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ETNOBOTÁNICA, ECOLOGÍA Y POSIBLES PROCESOS DE DOMESTICACIÓN DE MALEZAS ÚTILES EN DIFERENTES AGROECOSISTEMAS EN SANTA MARÍA TECOMAVACA, OAXACA, MÉXICO.

TESIS

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PRESENTA

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Flora's Secret

Lovers in the long grass
look above them
only they can see
where the clouds are going
only to discover
dust and sunlight
ever make the sky so blue

Afternoon is hazy
river flowing
all around the sounds
moving closer to them
telling them the story
told by flora
dreams they never knew

Enya

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ÍNDICE

RESUMEN

Durante siglos, el cultivo de plantas ha sido acompañado por la presencia de plantas indeseadas llamadas malezas o plantas arvenses. En general, la mayor parte de la información disponible sobre estas plantas se dirige básicamente hacía su control o erradicación de los terrenos de cultivo. Estas plantas, sin embargo, también presentan utilidad para el hombre y por ello forman parte integral de los agroecosistemas tradicionales. De hecho, los agricultores tradicionales desarrollan varias actividades para facilitar su obtención y como consecuencia de esta interacción algunas de estas plantas muestran indicios de estar bajo un proceso incipiente de domesticación.

Este trabajo estudió la flora arvense asociada con la agricultura de subsistencia tanto de temporal como de riego, que se practica en Santa María Tecomavaca, una comunidad rural dentro de la porción oaxaqueña de la Reserva de la Biosfera Tehuacán-Cuicatlán, México. Dos hipótesis fueron planteadas en el trabajo. La primera postula que la utilidad y las formas de manejo de las plantas arvenses determinan su distribución en los sistemas agrícolas, resultando en una mayor distribución de plantas arvenses útiles y nativas en los sistemas agrícolas con menor uso de productos químicos. La segunda propone que las diferencias morfológicas, fitoquímicas y/o genéticas entre las plantas manejadas y silvestres indican que las poblaciones manejadas han sido sujetas y/o están bajo un proceso de domesticación incipiente. Los objetivos generales del trabajo fueron investigar el uso, el manejo y la ecología de las plantas arvenses que crecen dentro de diferentes sistemas de cultivo, así como también investigar los indicios de una posible domesticación incipiente en dos especies de arvenses elegidas.

Mediante trabajo de campo (colectas, entrevistas etnobotánicas abiertas y estructuradas y muestreos en campos de cultivo) y gabinete (revisión de floras y monografías taxonómicas, determinación), se obtuvo información para describir la diversidad de las plantas arvenses, el origen nativo o exótico de cada una de ellas, los usos locales y las formas de manejo que ejercen los campesinos sobre ellas, así como también su distribución dentro de cuatro diferentes sistemas de cultivo a lo largo de un gradiente de intensidad de manejo agrícola. Los resultados revelan que 161 especies pertenecientes a 40 familias y 103 géneros son encontrados como arvenses en los campos de cultivo estudiados, incluyendo tres especies endémicas de la región. De estas especies, 124 son nativas, 22 son exóticas y para las restantes 15 no se pudo determinar su origen fitogeográfico. El 91.9% de todas las especies arvenses presentan uno o más usos, siendo el forraje su uso más importante, seguido por su aplicación como medicina, alimento, ornamento, condimento y abono verde, entre otros. De las especies forrajeras, solo el 3.5% reciben alguna forma de manejo incipiente, mientras que el 29% de las especies con otro uso recibe alguna forma de manejo incipiente por parte de los campesinos. La forma de manejo más común es la tolerancia (21 spp.), seguido por la protección (7 spp.), el cultivo local (5 spp.) y el fomento (1 spp.). No obstante el interés por parte de los campesinos en la utilidad de las plantas arvenses, su distribución espacial no parece estar influenciada por las prácticas del manejo no-agrícola como la tolerancia, la protección o el fomento. El uso sistemático de herbicidas no-selectivos y sistémicos, sin embargo, si parece disminuir significativamente la riqueza de arvenses nativas.

Considerando las evidencias obtenidas con la metodología anterior se seleccionaron dos especies arvenses para su estudio morfológico, fitoquímico y genético, con el fin de determinar las diferencias entre las poblaciones manejadas y sin manejo y con ello comprobar la segunda hipótesis de este trabajo. Las especies fueron seleccionadas con base en criterios de utilidad, formas de manejo, presencia en hábitats tanto naturales como antropogénicos y variaciones morfológicas. Las especies elegidas son el Papaloquelite (*Porophyllum ruderale* var. *macrocephalum* (DC.) Cronquist: Asteraceae) y el Epazote (*Chenopodium ambrosioides* L.: Chenopodiaceae). Los resultados muestran la existencia de variantes asociadas a un gradiente de intensidad de manejo humano solo para una de las dos especies: Epazote. Esta variación se relaciona con el mejoramiento de su sabor, lo cual implica la disminución de sustancias de defensa química. Además, lo anterior coincide con la variación genética encontrada para las mismas variantes. Estos resultados son similares a los encontrados en otras especies utilizadas como verduras en otras regiones del mundo, ubicando a la evolución del Epazote bajo el modelo de la colonización dentro de la agro-ecología. Así, en contraste con el Papaloquelite para el cual no se encontró ninguna diferencia significativa entre variantes, el Epazote se encuentra aparentemente bajo un proceso de domesticación incipiente, al menos en la zona de estudio. Sin embargo, cabe destacar que ambas especies, así como otras bajo manejo humano, siguen evolucionando y su futura domesticación depende de las condiciones económicas, sociales y culturales imperantes, tanto en el tiempo como en el espacio.

Los resultados de este trabajo apoyan parcialmente la primera hipótesis. Así, aunque se encontraron más arvenses nativas en los sistemas agrícolas con menor uso de herbicidas, la proporción de arvenses útiles no cambió como se esperaba. Por lo tanto, se puede concluir que la distribución de las arvenses no depende de su utilidad, sino del manejo agrícola, y en particular, del uso de herbicidas no-selectivos y sistémicos. La segunda hipótesis del trabajo se puede aceptar en el caso de Epazote, pero no para Papaloquelite. En conclusión, la evidencia de un proceso de domesticación incipiente para *C. ambrosioides* señala que hoy en día hay especies de arvenses útiles que están evolucionando, y su documentación podría proporcionar información importante para aclarar aún más nuestro conocimiento sobre el proceso de la domesticación de plantas, tanto en el pasado y el presente, como en el futuro.

ABSTRACT

For centuries, plant cultivation has confronted the presence of unwanted plants or weeds. In general, most information available about these plants is directed towards their control or eradication from agricultural fields. Weeds, however, also present certain benefits and as such, form an integral part of traditional agro-ecosystems. In fact, traditional farmers develop various activities to aument their availability and in consequence of these human-plant interactions, some of these plants show indications of an incipient domestication process.

This work studied weeds associated with subsistence agriculture, both rain-fed and river-fed, which is practiced in Santa María Tecomavaca, a rural community within the Oaxaca portion of the Tehuacán-Cuicatlán Biosphere Reserve in Mexico. Two hypotheses were formulated in this work. The first postulated that utility and incipient management forms of weeds determine their distribution in agricultural fields, resulting in a major distribution of useful and native weeds within farming systems with less use of chemical products. The second hypothesis proposed that morphological, phytochemical and/or genetic differences between managed and wild weed populations indicate that managed populations have been and/or are under a process of incipient domestication. The general objectives of this work were to investigate uses, management forms and ecology of weeds growing within different crop production systems, as well as to investigate the indications of a possible incipient domestication process of two selected weed species.

Through field and laboratory work (weed collections, free and structured interviews, field sampling, taxonomic determination using Flora and floristic monographs), sufficient information was gathered to describe weed diversity, determine the native/exotic origin of each weed species, identify their local uses and management forms applied by local farmers, as well as to assess weed distribution within four different farming systems along a gradient of agricultural management intensity. The results present 161 species belonging to 40 botanic families and 103 genera within the studied fields, including three endemic species of the region. Of these species, 124 are native, 22 are exotic, although for 15 species, the phytogeographic origin could not be determined. Of all weeds, 91.9% present one or more uses, with fodder being the most important one, followed by application as medicine, food, ornament and mulch, amongst others. Of the fodder weeds, only 3.5% receive some kind of incipient management, in contrast with otherwise used weeds, of which 29% is managed in some way. The most practiced management form is tolerance (21 spp.), followed by protection (7 spp.), cultivation (5 spp.) and promotion (1 spp.). Notwithstanding the interest of the local farmers in the utility of weeds, their spatial distribution does not appear to be influenced by non-agricultural management practices like tolerance, protection or promotion. The systematic use of non-selective and systemic herbicides, however, seems to significantly diminish native weed richness.

Taking into account the evidence obtained above, two weeds were selected for the morphological, phytochemical and genetic study, in order to determine differences between managed and wild populations as postulated in the second hypothesis of this work. The weed species were selected based on criteria of utility, management forms, presence in habitats both natural and anthropogenic and morphological variations. The selected species were 'Papaloquelite' (*Porophyllum ruderale* var. *macrocephalum* (DC.) Cronquist: Asteraceae) and 'Epazote' (*Chenopodium ambrosioides* L.: Chenopodiaceae). The results highlight the existence of variants associated with a gradient in human management intensity for one of the two selected species: Epazote. This variation is related with an improvement of taste, which implies the reduction of substances related with chemical defense and coincides with the genetic variation found in the same Epazote variants. These results are similar to those from other species used as vegetables in other regions of the world and place the evolution of Epazote under the domestication model of simple colonization within the agroecological habitat. As such, in contrast with Papaloquelite, for which no significant differences were found among variants, Epazote appears to be under an incipient process of domestication, at least in the study zone. However, both species, like other plants under human management, continue to evolve and their future domestication strongly depends on economic, social and cultural conditions, both in time and space.

The results of this work partially support the first hypothesis. Even though there were more native weeds in farming systems with less herbicide use, the proportion of useful weeds did not change as expected. In conclusion, weed distribution does not depend on utility, but most likely on agricultural management, and in particular, on the use of non-selective and systemic herbicides. The second hypothesis of this work was accepted for Epazote, but not for Papaloquelite. The evidence of an incipient domestication process for Epazote confirms how, at present, there are useful weed species under evolution, and their documentation may provide important information in order to improve our knowledge about the plant domestication process, both in the past and the present, as in the future.

Xochipilli
Dios de las Flores

INTRODUCCIÓN GENERAL

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Antecedentes

Desde el inicio de la agricultura, los humanos han cultivado plantas en diferentes formas alrededor del mundo, dando lugar con ello a distintos sistemas agrícolas. Dentro de éstos sistemas de cultivo, sin embargo, se encuentran no solamente las plantas de interés económico, sino también aquellas plantas no deseadas, denominadas comúnmente malezas o malas hierbas. En general, las malezas pueden ser descritas como "*plantas impopulares o indeseables que crecen en lugares perturbados por el hombre*" (Harlan, 1929; Baker, 1965; Harlan & deWet, 1965; Baker, 1967, 1972, 1974). En terminos ecológicos se les describe como "*plantas colonizadoras de lugares perturbados*" (Challenger, 1998). Dependiendo del lugar en donde crecen, son llamadas "ruderales" (malezas asociadas con la vegetación secundaria, basureros, caminos, vías del tren, ríos, etc.) o "agrestales" o "plantas arvenses" (malezas asociadas con campos agrícolas) (Baker, 1967).

