	103°40.468"	11.94	0.0448
39 Puerta Nueva	PNU	Veracruz	Wild	18°26.714"	95°16.022"	19.40	0.0911
40 Comuapan	CMU	Veracruz	Wild	18°18.553"	95°09.317"	23.88	0.0966
41 S. Juan Seco	SEC	Veracruz	Wild	18°59.153"	97°04.651"	10.45	0.0537

42 Ojo de Agua	OJO	Veracruz	Wild	18°39.615"	96°17.192"	11.94	0.0534
43 Bajo de Chila	CHI	Oaxaca	Wild	15°55.448"	97°07.563"	5.97	0.0335
44 SgoJocotepec	JOC	Oaxaca	Wild	16°07.488"	97°26.274"	23.88	0.1053
45 El Charco	CHA	Oaxaca	Wild	16°26.648"	98°05.095"	19.40	0.0960
46 La Muralla	MUR	Oaxaca	Wild	16°57.669"	97°55.746"	5.97	0.0278
47 La Sabana	SAB	Oaxaca	Wild	17°11.855"	97°57.580"	16.42	0.0833
48 Camalotal	CAM	Oaxaca	Wild	17°57.342"	96°02.390"	25.37	0.1356
49 Los Ideales	IDE	Oaxaca	Wild	18°07.193"	96°23.312"	10.45	0.0640
50 Huautepec	HUA	Oaxaca	Wild	18°05.789"	96°47.757"	11.94	0.0512
51 Porvenir	POR	Oaxaca	Wild	16°02.231"	96°30.390"	10.45	0.0577
52 Gpe. Victoria	GPE	Oaxaca	Wild	15°59.564"	95°52.361"	14.93	0.0707
53 Terrero	TER	Oaxaca	Wild	16°26.648"	98°05.095"	14.93	0.0679
54 CIIDIR	CID	Oaxaca	Wild	17°01.542"	96°43.168"	23.88	0.1140
55 Hacienda	HDA	Oaxaca	Wild	16°58.852"	96°34.276"	19.40	0.0837
56 San Cristobal	CRI	Oaxaca	Wild	16°20.934"	97°05.649"	16.42	0.0835
57 La Cañada	CAÑ	Oaxaca	Wild	16°04.843"	97°07.375"	20.90	0.0926
58 Tenempa	TEN	Queretaro	Wild	21°26.753"	99°41.131"	17.91	0.1107
59 Ocampo	OCA	Tamaulipas	Wild	22°56.806"	99°27.701"	14.93	0.0855
60 Eureka	EUR	San Luis P.	Wild	21°35.982"	99°02.237"	13.43	0.0802
61 Comala	COM		Cultivated			13.43	0.0834
62 Saladete	SAL		Cultivated			10.45	0.0698
63 Dorientia	DOR		Cultivated			5.97	0.0361

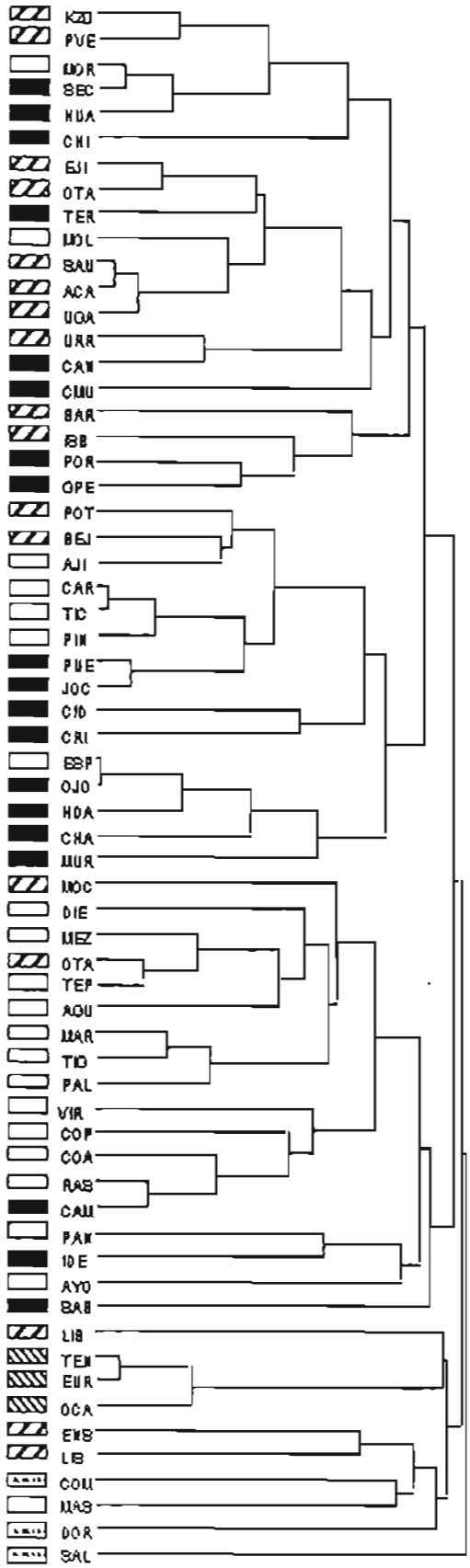
Table 2. Analysis of molecular variance (AMOVA) conducted for 60 RAPDs loci for the 60 wild and 3 cultivated population of tomato. Statistics includes degrees of freedom (d.f.), sum of squares, variance components, percentage of the total variance contributed by each component (% Total), and the statistics significance (*p*).

Source of variation	d.f.	Sum of squares	Variance components	% Total	*p*
(a)					
Wild vs cultivated	1	133.778	1.02866	15.68	0.00495
Among populations	61	3325.521	3.88118	59.15	< 0.0001
Within populations	797	1316.240	1.65149	25.17	< 0.0001
Cultivated (b)					
Among populations	2	176.921	7.06941	86.64	< 0.0001
Within populations	36	39.233	1.08980	13.36	< 0.0001
Wild (c)					
Among populations	59	3148.600	3.78287	69.27	< 0.0001
Within populations	761	1277.007	1.67806	30.7368	< 0.0001
Among regions (wild) (d)					
Among zones	3	749.858	1.09237	18.86	< 0.0001
Among populations	56	2398.742	3.02229	52.17	< 0.0001
Within populations	761	1277.007	1.67806	28.97	< 0.0001
Region 1 only (wild) (e)					
Among populations	15	588.385	3.05620	66.65	< 0.0001
Within populations	183	279.896	1.52949	33.35	< 0.0001
Region 2 only (wild) (f)					
Among populations	21	1015.720	3.08137	66.61	< 0.0001
Within populations	313	483.498	1.54472	33.39	< 0.0001
Region 3 only (wild) (g)					
Among populations	18	765.870	3.17243	60.82	< 0.0001
Within populations	225	459.798	2.04354	39.18	< 0.0001
Region 4 only (wild) (h)					
Among populations	2	22.620	0.69113	32.91	< 0.0001
Within populations	40	56.357	1.40893	67.09	< 0.0001

Figure Legends

Figure 1. UPGMA dendogram of wild and cultivated tomato populations

Figure 2. Map of geographical localization of the sampled populations. Number next to each symbol correspond to those given in Table 1.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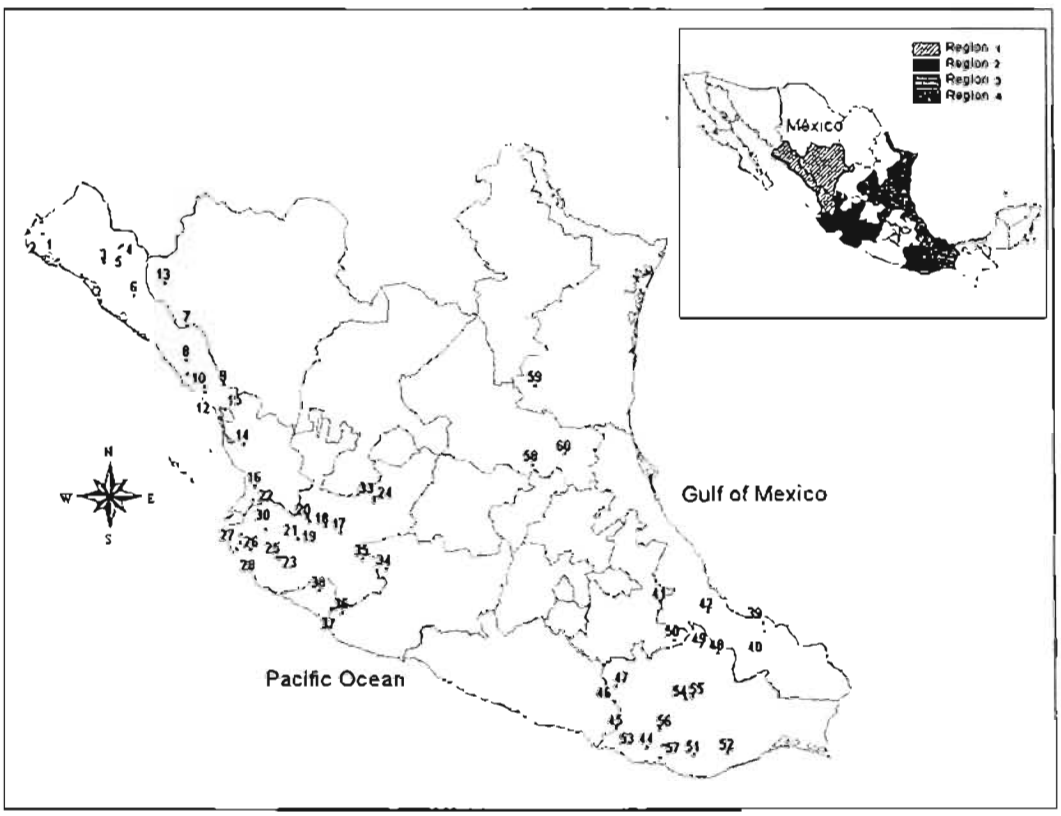
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CAPÍTULO IV

NATURAL SELECTION IMPOSED BY AN INVASIVE PEST (BEMISIA SPP.) UPON PLANT RESISTANCE IN WILD TOMATO (*SOLANUM LYCOPERSICUM* VAR. *CERASIFORME*) IN THE NORTHWESTER MEXICO

SELECCIÓN NATURAL IMPUESTA POR UN INSECTO INVASIVO (*BEMISIA SPP.*) SOBRE LA RESISTENCIA EN TOMATE SILVESTRE (*SOLANUM LYCOPERSICUM* VAR. *CERASIFORME*) EN EL NOROESTE DE MÉXICO

RESUMEN

En este estudio se examina la variación fenotípica dentro y entre poblaciones en la resistencia a una plaga invasiva (*Bemisia tabaci*), en cuatro poblaciones de tomate silvestres en la zona productora de tomate de mayor importancia en México (Sinaloa), y se estimó la magnitud de la selección natural sobre esta variación. En cada población de tomate silvestre se realizaron cruzas controladas para obtener el material genético (familias de medios hermanos paternos; diseño North Caroline I) que fue expuesto a los herbívoros en un experimento de jardín común. Los resultados demostraron la existencia de diferenciación poblacional en *Solanum lycopersicum* var. *cerasiforme* en la resistencia para mosquita blanca. La varianza genética aditiva para la resistencia fue detectada en tres poblaciones silvestres de tomate. Considerando las cuatro poblaciones como una sola, se detectó selección direccional para incrementar la resistencia por mosquita blanca, tanto en los valores fenotípicos y genéticos. También se detectó selección fenotípica para tasas relativas de crecimiento más altas. La relación entre la resistencia y tasa relativa de crecimiento varió entre poblaciones desde pendientes positivas, cercanas a cero, hasta pendientes significativamente positivas. Los resultados sugieren la existencia de un potencial coevolutivo en *Solanum lycopersicum* var. *cerasiforme* a la resistencia al a mosquita blanca, y por tanto con potencial de mejoramiento genético. El hallazgo de selección natural diferencial entre poblaciones sugiere la existencia de un mosaico geográfico de selección.

NATURAL SELECTION IMPOSED BY AN INVASIVE PEST (*BEMISIA SPP.*) UPON PLANT RESISTANCE IN WILD TOMATO (*SOLANUM LYCOPERSICUM* VAR. *CERASIFORME*) IN NORTHWESTERN MEXICO

Abstract.— In this study we examined the within and among population variation in plant resistance to an invasive pest species (*Bemisia spp.*) in four wild populations of tomato from the main area of tomato production in Mexico (Sinaloa state), and measured natural selection acting upon this variation. Controlled crosses were used to obtain genetic material (paternal half-sib families) from four populations and exposed to herbivores in a common garden experiment. The results demostrated the existence of population differentiation in *Solanum lycopersicum* var. *cerasiforme* in resistance to the invasive whitefly. Additive genetic variation for resistance was detected in three wild populations of tomato. Selection on both phenotypic and breeding values to decrease damage by *Bemisia* and to increase growth rate was detected if we consider all families of all four populations as a single population. The relationship between resistance and growth rate varied among populations, from family slopes positive or nearly zero, to significantly negative. These results suggest the potential for further selection, either natural or artificial, to the pest herbivore *Bemisia*.

INTRODUCTION

Much of the of intra- and inter-specific phenotypic variation of traits that mediate the interaction between species, particularly in host-enemies interaction, is thought to result from reciprocal effects on fitness between interacting species (Thompson 1994). This coevolutionary process is responsible of producing population structure decoupled from that produced by random events (Wright 1951, Spitze 1993). Coevolutionary processes between interacting species may give rise to adaptive radiations (Ehrlich and Raven 1964, Thompson 1994, Farrell 1998), with a distribution of traits among lineages explained by ancestor-descendant populations, but by independent adaptive evolution also (see Becerra 1997).

Interactions between species hardly occur with the same magnitude (i.e., reciprocal fitness effects) along the whole range of the interacting species, simply because (i) their ranges do not overlap completely, (ii) species vary geographically in abundance, (iii) or because populations possess different suites of characters and genetic variability that enhance or prevent evolutionary response. Thus, it is expected that not only selection might be present or absent in a particular locality, but that, when present, its magnitude on traits that mediated species interactions must logically vary geographically. The geographic mosaic theory of coevolution (Thompson 1999) states that due to selection mosaics there will be population differentiation in traits involved in species interactions. Also, reciprocal selection in some but not all localities would produce that traits-matching would be maladaptive in some locations and, because of this, no trait is expected to be favored across the whole range of the species (Thompson 1999).

Population differentiation in any trait is an ubiquitous phenomenon, either it is produced by selection or genetic drift (Wright 1951). However, under the selective mosaic hypothesis, we expect, first, that selection in a trait involved in species interactions would differ among populations and that the magnitude of differentiation must be distinct from that differentiation produced by drift or in selectively neutral traits (Spitze 1993). Although evidence of mosaic selection for different kinds of interactions exists [e.g., prey-predator (Brodie and Brodie 1991), host-parasite (Dybdhal and Lively 1996), plant-pollinator (Thompson 1999), seed-predators and plants (Benkman 1999), and plant-pathogen (Burdon and Thrall 1999)], few studies have analyzed the interaction between plants and herbivores. However, there is accumulating evidence of variation in selection on defensive traits among populations (Gomez and Zamora 2000, Valverde et al. 2001, Fornoni et al. 2004, Nuñez-Farfán and Schlichting 2005). In the present study we attempted to estimate the direction and magnitude of selection on plant resistance against the invasive herbivore whitefly (*Bemisia*), among populations of wild tomato (*Solanum lycopersicum* var. *cerasiforme*) in Northwestern Mexico.

Previous studies in the *Solanum-Bemisia* system in Northwestern Mexico documented that leaf trichome density is a component of resistance against whiteflies, and the existence of phenotypic differences among populations in this trait (Sánchez-Peña et al. In press). The phenotypic differences among populations are a common phenomenon that results from environmental factors. However, to what extent phenotypic differentiation is the result of differences in local selection regimes upon traits makes necessary to identify a factor that covary with fitness (Wade and Kalisz 1990, Schluter 2001). Yet, phenotypic differences among populations might result from phenotypic plasticity without underlying genetic differentiation. However, experiments

revealing that phenotypic differences among populations are retained in a common garden indicate underlying genetic differentiation (see Roff and Mousseau 2005 and references therein). Quantitative genetic studies seek to decompose the characters' phenotypic variance into its genetic and environmental components, in order to determine its potential response to selection (Falconer and Mackay 1995), and to estimate the extent of population differentiation (*Qst*, Spitze 1993). Also, direct and indirect effects of natural selection on traits of ecological importance can be estimated and contrasted among populations (see Schluter 2001). Both genetic variation and mosaic selection of traits are fundamental components of the raw material for coevolution among interacting species (Thompson 1999).

The study system

The interaction between the pest herbivore *Bemisia tabaci* (whitefly) and wild tomato (*Solanum lycopersicum* var. *cerasiforme*) was analyzed in four populations in the State of Sinaloa, in northwestern Mexico. This State is the main producer of cultivated tomato in Mexico (SAGARPA 2005). This generalist herbivore constitutes the main pest of tomato cultivars since it is the vector of many viral diseases (Martelli and Quacqarelli 1982, Idris and Brown 1998, Idris et al. 2001, Martins et al. 2001, Narasegowda et al. 2003). The first recorded outbreak of whitefly occurred in Greece in 1889 and described as *Bemisia tabaci* (McKenzie et al. 2004). In the USA it was considered as a pest until 1986 (McKenzie et al. 2004). Whitefly infestation in tomato cultivars of Sinaloa, Mexico was first recorded in the 1960s (Ramírez 1996) and became a serious problem in the region by 1991 (Martínez-Carillo 2003). It has been

reported losses of tomato production due to whitefly infestation can be as high as 100% in Australia (Stoner et al. 2003).

Surveys of new natural sources of resistance to whitefly among relatives of cultivated tomato have been carried out in some of its wild relative species of tomato (*S. cheesmaniae, S. chilene, S. chmielewwsky, S. galapagense, S. habrochaites, S. neorickki, S, penelli, S. pruvinum,* and *S. pimpinellifolium*), all placed in the genus *Solanum* (Darwin et al. 2003, Spooner et al. 2005). Cultivated tomato was domesticated from *Solanum lycopersicum* var. *cerasiforme* (Jenkins 1948, Rick 1978), and wild populations of this species are widely distributed in Mexico, including the Sinaloa state. Tomato was domesticated in Mexico and distributed to Europe by the Spaniards conquerors in the sixteen century (Jenkins 1948, Rick 1978). Wild tomato is a weed of many cultivars, including tomato, in Mexico (Sánchez-Peña et al. In press). Wild tomato show differences among populations in the state of Sinaloa in many vegetative and reproductive characters, as well as in their infestation levels by whitefly (Sánchez-Peña et al. In press).

In this study, we surveyed the within and among population variation in resistance to an invasive pest herbivore (*Bemisia spp.*) in four wild populations of tomato from the main area of tomato production in Mexico (Sinaloa state), and measured natural selection on this variation. Our goal was to assess, in these populations of *Solanum lycopersicum* var. *cerasiforme*, the genetic variation for resistance to whitefly, and simultaneously to measure the natural selection on traits related to plant resistance to this invasive pest.

MATERIALS AND METHODS

Experimental protocol

Seeds from wild plants of *S. lycopericum* var. *cerasiforme* were collected in each population during the reproductive season of 2000. Seeds of each individual plant (i.e., natural progenies) were kept separated in paper bags and labeled. The four populations studied are located along a latitudinal North-South transect of 400 km in the state of Sinaloa in Northwestern Mexico (Table 1). In October 2001, the seeds were sown in a greenhouse and only one individual per progeny was used for the crosses. The seedlings were transplanted to an experimental plot in November. By February 2002, plants reached maturity and the crosses began. Since wild tomato is hermaphroditic, plants were allocated randomly to function as male or female. Crosses were made following a North Carolina I design (Lawrence 1984), where each male (Sire) was crossed with two female (Dam) plants (Mitchell-Olds 1986; Nuñez-Farfán and Dirzo 1994; Roff 1997). The use of paternal half-sib families allows the estimation of additive genetic variance from the sire component of variance free from maternal and dominance effects (Mitchell-Olds 1986; Falconer and Mackay1995).

Because tomato produces flowers in inflorescences, all the floral buds but one in a given inflorescence were eliminated in order to left only the flower to be used as pollen recipient. To perform the crosses, the selected flower in an inflorescence of a given female plant was emasculated one day before anthers dehisced and then covered with a paper pollen bag; the next day, pollen from a male plant was deposited directly on the stigma. After pollination, the flower was labeled and bagged to avoid contamination with pollen from other plants. Since a wild tomato fruit produces between 20-30 seeds,

it was necessary to accomplish at least nine crosses between a given pair of male-female plants. At the end of crossing experiments, a total of 23, 26, 23, and 24 paternal half-sibs families were obtained for the populations of Ensenada, Jahuara, Limomba and Urraca, respectively. An average of 70 seeds for each full-sib family was obtained (140 seeds per paternal half-sib family).

Seeds of each full-sib family were germinated following the protocol mentioned above in October 2002. Prior to germination, seeds were treated with a Chloride solution (5%) to prevent fungal infections and to promote uniformity in germination time. Seedlings of twenty paternal half-sib families (40 full-sib families) of each population were introduced to the field under a randomized block design (two blocks; Cockran and Cox 1957). For each block, from 5-13 seedlings for each maternal family were planted. However, mortality left two paternal families in the Ensenada population with only one individual per block, and these families were eliminated from the final analyses. Data were gathered from 20 paternal half-sib families in Jahuara, Limomba and Urraca populations (N=363, 339 and 334, respectively) and from eighteen paternal half-sib families the Ensenada population (N=304) for a total of 1340 plants measured and used for the statistical analyses.