La mayoría de la literatura sobre malezas se enfoca en su nocividad y la competencia que establecen con los cultivos y por consecuencia, proporciona comúnmente información sobre su control y/o erradicación (Fryer, 1979; Mortimer, 1996; Cardina et al., 1997; Dekker, 1997; Norris, 1997; Thill & Mallory-Smith, 1997; Hidalgo et al., 1990). En la actualidad, la mayor parte del suministro de alimentos en el mundo depende fuertemente de un número reducido de especies vegetales llamadas en conjunto los "mega-cultivos" (Wilkes, 1995). La agricultura intensiva tiende a basarse en plantas altamente especializadas y destinadas al monocultivo, con lo cual también se tiende a la reducción de la diversidad genética de las plantas cultivadas (Rzedowski, 1978; Cox & Atkins, 1979). En consecuencia, la pérdida de diversidad en los sistemas de cultivo trae consigo repercusiones negativas en detrimento de la dieta y nutrición de la gente (Dewey, 1979). Al mismo tiempo, aunque los organismos no nativos juegan un papel muy importante en la economía y la cultura de muchas regiones en el mundo, su introducción indudablemente puede representar una amenaza para la biodiversidad nativa a nivel mundial (Ewel et al., 1999).

Afortunadamente, existen plantas que desde hace mucho tiempo sirven para satisfacer muchas de las necesidades humanas y entre ellas están varias de las consideradas como malezas (Rzedowski, 1978; Bye & Linares, 1983; Caballero, 1984; Casas et al., 1994; Caballero, 1995; Blanckaert, 2001; Casas et al., 2001; Paredes-Flores, 2001). Por ejemplo, las hierbas comestibles denominadas "quelites" han complementado la dieta básica de maíz, frijoles, chile y calabaza desde tiempos prehispánicos, enriqueciéndola con nutrientes y vitaminas importantes (Bye, 1981; Viveros & Casas, 1985). En contraste con la agricultura moderna que considera a todas las malezas como nocivas, los agricultores tradicionales reconocen el importante papel de las plantas no cultivadas que crecen espontáneamente entre sus cultivos (Chacón & Gliessman, 1982; Caballero, 1984; Casas et al., 1994, 2001). Además de proteger los suelos contra erosión, altas temperaturas y pérdida de nutrientes, las plantas arvenses presentan varios usos como comestible, medicinal, forraje, ornamental y ceremonial y aunque son principalmente utilizados en el hogar, ventas ocasionales en los mercados locales fortalecen la economía familiar (Espinosa-García & Díaz-Pérez, 1996; Vieyra-Odilón & Vibrans, 2001).

Desde el momento en que la gente tiene interés en algún producto útil de una planta, se desarrollan métodos para facilitar su obtención. Iniciando con la recolección, surgen distintas formas de manipulaciones con varias intensidades de interacción con las plantas de interés. El conjunto de estas prácticas ha sido llamado "manejo" y algunos autores prefieren utilizar el término "manejo incipiente", "manejo tradicional" o "cultivo in situ" para diferenciarlo de las prácticas agrícolas comunes. Se distinguen los siguientes grados de manejo incipiente: recolección, tolerancia, fomento o inducción, protección y transplante (Casas et al., 1997b). El manejo incipiente de arvenses es común en México (Casas & Caballero, 1995). Por ejemplo, recientes estudios etnobotánicos en el Valle de Tehuacán-Cuicatlán han registrado diferentes formas de manejo incipiente de especies arvenses que, desde hace mucho tiempo, son utilizadas por varios grupos humanos (Casas et al., 1997b; Blanckaert, 2001; Casas et al., 2001; Paredes-Flores, 2001; Van Diest, 2002; Rosas-López, 2003; Blanckaert et al., 2004; Vancraeynest, 2005; Avendaño et al., 2006; Paredes-Flores, 2006; Rodríguez-Arévalo et al., 2006). Así, durante la limpieza o el deshierbe de los campos de cultivo, los agricultores toleran plantas de algunas de las especies que ellos consideran útiles (Davis & Bye, 1982; Williams, 1985; Casas et al., 1996) y ciertas malezas comestibles pueden incluso ser protegidas, como lo describe Bye (1979) en Chihuahua.

Dentro del conjunto de sistemas agrícolas existe una variedad extensa de intensidades de manejo incipiente de plantas no-cultivadas. Es posible que una población de arvenses de un campo esté sujeta a una selección más intensiva que otra. Si este manejo se mantiene durante varios años, la selección artificial puede superar la fuerza del flujo génico y favorecer un genotipo con rasgos de interés humano. Evidencia de la evolución reciente bajo la influencia humana o domesticación incipiente está disponible y ejemplos de lo anterior se han documentado para algunas plantas arvenses útiles, como *Lepidium virginicum* L. (Bye, 1979), *Ibervillea millspaughii* (Cogn.) J. Jeffrey, *Melothria pendula* L. (Lira, 1988; Lira & Casas, 1998), *Jaltomata procumbens* (Cav.) J.L. Gentry (Davis & Bye, 1982), *Porophyllum ruderale* var. *macrocephalum* (DC.) Cronquist (Vázquez Rojas, 1991), *Solanum nigrescens* M. Martens & Galeotti, *Phytolacca icosandra* L. y *Chenopodium berlandieri* Moq. (Bye, 1998), *Amaranthus* spp. (Mapes et al., 1997), *Anoda cristata* (L.) Schl. (Bye, 1998; Rendón & Núñez-Farfán, 2001) y *Proboscidea louisianica* (Mill.) Thell. subsp. *fragans* (Lindl.) Bretting (Paredes-Flores, 2006), entre otras.

Por lo anterior, es evidente que la selección artificial del hombre es importante en la evolución de las plantas arvenses. La selección artificial se distingue de la selección natural en que, primero, la variabilidad genética depende de los cambios que hace el hombre en el medio en donde crecen las plantas de su interés, y segundo, en que la dirección e intensidad de la selección están dirigidas por diversos factores antropogénicos, como la cultura y la tecnología. De esta manera, el ser humano ha cambiado las presiones de selección natural sobre las plantas cultivadas, logrando que las plantas con rasgos desfavorables (i.e. que bajo condiciones naturales nunca les hubieran permitido sobrevivir) puedan permanecer. La intensidad y racionalidad de la selección artificial depende de algunos factores de la planta, tanto intrínsicos como extrinsicos: su importancia económica y cultural, su uso y destino comercial, así como también la forma en que se impone o libera cierta presión, y las características y el desarrollo de los sistemas agrícolas (Colunga García-Marín et al., 1986).

El desarrollo de la evolución determinado por la selección artificial es definido como "*el proceso de cambio de las frecuencias genéticas en las poblaciones cultivadas donde la fuerza predominante es la selección del hombre sobre las variaciones genéticas que se producen en el material que propaga*" (Schwanitz, 1966; Colunga García-Marín et al., 1986). Rindos (1984) define la domesticación como "*un proceso co-evolutivo mediante el cual un dado taxón diverge de su poza génica original y establece una relación simbiótica de protección y dispersión con el animal nutriéndose de el*". Otros autores la describen como "*un proceso mediante el cual los seres humanos determinan cambios en la estructura genética de las poblaciones, favoreciendo la frecuencia de genotipos que representan ventajas para su subsistencia y para el desarrollo de su vida social y cultural*" (Lira & Casas, 1998). En el contexto de este trabajo, la domesticación se considera como una co-evolución durante la cual las plantas presentan cambios que se mantienen artificialmente por el ser humano, y el ser humano adapta su comportamiento según estos cambios. La expresión máxima de esta evolución no solo es la planta domesticada, sino también el establecimiento de la agro-ecología y la aparición de plantas como las arvenses.

Un aspecto importante de la domesticación es que es un proceso continuo que puede afectar incluso las plantas ya domesticadas (Casas et al., 1997b). Se pueden distinguir tres formas principales de domesticación: incidente, especializado y agrícola (Rindos, 1984). La domesticación incidente es el resultado de la relación entre una comunidad no-agrícola y las plantas útiles en sus alrededores, como consecuencia directa de la necesidad de alimentarse. En las prácticas de selección resulta que algunos caracteres morfológicos obtienen una ventaja sobre otras. Los productos óptimos de este proceso son las primeras plantas domesticadas. Es importante notar que estas primeras plantas domesticadas no se originaron en un agro-ecosistema, sino que formaron parte importante del surgimiento de la agricultura misma, ya que la evolución de éstas plantas permitió nuevas interacciones entre humanos y la vegetación, resultando en la domesticación especializada. Los humanos empiezan a dispersar las plantas de interés más cerca o dentro de la zona habitada por ellos. Debido a las prácticas intensivas de protección y eliminación diferencial de plantas no deseadas, las plantas de interés humano se vuelven más y más abundantes en estas áreas. Estas interacciones humanas simbióticas con una comunidad de plantas en su ambiente local, dan lugar al desarrollo de sistemas agrícolas complejos. En la domesticación agrícola interactuan el comportamiento humano y la evolución vegetativa dentro del ambiente agrícola. La evolución de las plantas domesticadas se acelera después de la introducción de la preparación del terreno mediante fuego, el deshierbe, la irrigación, la labranza, etc.

Por definición, las plantas arvenses o malezas no existirían sin las prácticas agrícolas del ser humano. Por lo tanto, ellas son nuevos productos de la evolución (Harlan & deWet, 1965), lo cual las hace excelentes candidatas para el estudio de la evolución bajo la domesticación (Harlan, 1970; Baker, 1972, 1974; Begon et al., 1996). La adaptación a lugares perturbados ha introducido el desarrollo de muchos rasgos y una de las características más importantes de las plantas arvenses, es su plasticidad fenotípica. La capacidad de las arvenses de adaptarse a hábitats perturbados probablemente les proporciona una ventaja evolutiva.

La selección artificial ha dado lugar tanto a cambios deseados (de interés agronómico) como a cambios no deseados o inconscientes en las plantas domesticadas. Entre los primeros, se destacan los cambios morfológicos, como por ejemplo, el incremento del tamaño o el desarrollo de un color agradable o una forma más llamativa del producto deseado. También se ha seleccionado por adaptaciones químicas y fisiológicas, como la pérdida de toxinas y el mejor sabor de la parte comestible o la resistencia de la planta contra enfermedades y plagas, así como ventajas fenológicas como un hábito anual en lugar de uno perenne. Pero los cambios más fuertes se han efectuados a nivel de la reproducción, por ejemplo, autogamia en lugar de alogamia, pérdida de latencia de semillas, mayor tamaño de semillas, germinación rápida y uniforme, reducción de dispersión de las semillas y reducción de fertilidad de semillas en plantas con reproducción vegetativa (Baker, 1972; deWet & Harlan, 1975; Hawkes, 1983; Hanelt, 1986). Por otro lado, un cambio no deseado de la selección artificial es la pérdida de la diversidad genética de las poblaciones de plantas domesticadas, en comparación con la diversidad genética de las poblaciones silvestres originales (erosión genética) (Baker, 1972).

Desde los tiempos de de Candolle y Vavilov hasta los años '50, las plantas arvenses fueron consideradas como los progenitores de las plantas domesticadas (Vavilov, 1926; Anderson, 1952; Sauer, 1952). Hoy en día, la observación de que casi todas las especies domesticadas tienen su pariente arvense, generó la idea que ambas han evolucionado simultáneamente y condujo a la introducción del concepto de un complejo "domestico-arvense" (Harlan, 1965; Harlan & deWet, 1965): dos poblaciones separadas entre las cuales ocurre ocasionalmente, de forma local y por un número limitado de generaciones, un intercambio genético (flujo génico). Este modelo entonces propone que la planta arvense y la domesticada tienen un ancestro común. Por lo tanto, arvenses son consideradas como reservorios de germoplasma, intercambiándolo periódicamente con las domesticadas e incrementando así su diversidad genética. La relación actual entre maíz y teocinte (*Zea mays* ssp. *mexicana* (Schrad.) Iltís) es un notable ejemplo de ello (Harlan & deWet, 1965). Otro ejemplo es la hibridación de la maleza *Solanum x edinense* con la domesticada *S. tuberosum* en el centro del Valle de México, la cual se sabe que es la causa principal de la variabilidad de las razas locales de las papas cultivadas (Ugent, 1968). La dirección de la evolución a lo largo del *continuum* silvestre-arvense-domesticada (Bye, 1998) no es necesariamente en un solo sentido. En ciertas circunstancias dicho sentido puede ser reversible dependiendo de la intensidad y orientación de la selección natural y/o artificial sobre las especies (Harlan & deWet, 1965; deWet & Harlan, 1975; Chacón & Gliessman, 1982; Davis & Bye, 1982; Hawkes, 1983).