The experiment attempted to mimic the conditions that tomato producers of Sinaloa State provide to commercial varieties of tomato. In fact, the experimental plot employed in this study belonging to the Instituto Nacional de Investigaciones Forestales Agrícolas y Pecuarias (INIFAP) is surrounded by cultivars of tomato. These cultivars are attacked by the invasive whitefly *Bemisia* during plant development and usually controlled by the use of pesticides.

In the experimental plot, plants of all paternal half-sib families and populations were assigned to rows and position within a row randomly. Rows were separated by 1.8 m and plants within a row were spaced 1.5 m. Plants were watered regularly by employing drip irrigation and fertilized three times during the experiment (at establishment, growth and reproduction; 150:90:250 units of NPK ha^{-1}). Nitrogen (ammonium nitrate) was applied 50 units each time; phosphorus (ammonium sulfate) at a rate of 30 units each time, and potassium (potassium nitrate) was applied two times (growth and reproduction stage) with 125 units each. No pesticides were applied to the plants in order to allow colonization of tomato plants by white flies (*Bemisia tabaci*). Weeding control was done manually at regular periods.

Data collection

Each plant was monitored along time to record and measure the phenotypic characters, particularly plant resistance, growth and reproductive traits. Data were collected in every plant three times (at 60, 90 and 120 days after planting). In each census, the following measurements were made: plant height, number of inflorescences, number of matured fruits, and incidence of whiteflies (adults, eggs and larvae). The incidence of *Bemisia* (as a measure of plant resistance) was assessed by counting the number of adult flies in the leaf immediately below the most recently matured inflorescence. Previous studies indicate that this is a reliable estimator of fly abundance (Aviles 1997) and resistance (Sánchez-Peña et al. In press). In each sampling, the largest leaflet of the same leaf of tomato was collected from every plant and observed using a stereoscopic microscope (Leica MZ125) to count the number of eggs and larvae

laid by a female of *Bemisia*. For this, an area of 1 cm^2 in the central part of the leaf was observed under the microscope.

At the end of the experiment, all matured fruits per plant were collected individually, and the number of seeds per fruit was counted in a sample of ten fruits per plant. Fruit-set was calculated as the number of fruits divided by the number of inflorescences. The relative growth rate was calculated for each plant as RGR = {(plant height at 90 days – Plant height at 120 days)/30 days}. Height is an important estimator of growth rate because leaves, inflorescences and fruits are deployed along the stem.

Statistical Analyses

Phenotypic variability among populations

Differences in the average values of six variables [plant resistance (number of *Bemisia* flies), RGR, fruit number, inflorescences number, fruit-set, and total seed number] of each plant among populations were assessed through a multivariate analysis of variance (MANOVA). In addition, separate analyses of variance (ANOVA) were preformed to determine which character contributed to the differences detected by the MANOVA. Post hoc tests (Fisher's Protected LSD) were carried out to compare the average values of each trait among populations.

Given that the levels of plant infestation by white flies was monitored three times during the season, differences between population, time, and population by time interaction were analyzed by means of a Repeated Measures ANOVA (Sokal and Rohlf 1995).

Heritability

Estimates of the narrow sense heritability (h^2) of each character, in each population, were obtained by estimating the variance components for Sires, Dams and Error, after executing a nested analysis of variance containing as sources of variation Sires and Dams within Sires. The intra-class correlation of Sires (t_s), is equivalent to 1/4 of the additive genetic variance (i.e., $V_a = 4\sigma^2_{sires}$), and in the case of paternal half-sib families it is free from dominance and maternal effects (Mitchell-Olds 1986; Falconer and Mackay1995). Hence, h^2 is calculated as: $h^2 = 4\sigma^2_{sires}/\sigma^2_{total}$, where σ^2_{sires} is the expected component of variance attributable to Sires, and σ^2_{total} is the total phenotypic variance of the trait. In this case, $\sigma^2_{total} = \{\sigma^2_{sires} + \sigma^2_{dams} + \sigma^2_{error}\}$, where σ^2_{dams} is the expected variance component due to Dams nested within Sires and σ^2_{error} is the expected component of variance due to error (progenies within Dams, within sires; Falconer and Mackay1995).

Standard errors of the estimated heritabilities were obtained by means of a Jackknife procedure, removing one paternal half-sib family each time, and running the nested analysis of variance (Berenbaum et al. 1986). At each iteration, one pseudo-value (θ_i) is calculated as

$$\theta_i = fh^2 - (f-1)h^2_{-1}, \qquad (1)$$

where f is the number of families, h^2 is the true heritability, and h^2_{-1} is the heritability with the ith family deleted. The mean of all θ_i ($\bar{\theta}$) is a nearly unbiased estimator of h^2, with a standard error estimated as:

$$SE_{\bar{\theta}} = \sqrt{\frac{\sum\left(\bar{\theta} - \theta_i\right)^2}{f(f-1)}} \qquad (2)$$

Genetic Correlations

The phenotypic and genetic correlations among characters were obtained for each population separately. Phenotypic correlations were calculated by standard Pearson product-moment correlation coefficient (Arnold 1981; Via 1984), considering each individual as an observation. Genetic correlations were calculated through product-moment correlations of breeding values of the characters (Arnold 1981; Via 1984).

Genetic differentiation among populations

In order to estimate the amount of genetic differentiation among populations of wild tomato for each quantitative character measured, a Nested Analysis of variance was carried out. The sources of variation included Populations, Sires within populations, and Dams nested within Sires (Model II, Sokal and Rohlf 1995). All variables were declared as random and the variance components were obtained. The coefficient of genetic differentiation in quantitative traits, Q_{st}, can be estimated as

$$Q_{st} = V_{pop}/(V_{pop} + 2V_a), \qquad (3)$$

where V_{pop} is the variance among populations (obtained from the variance component of population), and V_a is the additive genetic variance estimated by the Sire component of variance ($V_a = 4\sigma^2_{sires}$) (Spitze 1993; Widén et al. 2002; Cano et al. 2004). The significance of the Q_{st} of each character was estimated through a Jackknife procedure (Sokal and Rolhf 1995). To do this, a nested analysis of variance is estimated removing

one family each time, obtaining the pseudo values, θ_i, its sample mean, $\bar{\theta}$, and standard error, $SE_{\bar{\theta}}$, in similar way to the procedure employed for heritabilities (see equations 1 and 2).

Natural selection

Natural selection imposed by whiteflies (plant resistance) and plant's relative growth rate (RGR) was estimated in each population. In addition, we estimated the selection gradients on the same two characters considering all individuals as a single whole population. Selection gradients were estimated using multiple regression analysis of relative fitness (w_i) as a function of resistance to *Bemisia* and RGR (Lande and Arnold 1983; Núñez-Farfán and Dirzo 1994). The directional selection gradients were estimated with the model

$$w_i = \beta_0 + \sum_{i=1}^{n} \beta_i x_i + \varepsilon \ , \qquad (4)$$

whereas the stabilizing/disruptive selection gradients were obtained with the model

$$w_i = \beta_0 + \sum_{i=1}^{n} \beta_i' x_i + \sum_{i=1}^{n} \frac{1}{2} \gamma_{ii} x_i^2 + \sum_{i=1}^{n} \sum_{j>i}^{n} \gamma_{ij} x_i x_j + \varepsilon \ , \qquad (5)$$

where x_i are the independent variables, w_i is the relative individual fitness, β_i are the partial regression coefficients; γ_{ii} and γ_{ij} are the quadratic coefficients. β_i is interpretable as the directional selection gradient and its sign indicates the direction of change expected from selection acting directly on trait x_i. γ_{ii} is the quadratic coefficient and indicates the presence of a curvature in the relation between fitness and trait x_i

(Mitchell-Olds and Shaw 1987; Phillips and Arnold 1989). Significant γ_{ij} coefficient suggest the presence of correlative selection on two given traits, x_i and x_j.

The selection analyses were performed for both phenotypic (i.e., phenotypic selection; Lande and Arnold, 1983) and genetic values of character (i.e., genetic selection; Rausher 1992) in each population independently and for the whole population. The phenotypic selection was obtained on the individual plant values, whereas the genotypic selection was performed on the Sires, breeding values for each trait examined. Selection on breeding values avoid biases in the estimation of selection gradients caused by environmentally induced correlation between fitness and the examined traits, and measures selection directly on additive genetic variance (Rausher 1992). Selection gradients and their standard errors were estimated using the Jackknife procedure. This method allows approximating *t*-tests of significance, which are robust to deviations from normality and to heterogeneity of residual variances (Mitchell-Olds 1989).

The total of number of seeds per plant was used as measure of fitness. Relative fitness (w_i) of a given plant was estimated as $w_i = W_i/\overline{W}$, where W_i is the total number of seeds produced per plant i, and $\overline{W}$ is the average of seed number in the population. Thus, $\overline{w}$ = 1 (Lande and Arnold 1983).

Contrasting selection among populations

An ANCOVA of w_i was performed in order to test whether selection on plant resistance and RGR differed among populations. In this analysis plant resistance and RGR were entered as covariates and population was considered a fixed factor. A significant RGR × population and/or resistance × population interaction would indicate

that the magnitude/direction of selection on plant resistance and RGR differ among populations. These analyses were performed at the phenotypic and breeding values levels.

Relationship between level of infestation and RGR

In order to assess the possible differences in the relationship between the level of infestation by white flies and RGR within each paternal half-sib family, an ANOVA of the slopes (betas) was compared among populations. For this, the slope of the relationship of RGR as a function of white flies infestation was obtained for each paternal half-sib family of each population. Differences among populations in the average values of the slope would be indicative of differences in magnitude of the potential costs in terms of RGR after white fly infestation, or even in the mean direction of the relationship. A post hoc test was performed to compare the mean slope among populations (Fisher's Protected LSD Test; Superanova v. 1.11)

Prior to all statistical analyses, variables expressed as counts (number of adults, larvae, and eggs of *Bemisia*, inflorescences, fruits, seeds) were $\log_{10}$ transformed; proportions were arcsine transformed (fruit-set). All analyses were performed using the JMP® statistical package (SAS Institute 1995), except when indicated. For depiction, values were back transformed to their scale of measurement.

RESULTS

Phenotypic variability among populations

A MANOVA indicated significant differences among populations for all six characters measured and no differences between blocks (Table 2A). Similarly, univariate ANOVAs (excluding blocks) detected differences among populations in average values of each character (Table 2B-G). Post-hoc tests detected differences among all populations for resistance to white flies (Fig. 1A). The Jahuara and Limomba populations had the lowest levels of infestation, whereas Ensenada and Urraca were the most susceptible. Relative growth rate (RGR) was higher and similar for Ensenada and Jahuara, and lower and similar for Limomba and Urraca (Fig. 1B). The average values for three reproductive characters (inflorescences, fruits and fruit-set) displayed the same pattern among populations, with Jahuara, the most resistant, having the higher mean value followed by Ensenada and Urraca, and the significantly lowest value displayed by Limomba (Fig. 1C-E). In contrast, Ensenada, the most infested by white flies, was the population with the lower average value of seed number. Again, Jahuara displayed the higher number of seeds per plant (Fig. 1F).