Después de varias décadas de investigación sobre los mecanismos biológicos de la domesticación, todavía quedan muchas dudas. Afortunadamente, las técnicas moleculares modernas presentan soluciones para resolver diferentes preguntas sobre la evolución y la domesticación. Los métodos avanzados involucran híbridos, el análisis de aloenzimas y los marcadores moleculares como los RAPDs, RFLPs, AFLPs y microsatélites, entre otros. Ellos proporcionan información indispensable para mejorar el entendimiento de la domesticación. Entre otros, estos estudios pueden ayudar en la determinación del posible progenitor de una planta domesticada, encontrar o verificar sus centros de origen, llenar el vacío de conocimiento que existe entre el uso de una planta silvestre y la aparición de la primera planta domesticada, distinguir procesos de domesticación incipiente que pueden ser estudiados en el presente, o ayudar a detectar los genes responsables de la adaptación a la selección artificial, dándonos mucha información sobre sus mecanismos.

El entendimiento de la agroecología, las formas de manejo y los usos locales de las plantas arvenses puede contribuir al fortalecimiento de la agricultura tropical en el futuro, con mucho mayor grado de capacidades de manejo integral, lo cual los agricultores tradicionales han desarrollado durante siglos. Al mismo tiempo, la identificación de los organismos nativos potencialmente útiles que han sido generalmente olvidados a través de los años y su posible proceso de domesticación, puede proporcionar beneficios económicos, sociales y ambientales (IPGRI, 2002). Más aún, dicho conocimiento puede también proporcionar herramientas a la agricultura de zonas templadas para un mejor manejo y aprovechamiento de sus malezas. Adicionalmente, el estudio detallado del impacto del hombre en la evolución y domesticación de plantas anuales pudiera clarificar algunos aspectos de la evolución vegetal y revelar información acerca de las estrategias locales de manejo ambiental que a su vez contribuyan a diseñar mejores estrategias de conservación.

Por todo lo anterior, el presente trabajo estudió la diversidad florística, la ecología, los usos y las formas de manejo incipiente de la flora arvense en diferentes sistemas agrícolas de Santa María Tecomavaca, Oaxaca, con el fin de seleccionar dos posibles plantas arvenses, adecuadas para el estudio posterior de la domesticación incipiente mediante evidencias etnobotánicas, morfológicas, fitoquímicas y genéticas.

A continuación, se formulan algunas preguntas que se pretenden resolver en este trabajo:

I. Preguntas relacionadas con la etnobotánica y ecología de plantas arvenses:

p_1 ¿Qué utilidad tienen las plantas arvenses?

p_2 ¿Qué formas de manejo incipiente ejercen los campesinos sobre las plantas arvenses que crecen en sus sistemas de cultivo?

p_3 ¿Son las diferencias de distribución de las plantas arvenses atribuibles a su utilidad?

p_4 ¿Existen diferencias en la utilidad de las plantas arvenses nativas e introducidas?

p_5 ¿Existe una influencia del uso de productos químicos en la proporción de plantas arvenses nativas e introducidas en los diferentes campos de cultivo?

II. Preguntas relacionadas con la domesticación incipiente de plantas arvenses:

p_6 ¿Existen diferencias morfológicas y/o fitoquímicas entre plantas arvenses de poblaciones bajo distintas intensidades de manejo incipiente?

p_7 ¿El grado de manejo incipiente influye en la morfología y/o fitoquímica de las partes útiles de las plantas arvenses?

p_8 ¿Existen diferencias genéticas entre las plantas manejadas y sus contrapartes no-manejadas de la misma especie?

Objetivos

Los OBJETIVOS GENERALES de este trabajo son:

O_1 Investigar el uso, el manejo y la ecología de las plantas arvenses que crecen dentro de diferentes sistemas de cultivo.

O_2 Investigar los indicios de una posible domesticación incipiente en dos especies de arvenses elegidas.

Los OBJETIVOS ESPECÍFICOS son:

O_1

- o_{1a} Construir una base de datos de las plantas arvenses presentes en los diferentes sistemas de cultivo del área de estudio.
- o_{1b} Describir el uso y las prácticas de manejo de que son objeto las arvenses.
- o_{1c} Investigar la utilidad y distribución de las arvenses nativas e introducidas en diferentes sistemas de cultivo.

O_2

- o_{2a} Analizar las diferencias morfológicas y fitoquímicas entre poblaciones manejadas y silvestres de dos arvenses.
- o_{2b} Analizar las diferencias a nivel genético entre poblaciones manejadas y silvestres de dos arvenses.

Hipótesis

De acuerdo a los objetivos de este proyecto, se postulan las HIPÓTESIS GENERALES de la siguiente manera:

H_1 La utilidad y las formas de manejo de las plantas arvenses determinan su distribución en los sistemas agrícolas, resultando en una mayor distribución de plantas arvenses útiles y nativas en los sistemas agrícolas con menor uso de productos químicos.

H_2 Las diferencias morfológicas, fitoquímicas y/o genéticas entre las plantas manejadas y silvestres indican que las poblaciones manejadas han sido sujetas a y/o están bajo un proceso de domesticación incipiente.

Para poder rechazar o aceptar las hipótesis generales, se formularon las HIPÓTESIS ESPECÍFICAS:

H_1

h_{1a} Las plantas arvenses tienen utilidad y están sujetas a diferentes formas de manejo incipiente en los diferentes sistemas de cultivo.

h_{1b} Las diferencias en la distribución de las plantas arvenses dentro de diferentes sistemas de cultivo son atribuibles a su utilidad.

h_{1c} Las plantas arvenses nativas tienen más utilidad que las arvenses introducidas y los sistemas agrícolas con mayor uso de productos químicos tienen una mayor abundancia y cobertura de plantas arvenses introducidas que nativas.

H_1

h_{2a} El grado de manejo influye gradualmente en las características morfológicas y/o fitoquímicas de las plantas arvenses.

h_{2b} Las poblaciones de una especie arvense sujetas a distintas formas de manejo son genéticamente diferentes entre sí.

A continuación, se presenta el desarrollo de la tesis y sus capítulos, indicando las hipótesis específicas que se investigan en cada parte para poder rechazar o confirmar las hipótesis generales (Tabla 1).

La tesis esta organizada en seis partes. Primero, la INTRODUCCIÓN GENERAL presenta los antecedentes, las preguntas, los objetivos, las hipótesis y el área de estudio de la investigación. Después siguen cuatro capítulos temáticos. El CAPÍTULO I discute la diversidad, etnobotánica y distribución de las plantas arvenses en los diferentes sistemas agrícolas en la zona de estudio (Blanckaert et al.: Agriculture, Ecosystems & Environment (2007) 119: 39-48). El CAPÍTULO II investiga la importancia de la utilidad de las plantas arvenses en su distribución (Blanckaert & Lira-Saade: Boletín de la Sociedad Botánica de México (en revisión)). El CAPÍTULO III estudia la problemática de las plantas arvenses nativas e introducidas (Blanckaert et al.: Biological Conservation (en revisión) y el CAPÍTULO IV se enfoca en los indicios de la domesticación incipiente de dos arvenses útiles (Blanckaert et al.: Economic Botany (en revisión). Finalmente, el trabajo termina con una DISCUSIÓN GENERAL de los resultados encontrados, seguidos por los apéndices y las láminas fotográficas.

Tabla 1. Estructura de la tesis e interrelaciones entre preguntas e hipótesis.

<table>
<tr><td colspan="5">Introducción General</td></tr>
<tr><td rowspan="7">Manejo Humano y Distribución de la Flora Arvense General</td><td colspan="4">H_1 La utilidad y las formas de manejo de las plantas arvenses determinan su distribución en los sistemas agrícolas, resultando en una mayor distribución de arvenses útiles y nativas en los sistemas agrícolas con menor uso de productos químicos.</td></tr>
<tr><td>Capítulo I.</td><td colspan="3">Recursos No Cultivados y el Conocimiento Indígena en la Producción Semiárida en México.</td></tr>
<tr><td></td><td>p_1
p_2</td><td>⇨</td><td>h_{1a} Las plantas arvenses tienen utilidad y están sujetas a diferentes formas de manejo incipiente en los diferentes sistemas de cultivo.</td></tr>
<tr><td>Capítulo II.</td><td colspan="3">¿Influye el Manejo Incipiente en la Distribución de Arvenses Útiles? Observaciones de Santa María Tecomavaca.</td></tr>
<tr><td></td><td>p_3</td><td>⇨</td><td>h_{1b} Las diferencias en la distribución de las plantas arvenses dentro de diferentes sistemas de cultivo son atribuibles a su utilidad.</td></tr>
<tr><td>Capítulo III.</td><td colspan="3">Herbicidas Facilitan la Invasión de Arvenses Exóticas en la Reserva de Biosfera Tehuacán-Cuicatlán, México.</td></tr>
<tr><td></td><td>p_4
p_5</td><td>⇨</td><td>h_{1c} Las plantas arvenses nativas tienen más utilidad que las arvenses introducidas y los sistemas agrícolas con mayor uso de productos químicos tienen una mayor abundancia y cobertura de arvenses introducidas que nativas.</td></tr>
<tr><td rowspan="4">Evolución en Dos Arvenses Elegidas</td><td colspan="4">H_2 Las diferencias morfológicas, fitoquímicas y/o genéticas entre las plantas manejadas y silvestres indican que las poblaciones manejadas han sido sujetas a y/o están bajo un proceso de domesticación incipiente.</td></tr>
<tr><td>Capítulo IV.</td><td colspan="3">Indicios de Domesticación Incipiente de Dos Arvenses Comestibles en México Semiárido: Evidencias Etnobotánicas, Morfológicas, Fitoquímicas y Genéticas.</td></tr>
<tr><td></td><td>p_6
p_7</td><td>⇨</td><td>h_{2a} El grado de manejo influye gradualmente en las características morfológicas y/o fitoquímicas de las plantas arvenses.</td></tr>
<tr><td></td><td>p_8</td><td>⇨</td><td>h_{2b} Las poblaciones de una especie arvense sujetas a distintas formas de manejo son genéticamente diferentes entre sí.</td></tr>
<tr><td colspan="5">Discusión General y Conclusiones</td></tr>
</table>

Área de Estudio

México es un país muy adecuado para realizar estudios sobre plantas arvenses, ya que posee aproximadamente 3,000 especies de plantas arvenses (Villaseñor & Espinosa-García, 2004) y se encuentra dentro de uno de los centros de domesticación más importantes en el mundo (Bye, 1998; Hernández-Xolocotzi, 1993). A lo largo de una historia cultural de probablemente más de 14,000 años, los grupos humanos que han habitado el territorio de este país han desarrollado un extraordinario complejo de formas de interacción con las plantas. Para ello, han contado con una amplia gama de posibilidades representada por su flora vascular conformada por más de 25,000 especies.

Una de las zonas de México que llaman más la atención en este contexto es el Valle de Tehuacán-Cuicatlán. Este valle constituye una zona árida localizada en el sureste del estado de Puebla y el noreste de

Oaxaca, entre los 17°39´ y los 18°53´ de latitud norte y los 96°55´ y 97°44´ de longitud oeste. Tiene un promedio anual de precipitación de 300 mm y una vegetación principalmente representado por el matorral xerófilo (Valiente-Banuet et al., 2000). El Valle de Tehuacán, además, es considerado como una de las zonas de mayor diversidad vegetal y cultural de México, tomando en cuenta que en su área relativamente pequeña (10,000 km^2) confluyen cerca de 2,800 especies de plantas (casi 13% de ellas endémicas) y siete de los 52 grupos étnicos que aún existen en el país (Nahuas, Popolocas, Mazatecos, Chinantecos, Ixcatecos, Cuicatecos y Mixtecos) (Dávila et al., 2002). Por lo anterior, entre otras cosas, este valle es considerado como un centro de megadiversidad y endemismo a nivel mundial por la Unión Internacional para la Conservación de la Naturaleza y ha sido decretado como una Reserva de la Biosfera (IUCN, 1998).

La Reserva de la Biosfera Tehuacán-Cuicatlán ha tenido gran importancia para la reconstrucción de la prehistoria de la región cultural conocida como Mesoamérica, ya que en algunas de sus cuevas se ha encontrado una de las evidencias más antiguas de domesticación de plantas y origen de agricultura en el Nuevo Mundo (MacNeish, 1967, 1992). Asimismo, estudios recientes han revelado que más de 800 especies son utilizadas por la gente en todo el Valle de Tehuacán-Cuicatlán y que aproximadamente 120 de ellas son plantas que pudieran considerarse como ruderales (Casas et al., 2001; Paredes-Flores, 2001). Ningún esfuerzo, sin embargo, ha sido hecho hasta ahora para determinar en detalle el verdadero papel de estas plantas en la subsistencia de las comunidades humanas de la zona y mucho menos el posible papel del manejo humano en su evolución.

Para la realización de este proyecto, se ha elegido el municipio de Santa María Tecomavaca, una comunidad rural de aproximadamente 1,837 habitantes (INEGI, 2000), ubicada en la parte sureste de la Reserva de la Biosfera Tehuacán-Cuicatlán (17°57’48”N y 97°00’26”O; elevación 612 msnm), en la región de la Cañada, en el Distrito de Teotitlán de Flores Magón, Oaxaca (Figura 1). El clima local es semiárido con una temperatura anual promedia entre 18°C y 22°C. Las lluvias llegan en verano (Julio-Septiembre), durante una época de aproximadamente tres semanas. La precipitación anual promedio es entre 600-800 mm (INEGI, 2005).

Territorialmente, el municipio está conformado por tres localidades: Santa María Tecomavaca, que es la cabecera municipal, Buena Vista con categoría de núcleo rural y la localidad de Santiago el Viejo, catalogada como ranchería. Los habitantes son mestizos con descendencia Mazateca. De las 539 personas reportadas como población ocupada (año 2000), 323 se dedican a labores agropecuarias, 60 trabajan en el sector secundario y 153 en el terciario. Según el censo del 2000, en ese año, 307 o 310 personas mayores de 5 años hablaban lengua indígena, cifra que representa 19.26% de la población mayor de esa edad. De ellas, 8 personas fueron registradas como monolingües. En la cabecera predominan los hablantes de español, mientras que en términos relativos en los dos poblados la lengua indígena sigue siendo un medio vigente de comunicación (Grupo Mesófilo, 2001).

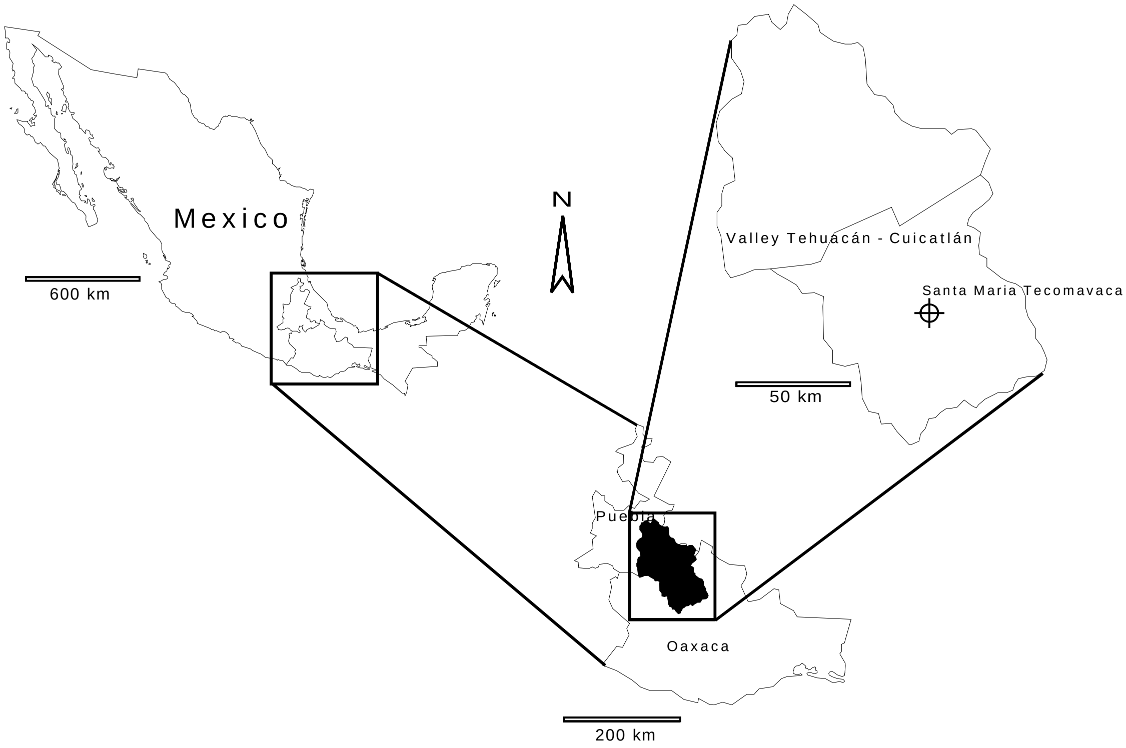

Figura 1 Ubicación del municipio de Santa María Tecomavaca dentro de la Reserva de la Biosfera Tehuacán-Cuicatlán.

La vegetación predominante es la Selva Baja Caducifolia, la cual incluye las siguientes especies: *Pachycereus marginatus* (DC.) Britton & Rose, *Cephalocereus columna-trajani* (Karw. ex Pfeiff.) K. Schum., *Mitrocereus fulviceps* (F.A.C. Weber ex K. Schum.) Backeb. ex Bravo, *Plumeria rubra* L., *Bursera morelensis* Ramirez, *B. schlechtendalii* Engl., *B. submoniliformis* Engl., *B. aptera* Ramirez, *Acacia angustissima* (Mill.) Kuntze, *Amphipterygium adstringens* (Schltdl.) Standl., *Actinocheita filicosa* (DC.) F.A. Barkley, *Stenocereus stellatus* (Pfeiff.) Riccob., *Mammillaria sphacelata* Mart., *M. supertexta* Mart. ex Pfeiff., *M. haageana* Pfeiff., *Ferocactus flavovirens* (Scheidw.) Britton & Rose, *F. recurvus* (Mill.) Borg, entre otras. También se encuentra el Cardonal de *Pachycereus weberi* (J.M. Coult.) Backeb., el Cardonal de *Cephalocereus columna-trajani,* el Bosque de Encinos con vegetación secundaria, el Bosque de Galería y la Vegetación riparia (Grupo Mesófilo, 2001).

Lo que hace particularmente interesante a Santa María Tecomavaca en el contexto de éste proyecto, es la coexistencia de varios sistemas agrícolas de los cuales se obtienen numerosos productos agrícolas. Se encuentra la agricultura tradicional de milpa con combinaciones de maíz (*Zea mays* L.) y calabaza (*Cucurbita* spp.), el cultivo extensivo de limón (*Citrus aurantifolia* (Christm.) Swingle), papaya (*Carica papaya* L.) o mango

(*Mangifera indica* L.), así como también monocultivos intensivos de melón (*Cucumis melo* L.). Otros productos que se cultivan son: caña de azucar (*Saccharum officinarum* L.), frijol (*Phaseolus vulgaris* L.), chile (*Capsicum* spp.), tomate (*Physalis philadelphica* Lam.), jitomate (*Lycopersicon esculentum* Mill.), chicozapote (*Manilkara zapota* (L.) P. Royen) y sandía (*Citrullus lanatus* (Thunb.) Matsum. & Nakai) (Grupo Mesófilo, 2001). Esta diversidad de sistemas agrícolas, seguramente también encierra numerosas estrategias de manejo de las plantas que crecen espontáneamente en ellos.

La superficie cultivada de Santa María Tecomavaca dispone de un sistema de irrigación proviniendo de dos fuentes de agua: (1) el Río Salado, que proporciona agua con altas niveles de sales y (2) los cerros cercanos, que proporcionan agua dulce de lluvia. Los canales que vienen del Río Salado contienen agua durante todo el año, mientras que los canales de agua dulce de los cerros solo transportan agua durante la época de lluvias. Los animales como ganado vacuno, caprino, caballar y de burros forman parte integral de los sistemas agrícolas, ya que son ocasionalmente dejados para pastar en los campos después de la cosecha o antes de la preparación del suelo.

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Capítulo I

Recursos No Cultivados y el Conocimiento Indígena en la Producción Semiárida de México

Blanckaert, I., Vancraeynest K., Swennen R.L., Espinosa-García F.J., Piñero D. & Lira-Saade R.
Non-crop resources and the role of indigenous knowledge in semi-arid production of Mexico.

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RESUMEN

En este trabajo, se investigó la flora arvense asociada con la agricultura de subsistencia en la Reserva de la Biosfera Tehuacán-Cuicatlán, una región semiárida de México. Los objetivos fueron describir la diversidad de plantas arvenses, sus usos locales, el conocimiento indígena y las formas de manejo que ejercen los campesinos sobre dichas plantas, así como también investigar la distribución de plantas arvenses dentro de cuatro diferentes sistemas agrícolas a lo largo de un gradiente de intensidades de manejo agrícola. En total, 161 especies arvenses pertenecientes a 40 familias y 103 géneros fueron encontrados, incluyendo tres especies endémicas de la región. Aproximadament, el 92% de todas las especies arvenses presentaron uno o más usos, siendo el forraje el uso más importante, seguido por aplicaciones para medicina, alimento y ornamento. La experiencia y el conocimiento de los campesinos locales y la diversidad de arvenses útiles asociadas con una gran variedad de sistemas agrícolas locales, indican que la agricultura tropical de pequeña escala dentro de un país en desarrollo puede ser combinada con la conservación in situ de recursos no-cultivados útiles.

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Non-crop resources and the role of indigenous knowledge in semi-arid production of Mexico

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Abstract

In this paper, weed flora associated with small-scale farming in the semi-arid Tehuacán-Cuicatlán Biosphere Reserve (Mexico) was investigated. The objectives were to describe weed floristic diversity, local uses, indigenous knowledge and farmers' management as well as weed distribution in four different crop production systems along a gradient of agricultural management intensity. In total, 161 weed species belonging to 40 families and 103 genera were found, including three endemic species of the region. Approximately, 91.9% of all weed species had one or more uses, fodder being the most important one, followed by medicinal, edible and ornamental uses. The experience and knowledge of local farmers and the biodiversity of useful weed resources associated with a large variety of local crop production systems, indicated how small-scale tropical agriculture in a developing country may be compatible with in situ conservation of useful non-crop resources.