Resistance to Bemisia

The time-course abundance of adults, eggs and larvae of *Bemisia* wild tomato plants, shows a higher abundance 90 days after transplanting (Fig. 2). There is a correspondence in abundance of adults, eggs, and larvae. Also, it is clear that the populations of Jahuara and Limonba showed lower levels of infestation, at any time and for all stage of *Bemisia* than the Ensenada and Urraca populations (Fig. 2). The repeated measures ANOVAs detected a significant effect of population, time, and the interaction

population x time for the number of adults, eggs, and larvae of whiteflies on tomato plants (Table 3). This result indicates a consistency in the average values of resistance among populations.

Genetic variance within populations

Low but significant amounts of additive genetic variation were detected for most traits. The Ensenada population displayed significant heritabilities for five out of six characters, whereas the population of Jahuara did it only in one character (Table 4). Plant resistance to *Bemisia* and fruit set were the characters that had significant heritabilities in most populations of wild tomato. Only one of the resistant populations, Limonba, there was no evidence of additive genetic variance for resistance (Table 4). The higher estimates of heritability for resistance were found in the two populations (Jahuara and Urraca). A low but significant heritability for RGR was only found in the population of Limomba. In the same way, significant additive genetic variance in fruit number was only detected in the population of Ensenada. In contrast, significant heritabilities for fruit set were detected in all but Jahuara populations. Inflorescence number had significant heritabilities in Ensenada and Urraca. Finally, additive genetic variation for seed number was only found in Ensenada population(Table 4).

Genetic differentiation among populations

The three-level nested analysis of variance with Population, Sires, Dams within Sires, and progenies within Dams (error), as sources of variation performed for each character to estimate the variance components and Q_{st}, revealed high values of population differentiation for all characters. Values of Q_{st} ranged from 0.69 for fruit set up to 1 for

inflorescences number (Table 4). Population differentiation in resistance to *Bemisia* was also high (Q_{st} = 0.77).

Phenotypic and genetic correlations

Most phenotypic correlations among traits measured in wild tomato were statistically significant for all populations (Table 5A-D). Correlations between whitefly infestation and all other characters were negative, and significant in all populations except in Jahuara. In the other three populations these correlations took values between -0.086 (RGR, Urraca) and -0.369 (fruits, Ensenada). Correlations between RGR and reproductive values were all positive in three populations, ranging from 0.077 (fruit-set) to 0.223 (total seeds) both in Limonba (Table 5C). In contrast, at Jahuara population, the correlations were negative and statistically significant, except for total seed number (Table 5B). Finally, the correlations among reproductive traits were all positive and statistically significant, ranging from 0.286 (fruit set vs total inflorescence at Limonba) up to 0.9658 (total seeds vs total fruits at Ensenada).

Most genetic correlations were not statistically significant, except for some correlations between reproductive characters in each population (Table 5A-D). The lowest significant correlation was detected between inflorescence number and fruit set (r = 0.553 at Limonba; Table 5B), whereas the highest correlations was observed between total seed and total fruits (r = 0.909 at Ensenada; Table 5A). Clearly, with the number of families analyzed per population we were unable to detect significant correlations lower than 0.5 (i.e. at least 32 families must be measured with an $\alpha = 0.05$, and a power of the test, $1-\beta = 0.85$).

Natural selection in the whole population

Selection on resistance and relative growth rate, this latter being assumed as a component of tolerance to herbivores, was estimated, first, considering all plants in the experimental plot as a whole population, given that these were grown in the same physical environmental conditions and exposed to the same herbivores. Secondly, selection was estimated in each population. In both analyses the gradients of selection were obtained for both the phenotypic and breeding values.

The linear gradients of selection on phenotypic values for resistance to *Bemisia* and for RGR were both statistically significant but with opposite signs. The number of flies was negatively related to relative plant fitness, whereas RGR was positively associated with it (Table 6). Similarly, the quadratic gradients of selection for both characters were found to be statistically significant and negative (Table 6; Fig. 3E). No correlative selection among traits was detected.

The selection analysis performed on the breeding values detected selection on resistance of similar magnitude and direction to that showed by the phenotypic analysis. In contrast, no directional selection was detected for RGR, and none of the second order selection gradients were found to be statistically significant (Table 7).

Selection within populations

Similar magnitude and direction of phenotypic selection on resistance was detected in all populations, except for the Jahuara population. In all populations the quadratic term of resistance was found to be negative and statistically significant (Table 6, Fig. 3).

Simultaneously, positive directional selection for RGR was detected in two populations (Limonba and Urraca) (Table 6, Figs. 3 C, D). There is no evidence of curvilinear selection on RGR in any populations of wild tomato (Table 6). The correlative selection gradient between RGR and plant resistance only was statistically significant at the Ensenada population (Table 6, Fig. 4A).

The within-population selection analysis on breeding values, failed to detect any significant selection gradient, and none of the ANOVA models were significant for either the linear or quadratic selection gradients (Table 7). These results suggest a potential limitation to reject a probable false null hypothesis (e.g., power of the test).

The fitness response of populations differed significantly (Table 7). A significant effect of growth and resistance on fitness was detected at phenotypic level but not at breeding values level (Table 8), supporting the selection results presented above. Additionally, significant growth × population and resistance × population interaction indicates that the patterns of selection on growth and resistance differed among populations (Table 8).

Relationship between level of infestation and RGR

The analysis of the relationship between the level of infestation by whiteflies and RGR within each paternal half-sib family indicated differences among populations in the direction and magnitude of the average slope ($F_{(3, 74)} = 3.293$, $P = 0.025$, $R^2 = 0.11$). These results support previous results and indicate different costs in terms of RGR imposed by whiteflies among populations. In resistant populations (Jahuara and Limonba) where the levels of infestation were low, the relationship was positive or

nearly zero. In contrast, in the susceptible populations (Ensenada and Urraca) the mean slopes of the relationship RGR vs. resistance were significantly negative (Fig. 4).

Discussion

The results of this study demonstrated the existence of population differentiation in *Solanum lycopersicum* var. *cerasiforme* in resistance to the invasive whitefly, supporting previous studies (Sánchez-Peña et al., in press). Furthermore, there is evidence of differential selection upon plant resistance given that no selection was detected in one population of wild tomato (cf. Table 6). Since additive genetic variation for resistance was detected in three populations, the potential for an evolutionary response is plausible in this species. Although additive genetic variation in growth rate was detected in only one population (Limomba), significant positive selection for this trait was also detected. Considering all families, of all populations, as a single population, selection on both phenotypic and breeding values to decrease damage by *Bemisia* and to increase plant growth rate was detected, suggesting the potential for further selection, either natural or artificial. Finally, high levels of population differentiation for all quantitative characters, including fitness related traits, were found.

Population differentiation among populations of wild tomato

Wide variability among populations in the phenotypic characters measured in wild tomato plants was detected, supporting previous analysis of the phenotypic variation in natural populations of this plant species in Sinaloa, Mexico (Sánchez-Peña et al., in press). Considering that phenotypic differences may be due to differences in the physical or biotic environment of the native localities where populations develop (Roff

2005), the present study attempted to determine if phenotypic variance for resistance to herbivores, growth rate, and reproductive characters, contained additive genetic variance useful for selection (Falconer and MacKay 1995). For most populations and most characters, low but significant heritabilities were detected indicating that genetic variance is not limiting factor for the evolution of trait mean values (Falconer and Mackay 1995; Roff 1997; Lynch and Walsh 1998). However, the analysis of phenotypic variance taking into account not only paternal half-sib families but the population as well, indicated that this source of variation explained a large fraction of phenotypic variability, and less variance was accounted by the paternal families within each population. This resulted in the detection of low heritabilities, and high values of population differentiation in quantitative traits (Q_{st}) for most traits. This result suggests that in the populations of wild tomato there are small amounts of additive genetic variance, perhaps due to high levels of inbreeding. Wild tomato, as other species of *Solanum*, is a selfer annual (Rick 1973), and thus inbreeding and drift might reduce the amount of genetic variance and increase population differentiation. Evidence from many plant species indicates that the mating system is of utmost importance in determining the level of population differentiation. In general, selfers tend to show the highest levels of population differentiation (F_{st}) for neutral or nearly neutral loci (Hamrick and Godt 1996).

Because population differentiation can be produced either by selection and drift, it is relevant to contrast the level of differentiation in quantitative traits of putative importance for adaptation to the environment. These traits, if subject to present or past selection, are expected to show higher values of differentiation than neutral traits (Spitze 1993; Cano et al. 2004). In fact, in this study, values estimated of Q_{st} were all

high and significant ($0.69 \leq Q_{st} \leq 1$). On the other hand, an AMOVA of the genetic variance among 60 populations of wild tomato from Mexico, estimated from RAPDs markers, indicated that about 69% of the variation is accounted by differences among populations, and hence have a strong population structure (Sánchez-Peña unpublished data). Thus, these figures and the high standard errors of Q_{st} estimated do not allow us to conclude that differentiation in quantitative traits is different from that estimated for neutral markers. The results, however, reinforce the view that there is a small amounts of genetic variation within populations of wild tomato, perhaps due to inbreeding. However, there is a possibility that populations of wild tomato have been subject to continuous selection to increase resistance in their local populations (at least in the two highly resistant Jahuara and Limonba), reducing additive genetic variation. But testing this hypothesis implies necessary the exposure to genetic variation (e.g., employing F_2 progenies; see Núñez-Farfán and Schlichting 2005) in each locality and performing reciprocal transplants together with the manipulation of the putative selective agent (e.g., exclusion of herbivores; Rausher, 1996) to determine the hypothesis of fixation of the highly resistant genotypes. Also, the use of neutral codominat markers (e.g., microsatellite loci) might produce an accurate estimation of population differentiation of wild tomato (F_{st}), to be contrasted with the estimator of population differentiation in quantitative traits (Q_{st}). Thus, it is possible to determine the role of selection in differentiating the populations for traits that mediate the interaction with its herbivores.

Differential selection of resistance in wild tomato populations

The main goal of this study was to determine the possible existence of a mosaic selection for resistance to the invasive herbivore *Bemisia spp*. Despite whitefly is a

naturalized herbivore in agricultural systems, and that it is not expected that defensive mechanisms of wild tomato (e.g., trichomes) evolved to cope with this herbivore, there is evidence of coevolutionary responses in agricultural systems (see Rausher, 2001), as long as additive genetic variation in defensive traits is not nil. Considering that the whitefly is the vector of viral diseases in cultivated tomato, different wild relatives of tomato have been analyzed as a source of resistance (Lepidot *et al.*, 2001; Martins *et al.* 2001; Narasegowda *et al.* 2003). Some species (e.g. *S. habrochaites*) show high levels of resistance due the presence of abundant glandular trichomes on leaf surface (Heinz and Zalom 1995; Nombele *et al.* 2000; Leite et al. 2001; Li *et al.* 2002; Sanchez-Peña et al. in press). Populations of wild tomato in Sinaloa Mexico vary in their leaf trichome density and this is negatively correlated with whitefly abundance (Sánchez-Peña et al. In press). Thus, if whitefly constitute a current selective agent to wild tomato (i.e., its abundance on a plant covary with fitness), it is possible to expect differences in selection among different populations of wild tomato, if there is phenotypic variation in the defensive trait. The results found in this study supported our expectations, because selection to reduce whitefly incidence was detected in three out of four populations. Interestingly, selection on resistance was absent in the Jahuara population which possess high average value of leaf trichome density (Sanchez Peña et al. In press). This reduced phenotypic variation resulted in very low levels of whitefly infestation as to produce differences in plant fitness among individuals. In consequence, statistical analysis revealed differences among populations in the effect of resistance upon fitness and hence in selection (interaction resistance x population; cf. Table 8). When the relationship between growth rate and level of infestation by whitefly is analyzed among paternal half-sib families in each population, it is clear that infestation affects

differentially growth rate: the average slope differed among populations, from positive or nearly zero to significant negative values (cf. Fig. 4). This, in turn indicated that selection is affecting correlation among traits, and changes in character mean value through indirect selection. This is exemplified in Ensenada population, where selection in resistance and correlative selection between resistance in growth rate, but no direct selection on growth rate (cf. Table 6).

According to the geographic mosaic of the coevolution theory (Thompson, 1999), the system whitefly and wild tomato possess some of its components, namely 1) variable outcomes of interaction, and hence 2) variable rates and mosaic selection. Further studies must address the question regarding the adaptive significance of resistance and its components across the distribution range of wild tomato in northwestern Mexico, to test potential mismatches between characters.

Conclusions

Two aspects of the present study are relevant in the context of crop improvement and evolution. First, Mexico is regarded as the center of domestication of cultivated tomato and given that *S. l.* var. *cerasiforme* is considered its wild closest relative, future plans of crop improvement and gene transfer become feasible. Second, the existence of genetic variation in yield traits and for pest resistance in natural populations of wild tomato constitutes the raw material for further selection and evolution.

Table 1. Geographic location and environmental conditions of four populations of wild tomato (*Solanum lycopersicum* var. *cerasiforme*) from the State of Sinaloa, Mexico.

Population	Latitude (N)	Longitude (W)	Elevation (m)	Mean annual temperature (°C)	Mean annual precipitation (mm)
Ensenada	24°00"	106°40"	40	24.7	691.1
Jahuara	26°00"	108°55"	56	24.9	301.2
Limonba	25°35"	107°20"	1120	16.6	1229.6
Urraca	23°04"	106°17"	36	24.1	812.1

Table 2. MANOVA performed on morphological RGR, and plant resistance and reproductive characters in four populations of wild tomato (*Solanum lycopersicum* var. *cerasiforme*) in Northwest Mexico. ANOVA for each character (B-F). R^2 = explained variance.

A) MANOVA

Source	Wilks' λ	*F*	df numerator	df denominator	*P-value*
Population	0.3398	103.467	15	3244	<0.0001
Block	0.9962	0.883	5	1175	0.4911
Population* Block	0.9428	4.663	15	3244	<0.0001

ANOVA

B) Plant Resistance (Whitefly number)

Source	df	SS	MS	*F*	*P-value*	R^2
Population	3	42.0243	14.008	181.24	<0.0001	0.350

C) Relative Growth Rate

Source	df	SS	MS	*F*	*P-value*	R^2
Population	3	14.7542	4.9180	18.16	<0.0001	0.050

D) Total inflorescences

Source	df	SS	MS	*F*	*P-value*	R^2
Population	3	1.48459	0.494	33.76	<0.0001	0.016

E) Total fruits

Source	df	SS	MS	*F*	*P-value*	R^2
Population	3	10.4031	3.467	65.78	<0.0001	0.169

F) Fruit Set

Source	df	SS	MS	*F*	*P-value*	R^2
Population	3	11.881	3.960	100.03	<0.0001	0.233

G) Total seeds

Source	df	SS	MS	*F*	*P-value*	*R*
Population	3	2.7715	0.923	14.371	<0.0001	0.043

Table 3. Repeated measures ANOVA of the number of adults (A), eggs (B), and larvae (C) of white flies *Bemisia sp.* on individual plants of wild tomato (*Solanum lycopersicum* var. *cerasiforme*) from four populations of Sinaloa, Mexico. Analyses were performed on log transformed values.

A) ADULTS

Source of Variation	df	Wilk's Lambda	Exact F	Prob>F
Population	3, 1307	0.5099	222.17	<0.0001
Time	2, 1306	1.9701	1286.48	<0.0001
Population x Time	6, 2612	0.8868	26.94	<0.0001

B) EGGS

Source of Variation	df	Wilk's Lambda	Exact F	Prob>F
Population	3, 1307	0.2836	123.59	<0.0001
Time	2, 1306	0.4541	296.57	<0.0001
Population x Time	6, 2612	0.9694	6.81	<0.0001

C) LARVAE

Source of Variation	df	Wilk's Lambda	Exact F	Prob>F
Population	3, 1307	0.1558	67.89	<0.0001
Time	2, 1306	0.0785	51.27	<0.0001
Population x Time	6, 2612	0.9605	8.85	<0.0001

Table 4. Estimates of narrow-sense heritability (SE) for six characters of *Solanum lycopersicum* var. *cerasiforme*, and the corresponding Q_{st} values (SE). Standard error for both estimates was estimated through Jackknife procedure. Figures in bold type indicated significant estimates.

	h^2				Q_{st}
Variable	Ensenada	Jahuara	Limonba	Urraca	
Plant Resistance (No. of *Bemisia* flies)	**0.03668** (0.0070)	**0.1583** (0.007)	-0.1375 (0.0679)	**0.1771** (0.0084)	0.7715 (0.242)
Relative growth rate	-0.0535 (0.0122)	-0.0131 (0.0399)	**0.0614** (0.0223)	-0.1859 (0.0790)	0.7744 (0.238)
Fruit number	**0.07162** (0.0051)	0.0184 (0.0324)	-0.0212 (0.0436)	-0.0431 (0.0470)	0.8534 (0.473)
No. of inflorescences	**0.0645** (0.0056)	0.02858 (0.0301)	-0.0728 (0.0532)	**0.0995** (0.0167)	1.0000 (0.000)
Fruit-set	**0.0904** (0.0040)	-0.0458 (0.0469)	**0.1377** (0.0449)	**0.1433** (0.0122)	0.6990 (0.095)
Total seed number	**0.0388** (0.0069)	-0.0616 (0.0124)	-0.2681 (0.1018)	-0.0661 (0.0517)	0.7346 (0.335)

Table 5. Phenotypic (above diagonal) and genetic (below diagonal) correlations between plant resistance, RGR, and reproductive characters in four wild tomato (*Solanum lycopersicum* var. *cerasiforme*) populations in Sinaloa, Mexico. N_1, N_2 are the sample size for phenotypic correlations and genetic correlation respectively, and significance of correlations is provided.

A) ENSENADA (N_1= 304 plants and N_2= 18 families)

Variable	Whitefly	RGR2-1	Total inflorescences	Total fruits	Fruitset	Total seeds
Whitefly		-0.1001^{a}	-0.3165^{c}	-0.3693^{e}	-0.3431^{e}	-0.3462^{e}
RGR2-1	0.0812^{ns}		0.1746^{a}	0.2192^{b}	0.1723^{b}	0.2210^{c}
Total inflorscences	-0.1178^{ns}	0.1248^{ns}		0.8497^{e}	0.5358^{e}	0.8034^{e}
Total fruits	-0.1362^{ns}	0.0492^{ns}	0.6768^{b}		0.8675^{e}	0.9658^{e}
Fruitset	-0.1072^{ns}	0.0177^{ns}	0.0752^{ns}	0.738^{c}		0.8472^{e}
Total seeds	-0.2693^{ns}	0.1427^{ns}	0.6199^{a}	0.9093^{e}	0.6223^{a}	

B) JAHUARA (N_1= 363 plants and N_2= 20 families)

Variable	Whitefly	RGR2-1	Total inflorescences	Total fruits	Fruitset	Total seeds
Whitefly		0.0691^{ns}	-0.0291^{ns}	-0.0673^{ns}	-0.0945^{ns}	-0.086^{ns}
RGR2-1	0.0866^{ns}		-0.1384^{b}	-0.1602^{b}	-0.1577^{b}	-0.0158^{ns}
Total inflorescences	0.1317^{ns}	-0.2715^{ns}		0.7825^{e}	0.3426^{e}	0.6203^{e}
Total fruits	-0.0025^{ns}	-0.391^{ns}	0.8725^{e}		0.8331^{e}	0.8521^{c}
Fruitset	-0.1697^{ns}	-0.3405^{ns}	0.382^{ns}	0.7719^{c}		0.7415^{e}
Total seeds	-0.206^{ns}	-0.2606^{ns}	0.6668^{b}	0.8465^{e}	0.7653^{c}	

C) LIMONBA (N_1= 339 plants and N_2 = 20 families)

Variable	Whitefly	RGR2-1	Total inflorescences	Total fruits	Fruitset	Total seeds
Whitefly		-0.0455^{ns}	-0.1806^{b}	-0.2361^{c}	-0.2271^{c}	-0.2377^{c}
RGR2-1	0.0847^{ns}		0.0871^{c}	0.1273^{a}	0.0772^{ns}	0.2234^{c}
Total inflorescences	-0.1346^{ns}	-0.1275^{ns}		0.7949^{e}	0.2865^{e}	0.6854^{e}
Total fruits	-0.0598^{ns}	-0.0753^{ns}	0.9084^{e}		0.7746^{e}	0.8651^{e}
Fruitset	0.0766^{ns}	0.1098^{ns}	0.5539^{a}	0.834^{e}		0.705^{e}
Total seeds	0.0178^{ns}	-0.0916^{ns}	0.7189^{c}	0.8332^{e}	0.7272^{c}	

D) URRACA (N_1= 334 plants and N_2 = 20 families)

Variable	Whitefly	RGR2-1	Total inflorescences	Total fruits	Fruitset	Total seeds
Whitefly		-0.086^{a}	-0.2279^{e}	-0.3025^{e}	-0.2802^{e}	-0.2896^{e}
RGR2-1	-0.1252^{ns}		0.0993^{a}	0.1864^{c}	0.1742^{c}	0.1739^{b}
Total inflorescences	-0.3691^{ns}	0.1772^{ns}		0.7641^{e}	0.3751^{e}	0.7247^{e}
Total fruits	-0.3904^{ns}	0.4265^{ns}	0.5724^{a}		0.8464^{e}	0.9518^{e}
Fruitset	-0.1223^{ns}	0.3983^{ns}	-0.1957^{ns}	0.6649^{b}		0.8083^{e}
Total seeds	-0.3505^{ns}	0.421^{ns}	0.3893^{ns}	0.9088^{e}	0.7067^{e}	

^{a} = P<0.05, ^{b} = P<0.005, ^{c} = P<0.001, ^{d} = P<0.0001, ^{e} = P<0.00001, ^{ns} = non significant

Table 6. Phenotypic selection gradients on resistance to *Bemisia tabaci* and on relative growth rate in *Solanum lycopersicum* var. *cerasiforme* in Northwetern Mexico. Analysis for each population and for the whole population are presented. Figures in bold indicate significant estimates (t-tests). The significance of the linear and quadratic Anova models is provided.