Keywords: Tehuacán-Cuicatlán Biosphere Reserve; Ethnobotany; Farmers' decisions; In situ conservation; On-farm research; Weed management; Weed diversity

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1. Introduction

In contrast with modern western agriculture, traditional tropical farmers recognize the additional value of non-cultivated plants (weeds) growing between their crops (Chacón and Gliessman, 1981; Bye, 1981). Recently, ethnobotanical investigations in the Tehuacán-Cuicatlán Biosphere Reserve have registered various forms of management and several uses of spontaneously growing species in different agro-ecosystems (Blanckaert et al.,

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2004; Casas et al., 2001; Paredes-Flores, 2001). At a given moment during crop cultivation, a farmer's weeding intensity decreases, thereby tolerating or even protecting certain useful weed species (Bye, 1979; Casas et al., 1996).

Recent works about biodiversity in the agricultural landscape have expressed the need for more basic research to understand the links between biodiversity, ecosystem function and sustainability (Gerowitt et al., 2003; Marshall et al., 2003; Toledo, 1995). Selection pressures applied by farmers' management, including the use of herbicides and their effect on diversity must be understood. Also, the identification of the most important weed species for biodiversity (for example, endangered or endemic species) together with the most threatening species for agricultural yield, may form an important step in combining effective weed control with more sustainable production methods (Marshall et al., 2003). For this, it is necessary to understand weed biology and diversity as well as the importance of indigenous knowledge and the impact of both traditional and modern agricultural management on the presence, abundance and distribution of useful/noxious weeds (Alcorn, 1984b; Altieri and Trujillo, 1987; Dekker, 1997).

This work presents information of weed flora associated with agricultural activities in a semi-arid region in Mexico. The objectives were: (1) to describe the floristic diversity, local uses, farmer's knowledge and management of the weedy flora and (2) to investigate the diversity and distribution of useful weeds in four different crop production systems along a gradient of management intensity in the rural community of Santa María Tecomavaca in the Tehuacán-Cuicatlán Biosphere Reserve, Mexico.

2. Materials and methods

Mexico is an appropriate country for weed investigation as it has ca. 3000 weed species (Villaseñor and Espinosa-García, 2004) and lies within one of the world's most important centres of plant domestication (Bye, 1993; Hernández-Xolocotzi, 1993). Especially of interest is the Tehuacán-Cuicatlán Biosphere Reserve, a semi-arid region located in the states of Puebla and Oaxaca. It is considered one of the most diverse and culturally important regions in Mexico and one of the world's most important centres of mega-diversity and endemism by the International Union for Conservation of Nature (IUCN, 1998). The coexistence of human settlements within a protected area makes this region interesting to explore possibilities for agriculture management in combination with in situ conservation of natural resources.

Santa María Tecomavaca is a rural community of approximately 1813 inhabitants (INEGI, 2000) situated in the southeast part of the Tehuacán-Cuicatlán Biosphere Reserve (17°57′48″N and 97°00′26″W; elevation 612 m above sea level), district of Teotitlán de Flores Magón, Oaxaca State, Mexico (Fig. 1). Inhabitants are mestizos with Mazatec backgrounds.

The local climate is semi-arid with a mean annual temperature between 18 and 22 °C. Rain falls in summer from July till September with mean annual precipitation between 600 and 800 mm (INEGI, 2005).

The dominant vegetation in the region is thorn scrub forest, with species like *Pachycereus marginatus* (DC.) Britton and Rose, *Cephalocereus columna-trajani* (Karw. ex Pfeiff.) K. Schum., *Mitrocereus fulviceps* (F.A.C. Weber ex K. Schum.) Backeb. ex Bravo, *Plumeria rubra* L., *Bursera morelensis* Ramirez, *B. schlechtendalii* Engl., *B. aptera* Ramirez and *Acacia angustissima* (Mill.) Kuntze, among others.

Farms in Santa María Tecomavaca are small-scale and highly diverse. There is multi-species agriculture like milpa (combining maize with squash), extensive fruit orchards of lime or papaya trees, as well as intensive short-cycle monoculture melon fields. The cultivated area of Santa María Tecomavaca has an irrigation infrastructure bringing water from two different sources: river-fed irrigation (with water coming from the "Rio Salado" river, which contains high salt levels) and rain-fed irrigation (with fresh water coming from the adjacent mountain range). The rain- and river-fed crop production systems result in a large variety of agricultural products like maize (*Zea mays* L.), sugarcane (*Saccharum officinarum* L.), Mexican lime (*Citrus aurantifolia* (Christm.) Swingle), beans (*Phaseolus vulgaris* L.), squash (*Cucurbita* sp.), melon (*Cucumis melo* L.), hot chilli peppers (*Capsicum* sp.), tomato (*Lycopersicon esculentum* Mill.), mango (*Mangifera indica* L.), papaya (*Carica papaya* L.), "chicozapote" or sapodilla (*Manilkara zapota* (L.) P. Royen) and watermelon (*Citrullus lanatus* (Thunb.) Matsum. and Nakai) (Grupo Mesófilo, 2001). Animals like cows, donkeys, horses and goats, also form an integral part of these crop production systems, as these animals are occasionally left to graze freely in the fields after harvest or before land preparation.

Field work in Santa María Tecomavaca was carried out in ca. 20 visits from September 2003 until December 2004. In order to establish a constructive relationship with the inhabitants of Santa María Tecomavaca, a formal presentation of the project was held in the community and the necessary permits were obtained from the corresponding authorities. Access to agricultural fields and households depended entirely on goodwill and available time of the local people.

2.1. *Weed flora of Santa María Tecomavaca*

A floristic inventory of all weed species from the study area was made. Permission was obtained to enter 10 randomly chosen agricultural fields to collect weed species along a random distance of minimum 500 m in each field. Collection continued until no new species were found. Fields were visited various times during the year. Up to five samples of each weed species, preferably with flower or fruit, were collected. Part of the collected plant samples was prepared according to conventional techniques (Alexiades, 1996) and one sample of each species was deposited in the

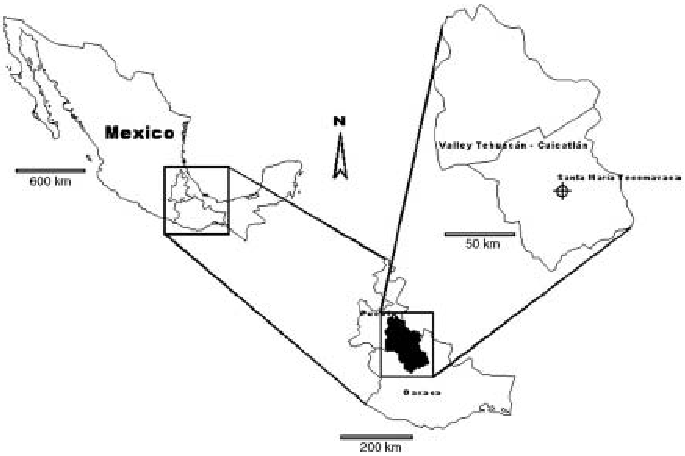

Fig. 1. Location of Santa María Tecomavaca in Oaxaca State, Mexico.

Iztacala Herbarium (IZTA) of the Universidad Nacional Autónoma de México (UNAM), Mexico. The other part of the sample was mounted in a portable field herbarium, for use during the subsequent ethnobotanical investigation.

The ethnobotanical investigation was conducted following the guidelines of participative observation (Martin, 1995). Free and structured interviews were held (Alexiades, 1996; Hernández-Xolocotzi, 1970; Martin, 1995); their format was elaborated based on the experience from previous studies in the region (Blanckaert et al., 2004; Clarysse, 2003; Paredes-Flores, 2001; Rosas-López, 2003; Van Diest, 2002). Free interviews included general information of the informant (personal dates, socio-economic situation) as well as data of weed species in the field herbarium: local names (Spanish, Náhuatl, Mazatec), uses (edible, medicinal, etc.), plant parts used, manner of plant preparation and management forms. In this work, weed management was not just related with control or eradication of weeds, but also included all activities associated with usefulness of weeds. In this context, weed management forms were categorized in five main groups (Alcorn, 1981; Casas et al., 1997): (1) not managed (i.e., not receiving any special attention from the farmer and eradicated when needed), (2) tolerated/spared (i.e., not removed by the farmer), (3) protected (i.e., receiving special care from the farmer, for example, a fence against free roaming animals or clearing space around the plant(s) of interest), (4) promoted (i.e., (un)consciously propagated by the farmer) and (5) cultivated (deliberately sown or planted by the farmer). Also questions concerning the noxiousness of weeds were asked, inviting informants to list weeds they consider noxious and the reasons why. On the other hand, structured interviews were held with the 27 farmers who collaborated with the in situ weed diversity and distribution assessment (see next section). Questions were asked concerning the farmer's crop production system (main crop, herbicide use, fertilizer use, mechanization, irrigation and labour). Additionally, each farmer named a list of local plant names and plant uses, based on the weed species present in situ (i.e., on his own field). To quantify the monetary input value of chemicals and herbicides, investments per month and per ha were calculated. All informants were selected as objectively as possible, albeit strict random sampling or stratified random sampling is rather difficult in a real situation (Alexiades, 1996). In total, 19 open interviews and 90 structured interviews were held in the community.

To study weed diversity and distribution in crop production systems with different management intensities, four specific crop production systems were chosen along a gradient of increasing input requirements of herbicides, fertilizers, labour and irrigation intensity, i.e., lime, milpa, papaya and melon, respectively. In total, 28 agricultural fields (owned by 27 farmers) were chosen in collaboration with the Committee of Communal Goods ("Bienes Comunales") and the Irrigation Committee ("Comité de Riego") of the village. Eight lime, seven milpa, six papaya and seven melon fields were selected at random, with an almost equal amount of fields per crop production type.

Fields were studied during the rainy season (July–October 2004), when herbaceous vegetation grew abundantly and almost everywhere across the whole area. Moreover, at that time farmers were more involved in weeding. Each field was surveyed only once, and had at the moment of assessment, a crop in a development stage similar to other fields with the same crop. Also, weed density was at or near its maximum at the assessment time.

Weed vegetation was assessed through the line-intercept method, a relatively fast method providing frequency, abundance and cover data for each weed species found (Canfield, 1941; Kent and Coker, 1992). Before sampling,

Table 1
Assigned value used in the calculation of farmer's indigenous knowledge (subjective allocation method)

Frequency of mentioning	Assigned value
>20	1
10–19	2
5–9	3
2–4	4
1	5

the optimal transect length for each crop production system was established (Kent and Coker, 1992). Species were identified with the established field herbarium. Newly registered species were labelled, dried, identified and included in the field herbarium for future reference.

2.2. *Data analysis*

To investigate the diversity and distribution of weeds in the four studied crop production systems, all floristic data matrices (containing presence/absence, abundance and cover data) were analysed using correspondence analysis (CA). This method is found most suitable to search for ecological and floristic variations between different sampling sites (Kent and Coker, 1992). Analyses were executed with the statistical program NTSYSpc Version 2.0 (Rohlf, 1997). Each data matrix contained 28 columns (representing fields) and 89 rows (representing weed species). The relationship between CA ordination patterns and external information was established through Spearman's non-parametric correlation coefficient and Mann–Whitney *U* non-parametric test (STATISTICA Version 6.0) (StatSoft Inc., 1998).

Indigenous knowledge was assessed as the farmer's capacity to mention local plant names and uses. Two methods were used to quantify farmer's plant knowledge: totalled method and subjective allocation method (Phillips, 1996). The first method supposes that the knowledge about each species is of equal importance, while the second method postulates that the knowledge of a species not known by the majority of farmers is more significant than the mentioning of a generally known species. Table 1 illustrates the values that were assigned for the frequency of mentioning.

3. Results

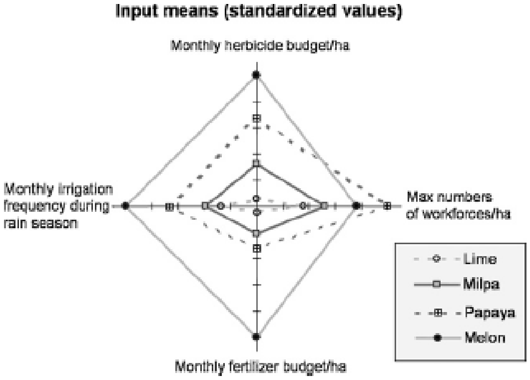

Fig. 2. Mean input factors for four crop production systems of Santa María Tecomavaca.

The intensity of agricultural management in the four studied crop production systems was estimated considering the following factors: (1) money invested in the application of agrochemicals (herbicide and fertilizer), (2) the amount and frequency of irrigation on the field and (3) the maximum number of contracted workers during land preparation, sowing or planting, application of agrochemicals, weeding and/or harvesting. The sequence "lime–milpa–papaya–melon" was found to represent a gradient of increasing management intensity (Fig. 2). Papaya and melon were intensive cash crop production systems, while milpa and lime were less intensively managed crop production systems, mainly aimed at on-farm auto-consumption with occasional selling.

3.1. *Weed diversity, uses, noxiousness and farmers' management*

In the agricultural fields of Santa María Tecomavaca, a total of 161 different weed species belonging to 40 plant families and 103 genera of Angiosperms were found. A complete list of weed species is available with the first author. The most representative plant families were Poaceae (25 species; 15.5%), Asteraceae (17 species; 10.6%), Malvaceae (16 species; 9.9%), Euphorbiaceae (14 species; 8.7%), Fabaceae (13 species; 8.1%) and Solanaceae (12 species; 7.5%).

Of all 161 weed species found, 148 species (91.9%) presented one or more uses. Moreover, 34 species (21.1%) were multi-purpose plants, meaning they presented several

Table 2
Weed uses in Santa María Tecomavaca

Use	No. of species	%
Fodder	113	76.4
Medicinal	30	20.3
Edible	17	11.5
Ornamental	9	6.1
Domestic	6	4.1
Toy	3	2.0
Spice	3	2.0
Soil ameliorant	2	1.4
Beneficial crop interaction	2	1.4
Construction material	1	0.7
Living fence	1	0.7

Note: total percentage of uses is >100% as several species are multi-purpose plants.

uses at the same time. Without doubt, the most important use was fodder (113 spp.; 76.4%), as most weeds were herbaceous annuals. The second most important use was medicinal (30 spp.; 20.3%), followed by edible (17 spp.; 11.5%) and ornamental (9 spp.; 6.1%) (Table 2). Several farmers also mentioned agro-ecological advantages of certain weeds. The dry material of *Viguiera dentata* (Cav.) Spreng (Asteraceae), for example, was often mixed with the soil during field preparation for soil enrichment and soil structure improvement.

Informants indicated two main reasons for weed noxiousness: (1) competition with the crop and (2) hindrance to the farmer and his activities on the field. Of the 24 species identified as most noxious in the interviews (Table 3), most species (17 spp., 70.8%) were considered competitive, while three species (12.5%) represented hindrance to the farmer. Four weed species (16.7%) were both competitive and hindering. In general, informants mentioned mostly members of the Poaceae family as noxious weeds. The two most mentioned noxious weed species were *Cyperus flavescens* L. (Cyperaceae) and *Chloris gayana* Kunth (Poaceae), both known as fast reproducers that are difficult to eradicate. Moreover, *C. flavescens* was particularly known to survive herbicide treatment and damage to aboveground plant parts. Species like *Viguiera dentata* (Cav.) Spreng (Asteraceae), *Abutilon mucronatum* J.E. Fryxell (Malvaceae), *Ricinus communis* L. (Euphorbiaceae), *Malvastrum americanum* (L.) Torr. (Malvaceae) and *Amaranthus hybridus* L. (Amaranthaceae) presented the ability to grow very tall, thereby disturbing the crop's development and in some cases even rendering field access difficult. The herbaceous vines, *Ipomoea purpurea* (L.) Roth., *Merremia dissecta* (Jacq.) Hallier f., *Merremia quinquefolia* (L.) Hallier f. (Convolvulaceae) and *Passiflora foetida* L. (Passifloraceae) were found to climb on the standing crop and cause direct damage. They were difficult to eradicate, especially in maize and lime fields. Species like *Solanum rostratum* and *Panicum* sp. spread over large areas in the field and complicated field preparation. Farmers were annoyed by species with thorns (*Cenchrus longispinus* (Hack.) Fernald, *Xanthium strumarium* L.) or sticky plant parts (*Mentzelia aspera* L.). Moreover, local beliefs affected farming practice. For example, some farmers were afraid to come near or pull out certain toxic weeds like *Datura stramonium* L., *D. inoxia* Mill. or *D. discolor* Greenm., as they believed that these species can provoke the loss of mind.

All noxious weeds had uses. Eight of them (33.3%) were even multi-purpose plants. The most important use of these weeds was fodder (75.0%), followed by medicinal (33.3%),

Table 3
Noxious weed species as mentioned by informants

Family	Species	Detailed noxiousness
Competition with crop		
Cyperaceae	*Cyperus flavescens*$^{\mathrm{F-M}}$	Fast growing, very difficult to eradicate
Poaceae	*Chloris gayana*$^{\mathrm{F}}$	Very fast reproduction, difficult to eradicate
Asteraceae	*Viguiera dentata*$^{\mathrm{F-M-A}}$	Fast reproduction, difficult to eradicate
Malvaceae	*Abutilon mucronatum*$^{\mathrm{T}}$	Fast growing, difficult to eradicate
Convolvulaceae	*Ipomoea purpurea*$^{\mathrm{F-O}}$	Twining vines covering entire crop (lime, maize)
Convolvulaceae	*Merremia quinquefolia*$^{\mathrm{F}}$	Twining vines covering entire crop (lime, maize)
Convolvulaceae	*Merremia dissecta*$^{\mathrm{M}}$	Twining vines covering entire crop (lime, maize)
Solanaceae	*Solanum rostratum*$^{\mathrm{F}}$	Fast growing, difficult to eradicate, with thorns
Poaceae	*Cenchrus incertus*$^{\mathrm{F}}$	Difficult to eradicate, noxious for crop (maize)
Poaceae	*Rynchelytrum repens*$^{\mathrm{F}}$	Fast reproduction and difficult to eradicate
Poaceae	*Panicum* sp.$^{\mathrm{F}}$	Fast growing, difficult to eradicate
Poaceae	*Panicum hirsutum*$^{\mathrm{F}}$	Noxious for crop (beans)
Malvaceae	**Sida puebliensis*$^{\mathrm{F}}$	Fast growing, difficult to eradicate
Solanaceae	*Datura* sp.$^{\mathrm{M}}$	Difficult to eradicate, toxic, noxious for crop
Euphorbiaceae	*Ricinus communis*$^{\mathrm{M-D}}$	Noxious for crop (maize)
Passifloraceae	*Passiflora foetida*$^{\mathrm{E-M-O}}$	Twining vines covering entire crop (lime)
Zygophyllaceae	*Kallstroemia hirsutissima*$^{\mathrm{F-M}}$	Difficult to eradicate, noxious for crop
Hindrance to farmers' activities		
Poaceae	*Cenchrus longispinus*$^{\mathrm{F}}$	Complicates field work, very thorny
Asteraceae	*Xanthium strumarium*$^{\mathrm{F}}$	Complicates field work, thorny
Loasaceae	*Mentzelia aspera*$^{\mathrm{F-B}}$	Complicates field work, sticky
Both competition and hindrance		
Malvaceae	*Malvastrum americanum*$^{\mathrm{F}}$	Slows crop growth, complicates field work, sticky
Amaranthaceae	*Amaranthus hybridus*$^{\mathrm{F-E}}$	Slows crop growth, complicates field work, irritating
Malvaceae	*Abutilon mollicomum*$^{\mathrm{F}}$	Slows crop growth, complicates field work
Papaveraceae	*Argemone ochroleuca*$^{\mathrm{M}}$	Slows crop growth, complicates field work, thorns

Weed uses: $^{\mathrm{F}}$fodder, $^{\mathrm{E}}$edible, $^{\mathrm{M}}$medicinal, $^{\mathrm{O}}$ornamental, $^{\mathrm{D}}$domestic use, $^{\mathrm{T}}$toy, $^{\mathrm{A}}$soil ameliorant, $^{\mathrm{B}}$beneficial crop interaction.
* Endemic species.

Table 4
Weed management forms in Santa María Tecomavaca

Management	No. of species	%
Non-managed	140	94.6
Tolerated	21	14.2
Protected	7	4.7
Cultivated	5	3.4
Promoted	1	0.7

Note: total percentage is >100% as several species receive multiple management forms.

edible (8.3%) and ornamental (8.3%) use. Less represented uses were domestic (i.e., used as utensil in the house), toy, soil ameliorant and beneficial crop interaction (each with 4.2%) (Table 3).

Still, weeding was an important activity in all four crop production systems of Santa María Tecomavaca. Only a small number of farmers (23.4%) mentioned specific management practices for useful weeds, such as tolerance/sparing, protection, promotion or cultivation. Of all 148 useful weed species, only a small number received some management (21 spp., 14.2%) (Table 4). The most common form of management was tolerance (21 spp.), followed by protection (7 spp.), cultivation (5 spp.) and promotion (1 sp.). Eight of these 21 managed species (38.1%) received multiple management forms, meaning that they were managed in different ways. Five of them were multipurpose plants.

The most tolerated or protected weeds were *Amaranthus hybridus* L., *Solanum americanum* L., *Porophyllum ruderale* var. *macrocephalum* (DC.) Cronquist and *Chenopodium ambrosioides* L. All these species were edible, and two of them were medicinal. Hence they were important enough for the local people to be tolerated or protected in the field.

Weeds were rarely transplanted, but the seeds of certain weed species were sometimes taken to the family homegarden and sown near the dwelling. This was the case for *P. ruderale* var. *macrocephalum*) and *C. ambrosioides*, amongst others. Within the homegarden, such weed species may receive intensive management. As a result, spontaneously growing plants may be found alongside tolerated, protected, promoted and cultivated species.

The use(s) of a weed influenced the management decision of the farmer. Weed species for fodder received little attention. Only three of 86 specific fodder species (3.5%) received some management (mainly tolerance). However, when a weed presented one or more additional non-fodder uses, management intensity increased (8 managed species of 26; 30.8%). A similar result was found for exclusive non-fodder species, as 10 species of 36 (27.8%) were managed. Clearly, even though fodder weeds represented an important component of the crop production system, weeds management practices were more directed towards differently used weeds. Indeed, use and management of weeds were found to be statistically dependent ($\chi^2 = 0.38$; $\alpha = 0.001$). As such, excluding fodder species, we concluded that almost one third (18 spp. of 62; 29.0%) received a certain form of management.