POPULATION	$\beta_{Resistance}$	β_{RGR}	Anova lineal model	$\gamma_{Resistance}$	γ_{RGR}	$\gamma_{ResistancexRGR}$	Anova quadratic model
ENSENADA	**-0.429****** (0.079)	0.168 (0.052)	$F_{(2, 252)} = 21.83$ $P < 0.0001$ $R^2_{adj} = 0.140$	**-0.651***** (0.173)	-0.031 (0.048)	**-0.333*** (0.144)	$F_{(5, 249)} = 12.69$ $P < 0.0001$ $R^2_{adj} = 0.187$
JAHUARA	-0.130 (0.083)	-0.004 (0.026)	$F_{(2, 332)} = 1.25$ $P < 0.28$ $R^2_{adj} = 0.001$	**-1.086*** (0.470)	-0.005 (0.023)	-0.176 (0.108)	$F_{(5, 329)} = 4.15$ $P < 0.001$ $R^2_{adj} = 0.045$
LIMOMBA	**-0.328***** (0.082)	**0.136***** (0.035)	$F_{(2, 296)} = 16.14$ $P < 0.0001$ $R^2_{adj} = 0.092$	**-0.807*** (0.383)	-0.032 (0.035)	-0.187 (0.149)	$F_{(5, 293)} = 7.92$ $P < 0.0001$ $R^2_{adj} = 0.104$
URRACA	**-0.342****** (0.069)	**0.146**** (0.054)	$F_{(2, 288)} = 17.11$ $P < 0.0001$ $R^2_{adj} = 0.100$	**-0.555***** (0.162)	-0.157 (0.081)	-0.106 (0.140)	$F_{(5, 285)} = 10.88$ $P < 0.0001$ $R^2_{adj} = 0.145$
WHOLE POPULATION	**-0.349****** (0.031)	**0.089****** (0.019)	$F_{(2, 1196)} = 75.17$ $P < 0.0001$ $R^2_{adj} = 0.110$	**-0.508****** (0.080)	**-0.050**** (0.017)	-0.101 (0.053)	$F_{(5, 1193)} = 42.54$ $P < 0.0001$ $R^2_{adj} = 0.147$

* $P < 0.05$, **$P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$

Table 7. Selection gradients on the sire breeding values of resistance to *Bemisia tabaci* and relative growth rate in *Solanum lycopersicum* var. *cerasiforme* in Northwestern Mexico. Analysis for each population and for the whole population is presented. Figures in bold indicate significant estimates (t-tests). The significance of the linear and quadratic Anova models is provided.

POPULATION	$\beta_{Resistance}$	β_{RGR}	Anova lineal model	$\gamma_{Resistance}$	γ_{RGR}	$\gamma_{ResistancexRGR}$	Anova quadratic model
ENSENADA	-0.371 (0.323)	0.114 (0.170)	$F_{(2, 15)} = 0.83$ $P = 0.45$ $R^2_{adj} = 0.0$	0.892 (5.477)	-0.166 (1.276)	-0.041 (4.107)	$F_{(5, 12)} = 0.280$ $P = 0.914$ $R^2_{adj} = 0.0$
JAHUARA	-0.272 (0.340)	-0.153 (0.144)	$F_{(2, 17)} = 9.63$ $P < 0.401$ $R^2_{adj} = 0.0$	-1.796 (7.487)	0.212 (0.809)	-4.882 (3.704)	$F_{(5, 12)} = 0.280$ $P = 0.914$ $R^2_{adj} = 0.02$
LIMOMBA	0.056 (0.535)	-0.077 (0.199)	$F_{(2, 17)} = 0.077$ $P < 0.925$ $R^2_{adj} = 0.0$	11.464 (9.265)	**2.576*** (1.121)	5.655 (4.225)	$F_{(5, 14)} = 2.788$ $P = 0.059$ $R^2_{adj} = 0.32$
URRACA	-0.324 (0.224)	0.490 (0.268)	$F_{(2, 17)} = 3.101$ $P = 0.071$ $R^2_{adj} = 0.181$	-1.012 (2.645)	-1.591 (4.211)	-3.961 (3.802)	$F_{(5, 14)} = 1.320$ $P = 0.311$ $R^2_{adj} = 0.077$
WHOLE POPULATION	**-0.381**** (0.061)	0.023 (0.070)	$F_{(2, 75)} = 19.40$ $P < 0.0001$ $R^2_{adj} = 0.324$	-0.294 (0.442)	0.006 (0.303)	-0.018 (0.350)	$F_{(5, 72)} = 7.62$ $P < 0.0001$ $R^2_{adj} = 0.300$

* P < 0.05, **P < 0.01, *** P < 0.001, **** P < 0.0001

Table 8. Analysis of covariance performed of the effects of growth (relative growth rate, RGR) and resistance, and differences among populations on relative fitness in plants of *Solanum lycopersicum* var. *cerasiforme*. Analysis based on individual values (phenotypic analysis) and paternal half-sib family mean values (breeding values).

	Phenotypic analysis				Breeding values analysis			
Source of variation	Df	SS	*F*	*P*-value	df	SS	*F*	*P*-value
Population	3	0.544	3.226	0.0219	3	0.0788	2.52	0.065
Resistance	1	3.045	54.14	<0.0001	1	0.0010	0.10	0.750
RGR	1	0.643	11.44	0.0007	1	0.0003	0.13	0.852
Population x resistance	3	0.677	4.017	0.0074	3	0.0690	2.21	0.095
Population x RGR	3	1.849	10.96	<0.0001	3	0.0834	2.67	0.054
Resistance x RGR	1	0.784	13.95	0.0002	1	0.0008	0.08	0.772
Population x resistance x RGR	3	0.227	1.349	0.2568	3	0.0701	2.25	0.091
Error	1171	65.85			62	0.6443		

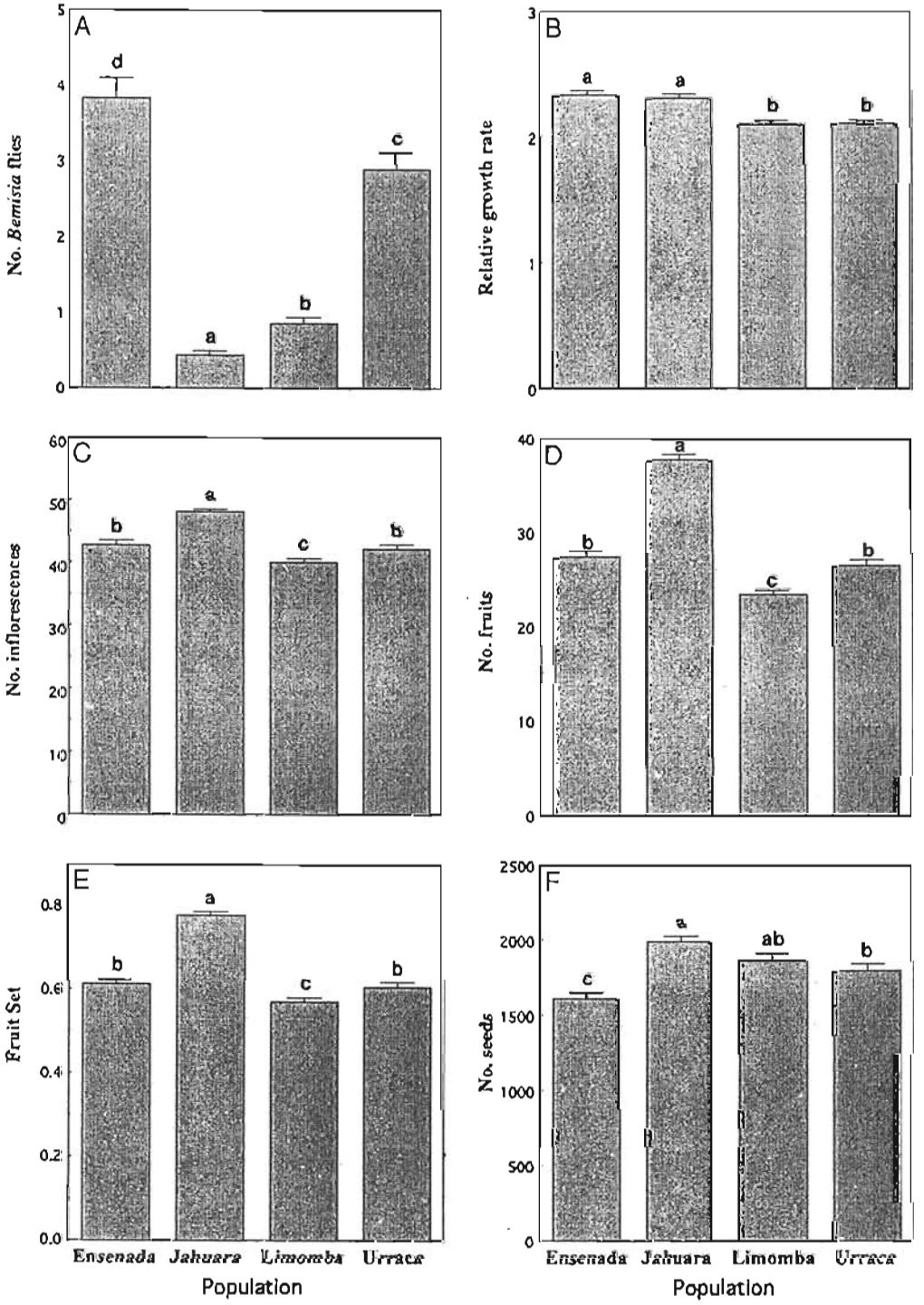

Figure 1. Mean values (±1SE) of plant resistance to *Bemisia tabaci*, relative growth rate, and four reproductive characters measured in plants of wild tomato (*Solanum lycopersicum var. cerasiforme*) from four populations of Sinaloa. Bars with different letters are statistically different, after Fisher's Protected LSD test.

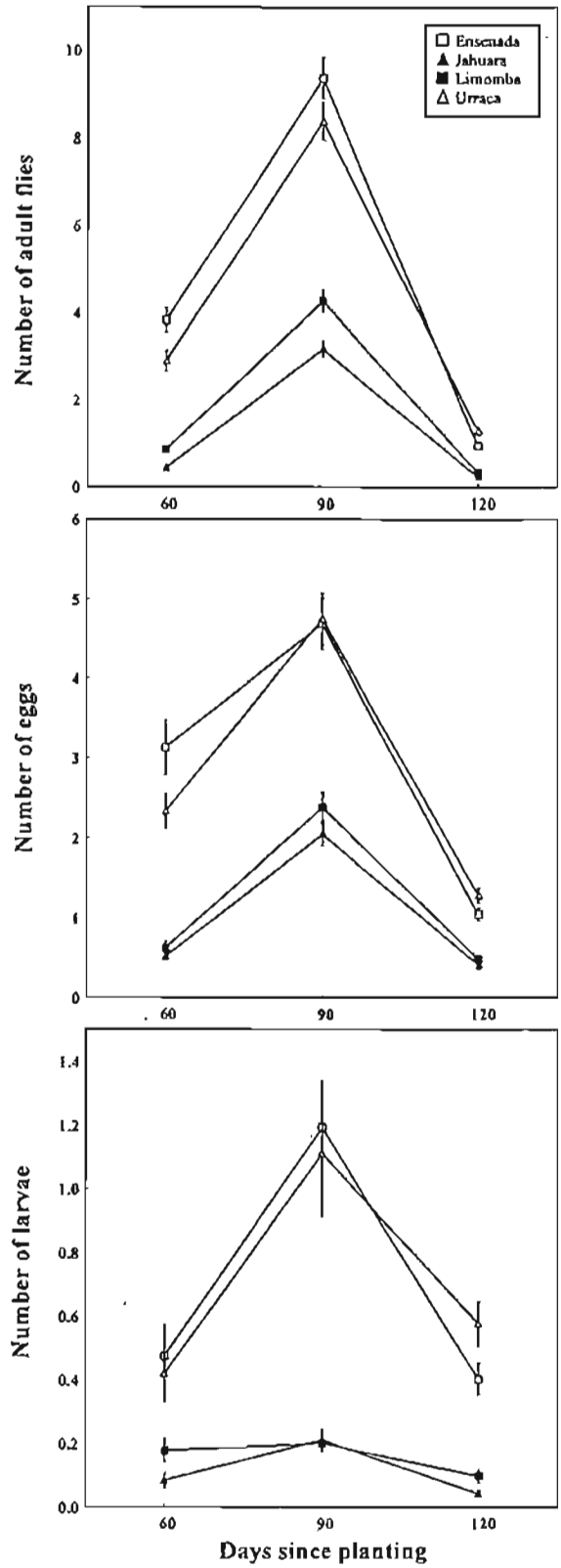
Ensenada
Jahuara
Limomba
Urraca
Number of adult flies
Number of eggs
Number of larvae
Days since planting
60
90
120

Figure 2. Mean (± SE) number of adults, eggs, and larvae of white fly (*Bemisia sp.*) in plants of *Solanum lycopersicum* var. *cerasiforme* from four populations of Sinaloa, Mexico.

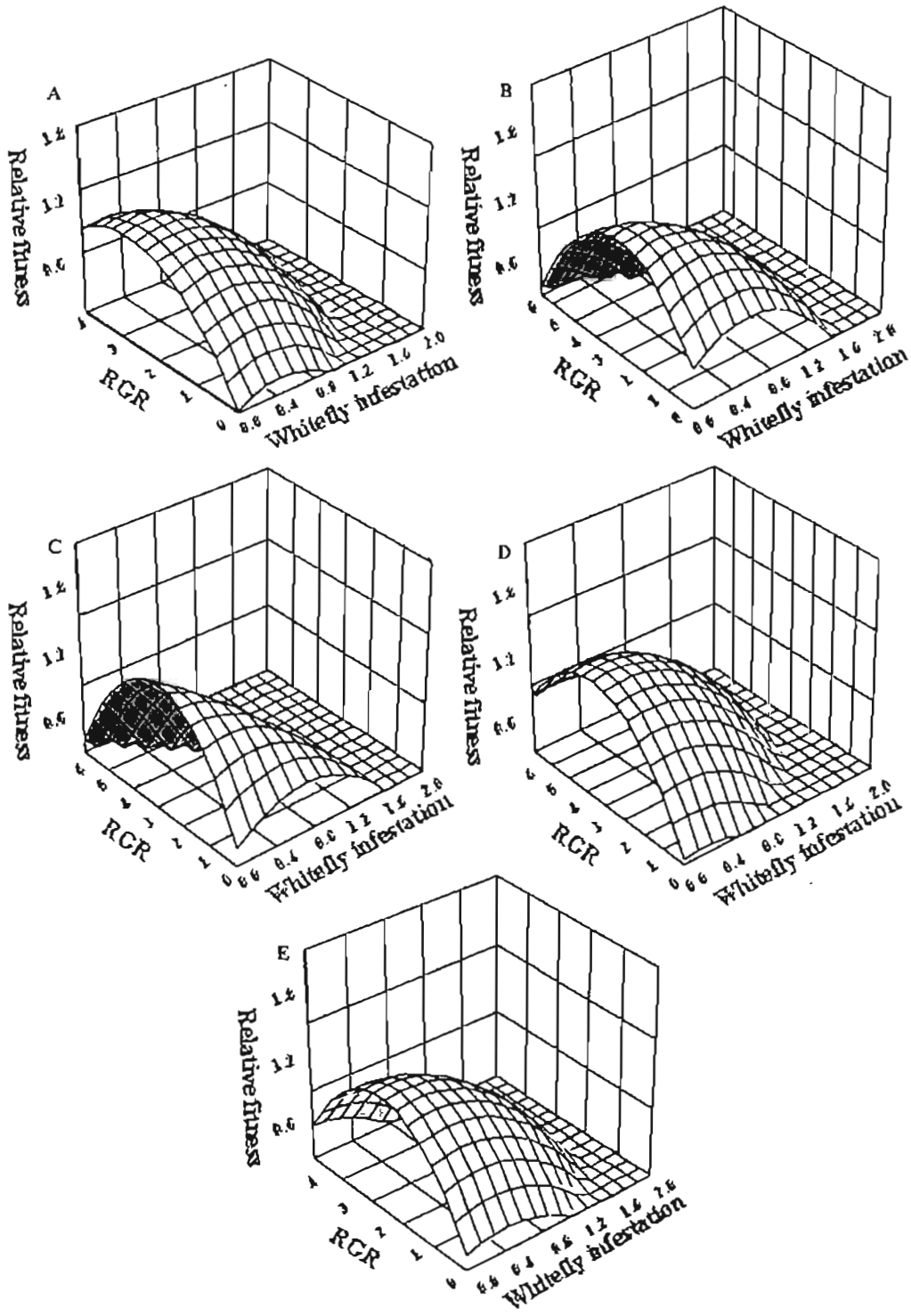

Figure 3. Selective surface of fitness as a function of relative growth rate (RGR) and plant resistance to whitefly (*Bemisia*) in four populations (A-D) and in the whole-population (E) of wild tomato (*Solanum lycopersicum* var. *cerasiforme*) from Sinaloa State, Mexico.

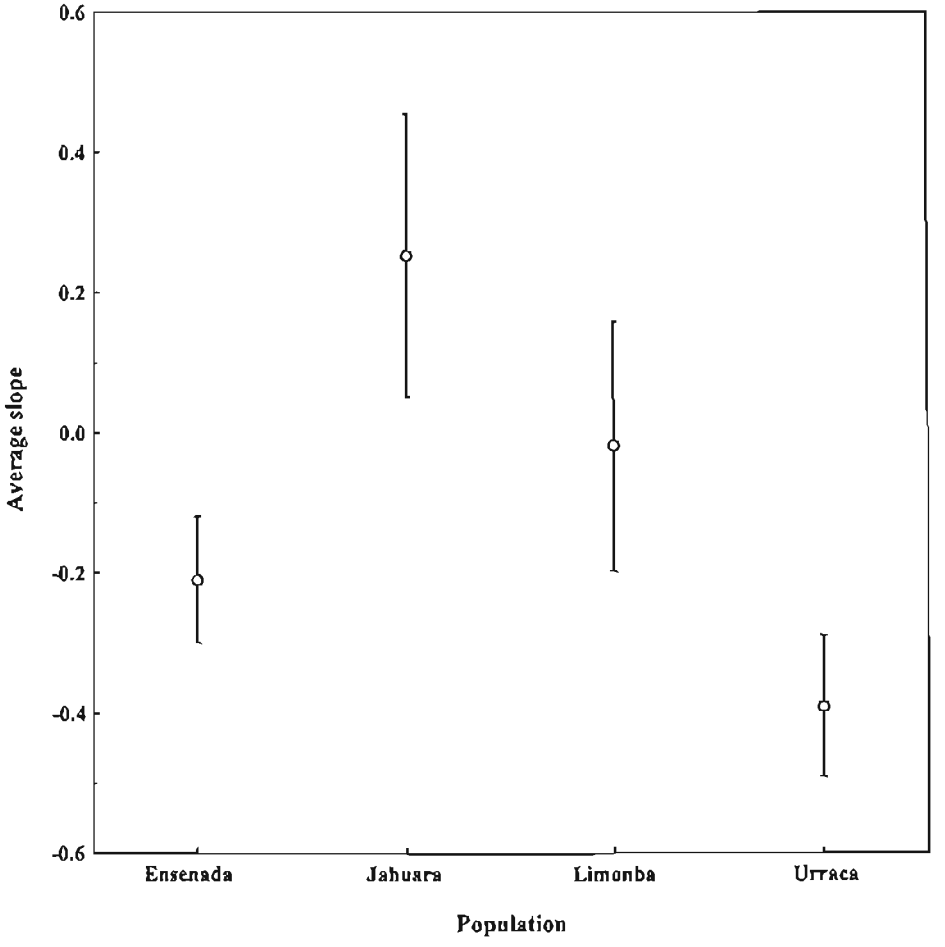

Figure 4. Average slope of the relationship between RGR as a function of resistance to whiteflies (*Bemisia sp.*) in four populations of wild tomato (*Solanum lycopersicum var. cerasiforme*) from Sinaloa.