The optimal transect length for each crop production system was established at 100 m. Of the 161 weed species found in the study area, 89 species (55%) were detected with the line intercept method. Weed floristic composition in the four crop production systems was highly variable. Evaluation of the three data sets (presence/absence, abundance and cover) indicated that only 13 species (14.6%) grew in more than 14 of the studied fields, with a maximum appearance of one species in 21 fields. The most widespread weed species were: *Chloris gayana* Kunth (Poaceae), *Chamaesyce hypericifolia* (L.) Millsp. (Euphorbiaceae), *Boerhavia erecta* L. (Nyctaginaceae), *Ipomoea purpurea* (L.) Roth. (Convolvulaceae), *Malvastrum americanum* (L.) Torr. (Malvaceae), *Amaranthus hybridus* L. (Amaranthaceae), *Panicum hirsutum* Sw. (Poaceae), *Waltheria americana* L. (Sterculiaceae), *Cyperus flavescens* L. (Cyperaceae), *Euphorbia heterophylla* L. (Euphorbiaceae), *Rhynchosia minima* (L.) DC. (Fabaceae), *Desmanthus virgatus* (L.) Willd. (Mimosaceae) and *Trianthema portulacastrum* L. (Aizoaceae). Not one single weed species grew in all fields

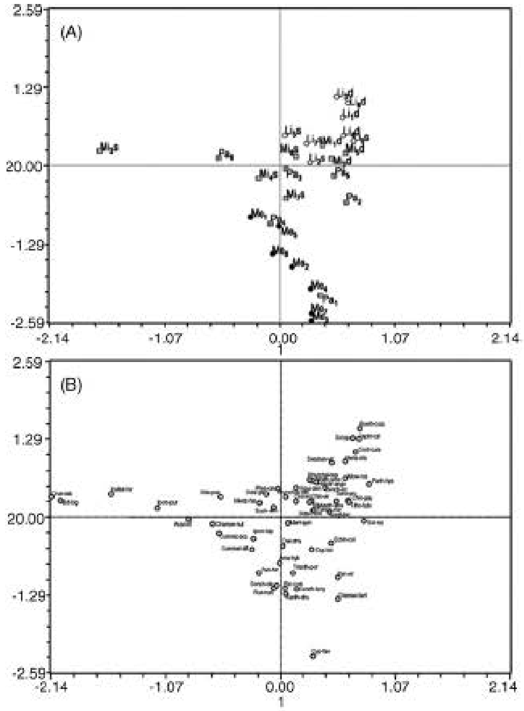

Fig. 3. Correspondence analysis using cover data excluding 36 species appearing in only one or two fields. (A) Ordination of the 28 studied agricultural fields (milpa [Mi ▨], lime [Li○], papaya [Pa ⊞] and melon [Me●]; fields were numbered according to moment of assessment), (B) ordination of the 89 weed species.

studied. More than half of all weed species (54 species; 60.7%) were found in only five fields of the 28 studied fields, whereas 23 species (25.8%) were found in one single field.

The following results were based entirely on the analysis of weed cover data because they incorporated presence/absence data and represented weed biomass information more accurately than abundance data. Also, cover data provided information on space occupied by weedy species, which was useful to interpret weed management and its effects. Moreover, abundance data were highly dependent on reproductive capacity and spatial dispersion, which are highly variable and not always correlated with biomass.

The CA analysis executed on the full data matrix (89 species and 28 fields) resulted in a very narrow group of fields, with four outliers, and was difficult to interpret (data not shown). The 36 weed species that appeared in only one or two fields did not represent information concerning general weed distribution patterns among fields and were therefore excluded from the analysis. A second CA analysis (53 species and 28 fields) resulted in the ordination graphs shown in Fig. 3.

In general, all crop production systems clustered together without clear separations, except for the milpa field Mi_2, where weed control was nearly absent as it had a different production goal (maize for animal fodder only). Two weed species covered a great part of this field: *Crusea calcicola* Greenm. (Rubiaceae) and *Bidens bigelovii* A. Gray (Asteraceae).

The first axis (Fig. 3A) explained 14% of the fields' variation, while the second axis explained 12%. These low values indicated large differences in weed cover between the different fields. On the other hand, weed cover in lime and melon fields was rather similar, while milpa and papaya fields tended to have a more variable weed cover. The second axis discriminated two main groups. First, a group containing all lime and all milpa fields (except Mi_2) plus four papaya fields, and a second group consisting of all melon fields with two papaya fields. In conclusion, weed cover of melon fields was distinct from the three other crop production systems, with papaya production the closest related crop production system, followed by milpa and then lime.

Close examination of the cover data matrix and the projection of the species into the space of the agricultural fields (Fig. 3B), showed that this tendency was caused by the uneven cover distribution of certain weed species. Table gives an overview of these species, which were dominant in one system, but (largely) dispersed or even non-existent in others. For example, 5 species were found with at least 80% of their total cover distributed in milpa fields only, while 10 species had at least 60% and 2 species at least 50% (Table 5). The cover of 17 weed species was significant for the

Table 5
Weed species and their uses as they appear in different crop production systems

Cover dominance	Crop production system			
	Milpa	Lime	Papaya	Melon
At least 80%	*Bidens bigelovii*^{F} *Crusea calcicola*^{F} *Ipomoea leptotoma*^{F} *Euphorbia heterophyla*$^{M–F}$ *Sanvitalia procumbens*^{F}	*Boerhavia coccinea*^{F} *Solanum erianthum*^{Ot} *Parthenium hysterophorus*^{M} *Tephrosia cinerea*^{F} *Abutilon mucronatum*$^{Ot/F}$ *Herissantia crispa*^{F}	*Sonchus oleraceus*$^{E–F}$ *Ruellia nudiflora*^{F} *Echinochloa colonum*^{F}	–
At least 60%	*Kallstroemia hirsutissima*$^{M–F}$ *Solanum rostratum*^{F} *Ipomoea purpurea*$^{O–F}$ *Merremia quinquefolia*^{F} *Mentzelia aspera*$^{Ot–F}$ *Physalis cinerascens*$^{M–Ot}$ *Boerhavia erecta*^{O} *Commelina diffusa*^{O} *Tithonia tubiformis*$^{O–F}$ *Acalypha arvensis*^{F}	*Viguiera dentata*$^{M–Ot–F}$ *Desmanthus virgatus*^{E} *Cenchrus incertus*^{F} *Cordia curassavica* *Crotalaria incana*^{F} *Heliotropium angiospermum*^{M} *Rhynchosia minima*^{F} *Chloris virgata*^{F} *Waltheria americana*$^{M–F}$	*Chamaesyce sp.*^{M} *Xanthium strumarium*^{F}	–
At least 50%	*Sida glabra*$^{Ot–F}$ *Amaranthus hybridus*$^{E–F}$	*Rhynchelytrum repens*^{F} *Sida rhombifolia*$^{Ot–F}$	*Sorghum bicolor*^{F} *Cenchrus longispinus*^{F} *Chamaesyce hypericifolia*^{F}	*Cyperus flavescens*$^{M–F}$
Total	17	17	8	1
Useful species for				
Fodder^{F}	14	12	7	1
Edible^{E}	1	1	1	0
Medicinal^{M}	4	4	1	1
Ornamental^{O}	4	0	0	0
Other^{Ot}	3	4	0	0

grouping of milpa and lime production systems while eight species for papaya fields and only one in melon fields. This clearly reflects management intensity in the different crop production systems. Also, dominant milpa weeds presented five uses, followed by four uses for lime weeds; papaya weeds had three uses and the single dominant melon weed had two uses. In conclusion, the availability of useful weed resources decreased from milpa and lime, over papaya to melon.

3.2. Farmers weed knowledge

Of all weed species, 103 species were known with a local Spanish name (64.0%), with only 2 species having Náhuatl names (*Tournefortia densiflora* M. Martens and Galeotti: ''hachinole'' and *Solanum lanceolatum* Cav.: "mocachane''). The latter species was the only one presenting also a Mazatec name (shuma'). Unfortunately, no informant was able to explain the significance of these indigenous names.

The relationship between farmer's indigenous knowledge (calculated with totalled and subjective allocation method) and age resulted in a positive correlation between farmers' age and plant knowledge. This indicated that plant knowledge tends to increase with increasing age, as has been reported previously (Boster, 1985).

The quantity of herbicide applied by farmers was not correlated with indigenous plant knowledge (data not shown). However, the decision whether a farmer used herbicides or not was linked with the farmer's plant name knowledge. The farmer that decided not to use herbicides had higher plant name knowledge, a difference that was significant using Mann–Whitney *U* non-parametric test ($P = 0.03$). There was a similar trend with plant use knowledge, but it was not significant (data not shown). No relation was found between farmer's age an herbicide use, which indicated that older farmers also used intensive production practices. No significant correlation was found between weed related factors (species number, Shannon's diversity index and Shannon's equitability index) and farmer's plant name and use knowledge.

4. Discussion

This work reports 161 different weed species belonging to 40 plant families and 103 genera for the municipality of Santa María Tecomavaca, a semi-arid region in Mexico. The most diverse plant families (Poaceae, Asteraceae, Fabaceae) were reported by Dávila et al. (2002) for the whole Tehuacán-Cuicatlán valley. The territory of Santa María Tecomavaca represented only 0.23% of the whole Oaxaca State, but harbours 14.5% of its total weed diversity (1113 spp.; Villaseñor and Espinosa-García, 1998). Three weed species were endemic to the States of Puebla and/or Oaxaca and distributed within the Tehuacán-Cuicatlán Biosphere Reserve (*Iresine discolor* Greenm., Amaranthaceae; *Florestina simplicifolia* B.L. Turner, Asteraceae and *Sida pueblensis* Fryxell, Malvaceae) (Méndez-Larios et al., 2004). Also, only a small proportion of the weeds (51 spp.; 31.7%) were found in the natural vegetation surrounding the village.

Approximately, 91.9% of all weed species found in Tecomavaca presented one or more uses. Specifically, their importance as fodder plants confirmed their role as an inherent part of the farming system. Farm animals were allowed to graze freely in the fields after harvest or before land preparation. Other farmers often cut weedy fodder plants to feed animals that were sheltered in the home-garden. Fodder weeds cut the costs for industrial animal feed purchases and increase the possibilities of survival of farm animals in times of drought, thus increasing financial security for rural families (Espinosa-García and Díaz-Pérez, 1996; Vieyra-Odilón and Vibrans, 2001). Other weed uses were medicinal, edible and ornamental as reported in other ethnobotanical investigations in the same region (Blanckaert et al., 2004; Casas et al., 2001; Paredes-Flores, 2001; Rosas-López, 2003; Van Diest, 2002), whereas certain weeds were known to present agro-ecological advantages (as soil ameliorant and inducing beneficial crop interaction). The availability of a large variety of edible and medicinal weeds enriches the daily diet of rural families as well as provides advantages for basic health. As such, the non-selective eradication of weeds would not only diminish the availability of useful resources for the local habitants, but also affect local food security.

Farmers' management decisions depended not only on aspects inherent to the crop production system and weed biology, but also on indigenous knowledge concerning usefulness/noxiousness of weeds. They recognized the usefulness of weeds, but eradicated them whenever they threatened their standing crop or obstructed agricultural activities. Only at the borders of the field or in a spot without intensive farming and also after the crop has reached a sufficiently mature stage, weeds were often tolerated. Fodder species did not receive specific attention due to their natural abundance, but almost one third of the otherwise used weed species (medicinal, edible, etc.) received a specific management. In addition, farmers with a higher plant name knowledge, tended to use less herbicides, which supports an earlier report (Alcorn, 1984a). The loss of indigenous knowledge is not only a loss for human culture, but also implies an impact on agricultural management, and this can help us to understand how the conservation of non-crop resources within small-scale tropical agriculture in a developing country can be supported.

Farmers' management intensity has its effect on local weed diversity. The dominant weed community within less intensely managed systems (milpa and lime) was more diverse than within papaya and melon systems, supporting previous reports and predictions from other countries

(Marshall et al., 2001; Marshall et al., 2003; Stoate et al., 2001).