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DISCUSIÓN GENERAL

El tomate es considerado el cultivo hortícola de mayor importancia en términos económicos (Nuez *et al.*, 2004). Existe consenso en ubicar el centro de origen del tomate cultivado en la región Andina compartida por Perú, Ecuador y Chile en Sudamerica; sin embargo no existe consenso para definir el lugar en donde se realizó la domesticacion, así como la taxonomía del mismo. Las evidencias científicas establecen que el centro de domesticación fue México (Jenkins, 1948; Rick, 1978) y que el tomate cultivado debe ser ubicado dentro del género *Solanum* y de la especie *lycopersicum*. Los últimos trabajos taxonómicos han logrado definir doce especies silvestres de tomate: *S. pinpinellifolium, S. chiesmanii, S. pennellii, S. habrochaites, S. neorickii, S. chiemilewskii, S. chilense, S. peruvianum, S. arcanum, S. corneliomuelleri, S. galapagense* y *S. huaylasense* (Peralta y Spooner, 2001; Darwin *et al.,* 2003; Spooner *et al.*, 2005; Peralta *et al.,* 2005), y una variedad o subespecie, también silvestre, dentro del tomate cultivado (*Solanum lycopersicum* var. *cerasiforme*).

Se ha reportado que las poblaciones silvestres de tomate, parientes de las plantas cultivadas constituyen un importante recurso genético en la búsqueda de genes resistentes a plagas o enfermedades (Stalker, 1980; Hernández-Verdugo *et al.*, 1998). La mosquita blanca (*Bemisia spp*) es una de las plagas de mayor importancia en tomate, ya que es el principal vector de enfermedades virales que impactan negativamente en la producción. En los parientes silvestres, tales como *L. pinpinellifolium, L. cheesmaniae, L. hirsutum, S. peruvianum* y S. *chilense* , se han encontrado niveles variables de resistencia a enfermedades virales (Kasrawi *et al.*, 1988; Pilowski y Cohen, 1974; Picó *et al.*, 1998), y por lo tanto han sido utilizados para transferir la resistencia a los tomates cultivados. Sin embargo, en esta tranferencia se presentan diferentes grados de barreras reproductivas

(Stevens y Rick, 1989; Sacks y St. Clair, 1998), las cuales podrían ser eliminadas si la resistencia se transfiere del ancestro más cercano al tomate cultivado. En este contexto es donde se inserta la importancia del presente esudio, que demuestra la existencia de variación genética para la resistencia a mosquita blanca. Los resultados indican la presencia de variación en los niveles de incidencia a la mosquita blanca y en la densidad de tricomas entre y dentro de las poblaciones de tomate silvestre y domesticado (cf. Capítulo II). Las poblaciones de tomate silvestre presentaron menor incidencia de mosquita blanca en comparación con la población de tomate cultivado. Este resultado está de acuerdo con estudios previos que indican que las poblaciones silvestres son más resistente al ataque de los herbívoros que las poblaciones cultivadas (Martins *et al.*, 2001; Freitas *et al.*, 2002; Tripathi y Varma, 2002). Es probable que estos elevados niveles de resistencia a la mosquita blanca en las poblaciones de tomate silvestre (*Solanum lycopersicum* var. *cerasiforme*) se deban a una respuesta a las presiones selectivas impuestas por la mosquita blanca, ya que esta interacción ha ocurrido en la misma área geográfica del Noroeste de México, al menos durante los últimos 50 años. La elevada variación observada entre y dentro de las poblaciones silvestres de tomate coincide con la variación en caracteres morfológicos y reproductivos y con la variación genética estimada con marcadores moleculares RAPD en estas poblaciones (Capítulo III). Por otro lado, la correlación negativa y significativa encontrada entre los niveles de incidencia de la mosquita blanca y el número de tricomas en las poblaciones silvestres y domesticada de tomate, indica que los tricomas en las hojas pueden constituir un componente de la resistencia de las plantas contra el ataque de este insecto.

Se ha demostrado que el ataque de insectos herbívoros puede eliminar o reducir el crecimiento y la capacidad de sobrevivencia y reproducción de la plantas (Crawley, 1997).

En este estudio se encontró que la incidencia de mosquita blanca se correlacionó significativamente con una reducción en el crecimiento y la producción de frutos de las plantas, lo que indica que el ataque de la mosquita blanca constituye un costo que se refleja en la adecuación de las plantas de tomate.

La introducción de resistencia a la mosquita blanca en el tomate por medio de la fijación de caracteres defensivos de las plantas, como es la alta densidad de tricomas, podría reducir la incidencia de enfermedades virales en este cultivo. Estos resultados demuestran la importancia de estudiar y mantener la variación genética presente en las poblaciones silvestres parientes de las plantas cultivadas.

Un recurso genético para ser explotado en los programas de mejoramiento debe tener amplia variacion genética. Los resultados de este estudio mostraron la existencia de variación genética dentro y entre las poblaciones de tomate silvestre y domesticado. El análisis molecular de varianza indicó que la mayor parte de la variación se encontró entre las poblaciones (cf. Capítulo III). Estos elevados niveles de diferenciación entre las poblaciones de tomate coinciden con los reportados para especies de plantas anuales que se autofecundan (Hamrick y Godt, 1996).

Una cantidad significativa (15.68 %; $P = 0.0049$) de la variación total se encontró entre el grupo de poblaciones silvestres y domesticadas, indicando una clara diferenciación entre ellas. Esto significa que el proceso de domesticación ha modificado la estructura genética de las poblaciones cultivadas de tomate. Estos resultados coinciden con los encontrados en poblaciones silvestres y domesticadas de chile analizadas con RAPDs por Oyama *et al.* (en prensa), que encuentran que las poblaciones silvestres y domesticadas se diferenciaron claramente, así como por el dendrograma y la gráfica obtenida por escalamiento multidimensional construidos con las matrices de distancias genéticas.

El dendrograma construido con la matriz de las distancias genéticas de las 60 poblaciones silvestres y las tres domesticadas de tomate, separó a la población domesticada Saladete del resto de las poblaciones, mientras que la población domesticada Comala fue la más similar a las poblaciones silvestres. Esta alta similitud de la población Comala con las poblaciones silvestres puede ser debido a que la variedad criolla Comala, haya intercambiado una mayor cantidad de genes con las poblaciones silvestres debido, a que los campesinos la han sembrado por varias décadas en las zonas de temporal del país, o bien a que el proceso de domesticación no ha producido grandes diferencias en esta población en relación a sus parientes silvestres más cercanos.

Las tres variedades cultivadas mostraron una cantidad significativamente menor de variación genética que las poblaciones silvestres. Este resultado está de acuerdo con la hipótesis general de que el proceso de domesticación ha reducido los niveles de variación genética en las poblaciones domesticadas (Ladzinsky, 1998).

Los niveles de polimorfismo genético promedio de 15.22 % y 9.95 % encontrados en las poblaciones silvestres y cultivadas, respectivamente, difieren de los reportados previamente para esta especie (Williams *et al.*, 1993), que encontraron un polimorfismo promedio de 24.5 % en las poblaciones silvestres y un polimorfismo de 2.8 a 20.3 % en las poblaciones cultivadas. Esto puede deberse en parte a que las poblaciones analizadas por Williams *et al.* (1993) provienen del centro de origen del género *Solanum*, mientras que las analizadas en el presente estudio pertenecen al centro de domesticación. Es posible que en el pasado estas poblaciones hayan sufrido cuellos de botella genéticos, produciendo una reducción en sus cantidades de variación genética de sus poblaciones.

La clara distinción entre las poblaciones de las diferentes regiones indica cierto grado de aislamiento entre los grupos de poblaciones y un flujo génico dentro de cada grupo. Esta

diferenciación y variación entre poblaciones fue confirmada al realizar el análisis cuantitativo de la resistencia a mosquita blanca en cuatro poblaciones silvestres de tomate (*Solanum lycopersicum* var. *cerasiforme*) de Sinaloa (cf. Capítulo IV). La diferenciación genética entre poblaciones se obtuvo no solamente para el carácter de resistencia, sino también para caracteres vegetativos y reproductivos. Estos resultados están en concordancia con la alta variación natural encontrada entre poblaciones de tomate (Sánchez-Peña *et al.*, en prensa); sin embargo, las diferencias fenotípicas pueden ser el resultado de las diferencias en las condiciones bióticas y abióticas en la que se encuentran las poblaciones (Roff y Mousseau, 2005).

El objetivo básico de la genética cuantitativa es conocer la contribución genética y ambiental de la variación fenotípica total (Falconer y Mackay, 1995). La contribución genética puede contener varianza debida a dominancia, la varianza aditiva y la varianza de interacción, siendo la varianza aditiva la de mayor importancia en los programas de mejoramiento, dado que sobre ésta actúa la selección (Falconer yMackay, 1995). En el experimento reportado en el Capítulo IV, la evidencia cuantitativa nos indica que existen cantidades significativas de variación genética aditiva para tres de las cuatro poblaciones, respecto al carácter de resistencia a mosquita blanca. Esto se confirmo en las estimaciones de la heredabilidad, que fueron diferentes de cero para las poblaciones de Urraca, Jahuara y Ensenada, mientras que ésta fue cero en Limonba. Estos resultados están en concordancia con los obtenidos en la variación fenotípica para la resistencia, donde se encontró que las cuatro poblaciones difieren para este carácter, y con estudios previos (Sánchez-Peña *et al.*, en prensa), en donde también se reporta diferenciación para resistencia a mosquita blanca en nueve poblaciones silvestres de tomate del noroeste de México. No obstante los valores pequeños (0.038-0.177) de las heredabilidades para un gran número de caracteres y

poblaciones, la significancia de éstos nos indica que la varianza genética no es una limitante para la evolución de estos caracteres (Falconer y Mackey 1995; Roff 1997; Lynch y Walsh 1998). Los bajos valores de heredabilidad sugieren que las poblaciones silvestres de tomate contienen pequeñas cantidades de varianza aditiva, posiblemente debido a los altos niveles de endogamia presente en las poblaciones de tomate. La mayoría de las poblaciones silvestres de tomate, al igual que otras especies de *Solanum*, son plantas autógamas (Rick 1973) lo que ocasiona que la endogamia y deriva reduzcan las cantidades de varianza genética dentro de las poblaciones, pero al mismo tiempo incrementan la diferenciación poblacional. Es posible que estos procesos hayan influido en la alta diferenciación poblacional encontrada para los caracteres cuantitativos en las poblaciones silvestres de tomate ($0.69 \leq Q_{st} \leq 1$).

Los resultados encontrados en el Capítulo IV nos indican que la mosquita blanca ha actuado como un agente selectivo en las poblaciones de tomate silvestre. Esto ha ocasionado niveles diferentes de resistencia a la plaga, lo cual fue demostrado en tres de cuatro poblaciones silvestres (Tabla 4). De la misma manera, se demostró que la mosquita blanca afecta de manera diferencial la tasa relativa de crecimiento y la adecuación de las poblaciones de tomate. Esto está en concordancia con dos aspectos de la teoría del mosaico geográfico (Thompson 1999) que plantea un mosaico de selección y en la interacción entre huéspedes-enemigos.

Finalmente, los resultados aquí presentados nos indican que los recursos genéticos presentes en las poblaciones silvestres de tomate de México deben ser motivo de estudios más profundos y al mismo tiempo deben de ser considerados en los programas de mejoramiento del cultivo del tomate.

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