The diminishing weed diversity with increasing management intensity represents a loss in biodiversity as plants form a basic keystone in the agro-ecosystem. Hence, western management techniques applied within a rural tropical community should be used with care as their effects have a different impact on small-scale rural societies compared with large-scale industrial farms in developed countries (Alcorn, 1984b; Vandermeer et al., 1998).

At present, the farmers of Tecomavaca selectively control their weeds and this knowledge should facilitate weed management programs aiming to combine effective weed control with in situ conservation of biological resources. The large variety of weeds found among the studied crop production systems confirmed the difficulty to formulate a general weed management program as described by Marshall and Arnold (1994). Weed control must be fine-tuned according to the crop production system, taking into account its most dominant weeds and farmer's uses. Weed management should not be uniform over the whole cultivated area. Instead, effective dosage of herbicides and localised application must be encouraged, thereby in addition reducing costs. However, additional experimental on-field research is needed to further develop these recommendations.

At the same time, farmers should receive more information about the influence of herbicide use on weed biodiversity and the role played by herbicides on the establishment of highly persistent weed species like *Cyperus flavescens* and *Chloris gayana*. In the year 2002, Mexico signed both the Cartagena Protocol on Biosafety to the Convention on Biological Diversity and the Stockholm Convention on Persistent Organic Pollutants. Weeds are an inherent part of agro-biodiversity and as such, it is in the interest of all that these international regulations are transformed into transparent legislation in order to initiate adequate promote programs that are able to reach the farmers in the rural communities.

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Capítulo II

¿Influye el Manejo Incipiente en la Distribución de Arvenses Útiles? Observaciones de Sta. María Tecomavaca, Oaxaca

Blanckaert, I. & Lira-Saade R.
Does incipient management influence the distribution of useful weeds? Observations from Santa María Tecomavaca, Oaxaca.

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En revisión

RESUMEN

Existe poca información sobre el efecto de manipulaciones antropogénicas en la distribución de plantas no cultivadas útiles dentro de campos de cultivo. Este trabajo investigó el manejo incipiente y la presencia, abundancia y cobertura de plantas arvenses útiles en cuatro sistemas agrícolas en Santa María Tecomavaca, una comunidad rural dentro de la Reserva de la Biosfera Tehuacán-Cuicatlán, México. Las plantas arvenses con mayor utilidad fueron manejadas más intensamente, crecían en un mayor número de sistemas agrícolas y terrenos que sus contrapartes con menor utilidad. Sin embargo, no fueron más abundantes ni presentaron una cobertura mayor. Al parecer, las plantas útiles en los terrenos fueron básicamente toleradas y/o protegidas, mientras que su fomento y/o cultivo se llevaba a cabo en los huertos familiares. En conclusión, la distribución de arvenses en los terrenos agrícolas de la zona de estudio, no está relacionada con su utilidad.

DOES INCIPIENT MANAGEMENT INFLUENCE THE DISTRIBUTION OF USEFUL WEEDS?

OBSERVATIONS FROM SANTA MARÍA TECOMAVACA, OAXACA.

¿INFLUYE EL MANEJO INCIPIENTE EN LA DISTRIBUCIÓN DE ARVENSES ÚTILES?

OBSERVACIONES DE SANTA MARÍA TECOMAVACA, OAXACA.

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ABSTRACT

There is little information on how anthropogenic manipulations affect the distribution of useful weeds within agricultural fields. This paper explores incipient management and the presence, abundance and cover of useful weeds in four farming systems of Santa María Tecomavaca, a rural community within the Tehuacán-Cuicatlán Biosphere Reserve, Mexico. Weeds with more uses were managed more intensely, grew within more farming systems and were found in more fields than their less useful counterparts. However, they were not more abundant, nor presented more cover. It seemed that useful plants were mainly tolerated and/or protected in the agricultural fields, while promotion and/or cultivation activities were found within homegardens. In conclusion, the distribution of weeds in agricultural fields within the study zone was not determined by their utility.

Key words: agrestals, non-agricultural weed management, Tehuacán-Cuicatlán Biosphere Reserve, semi-arid, useful weeds.

RESUMEN

Existe poca información sobre el efecto de manipulaciones antropogénicas en la distribución de plantas no-cultivadas útiles dentro de campos de cultivo. Este trabajo explora el manejo incipiente y la presencia, abundancia y cobertura de plantas arvenses útiles en cuatro sistemas agrícolas en Santa María Tecomavaca, una comunidad rural dentro de la Reserva de la Biosfera Tehuacán-Cuicatlán, México. Las plantas arvenses con mayor utilidad fueron manejadas más intensamente, crecían en más sistemas agrícolas y se encontraron en un mayor número de campos que sus contrapartes con menor utilidad. Sin embargo, no fueron más abundantes ni presentaron una cobertura mayor. Al parecer, plantas útiles en los terrenos fueron básicamente toleradas y/o protegidas, mientras que el fomento y/o cultivo se llevaba a cabo en los huertos familiares. En conclusión, la distribución de arvenses en los terrenos agrícolas de la zona de estudio, no fue determinado por su utilidad.

Palabras clave: malezas útiles, manejo no-agrícola, plantas arvenses, Reserva de la Biosfera Tehuacán-Cuicatlán, semi-árido.

Weeds are generally described as unpopular or unwanted plants which grow in agricultural fields and compete with crops for light, water, space and nutrients (Baker, 1965; Harlan and deWet, 1965, Baker, 1967, 1972, 1974). Ecology defines them as colonizers of sites which are perturbed by agricultural activities (Challenger, 1998) and they are, therefore, adapted to unstable habitats of which the future, as such, is often unpredictable (MacArthur, 1962; Grime, 1977; Sibly and Calow, 1983; Silvertown *et al.*, 1993).

Weed populations undergo periods of intense population growth with little competition, for example, when a new site is colonized. These periods, however, are interrupted by moments of high mortality, notwithstanding population density or the maturity of individuals. In such environment, plants assign much energy to growth and reproduction (Begon *et al.*, 1996). Hence, weed reproduction is generally characterized by the massive production of easily dispersible seeds and the persistence of latent structures in the soil, like seeds or vegetative reproduction organs (rhizomes, tubers and suckers), allowing weeds to maximize the establishment of large populations of different ages and sizes (Begon *et al.*, 1996).

Nevertheless, weed population structure and dynamics are altered by both natural and anthropogenic causes (Mortimer, 1996). The length of the fallow period in between subsequent crop cycles is determinant for the impact of artificial and natural selection. As such, an extensive fallow may weaken the effects of human perturbation and facilitate the establishment of species which, in the long term, will cause the disappearance of weeds from the site. Certain agricultural management activities, like the application of fertilizers or irrigation, may indirectly benefit weed seedling establishment (Mortimer, 1996), while weed seed dispersal may benefit from adherence in farmers' clothes or machinery (Vibrans, 1999). Others, however, like herbicides or ploughing, amongst others, are destined to obtain their maximal elimination (Marshall *et al.*, 2001). In general, the probability of weeds to reach maturity and begin seed production depends on the competitive capacity of the crop and the efficiency of weed control management (Fryer, 1979; Dekker, 1997).

Weeds are generally not considered plants of interest. For centuries, however, traditional farmers tolerate the existence of useful non-crop resources among their economically important domesticates (Bye, 1981; Chacón and Gliessman, 1982; Bye and Linares, 1983; Casas *et al.*, 1997b; Blanckaert *et al.*, 2007). Moreover, in order to obtain, secure or even increase the availability of these resources, people establish different kinds of interactions with varying intensity with these plants. These interactions involve collection, tolerance, protection, transplantation, promotion and cultivation of useful non-crop resources and are named incipient, traditional or non-agricultural management (Alcorn, 1981; Bye, 1993; Hernández-Xolocotzi, 1993; Casas and Caballero, 1995, 1996; Casas *et al.*, 1996, 1997a, 1997b, 2001) to distinguish them from standardized weed control, which, in the context of this paper, forms part of agricultural management.

The reason behind incipient management of weeds is their usefulness in the traditional cuisine, basic health or animal fodder, amongst others (Caballero, 1984, 1995; Espinosa-García and Díaz-Pérez, 1996; Blanckaert *et al.*, 2007). In fact, many weeds present one or several uses and may receive different forms of incipient management within the same community (Casas *et al.*, 1996). However, there is little information about the effect of these management forms within agricultural fields. Hence, the objective of this work is to investigate whether weed utility and incipient management forms influence weed distribution, postulating the hypothesis that differences in weed distribution within different farming systems are caused by the usefulness of weeds.

MATERIALS AND METHODS

The study region was the rural community of Santa María Tecomavaca (Oaxaca), localized in the southeastern section of the semi-arid Tehuacán-Cuicatlán Biosphere Reserve in Mexico (17°57’48”N and 97°00’26”W; elevation 612 meters above sea level; INEGI, 2000) (Figure 1). Inhabitants were mestizos with Mazatec backgrounds. The local climate was semi-arid with a mean annual temperature between 18 and 22°C. Rain fell intensely over a short three week period during summer (July – September), leaving the rest of the year dry (annual mean precipitation between 600 – 800 mm) (INEGI, 2005). The dominant vegetation in the region was thorn scrub forest, dominated by *Pachycereus marginatus* (DC.) Britton and Rose, *Cephalocereus columna-trajani* (Karw. ex Pfeiff.) K. Schum. and *Bursera morelensis* Ramirez, amongst others (Grupo Mesófilo, 2001).

Agriculture in Santa María Tecomavaca was small-scale and produced a wide variety of products in combination with animal husbandry (cattle, goats and horses, mainly). Given the semi-arid climate, agricultural activities were supported by an irrigation infrastructure providing water from two different sources: river-fed irrigation (bringing water from the ‘Río Salado’ river) and rain-fed irrigation (with fresh water coming from the adjacent mountain range). The most common farming systems in the study area were: (1) the milpa multiple cropping system with different combinations of maize (*Zea mays* L.), squashes (*Cucurbita* spp.) and beans (*Phaseolus* spp.), (2) Mexican lime orchards (*Citrus aurantifolia* (Christm.) Swingle), sometimes in combination with maize, (3) papaya orchards (*Carica papaya* L.) and (4) melon monoculture (*Cucumis melo* L.). The two first farming systems (milpa and lime) could be found under each of the two kinds of irrigation systems, while the two last systems (papaya and melon) were only found under river-fed irrigation in the study zone.

Between September 2003 and December 2004, the floristic composition of weeds within the study zone was assessed (Blanckaert *et al.*, 2007). Weed utility was determined through free and structured interviews following the guidelines of participatory observation (Martin, 1995; Alexiades, 1996), and local names, uses, plant parts used, plant preparation and incipient management forms were identified. In this work, all terms related with incipient, traditional and non-agricultural management of weeds do not refer to activities associated with their control of eradication, but include all human manipulations with respect to their importance as useful non-crop resources. In consequence, weed utility in this paper was associated with two measurable factors: (1) number of uses of each species and (2) the diversity of incipient management forms received.

Weed distribution was studied in 28 fields of the four farming systems mentioned above, with an almost equal amount of fields per crop production type. Each field was surveyed only once and had at the moment of assessment, a crop in a development stage similar to other fields with the same crop. Also, weed density was at or near its maximum at the assessment time. To obtain frequency, abundance and cover data, the line-intercept method was used (Kent and Coker, 1992). As such, the distribution pattern of each weed species was represented by the following quantitative characters: (1) number of different farming systems in which the species is found, (2) total number of fields were it is found (absolute frequency), (3) total number of plant individuals (absolute abundance), (4) total perpendicular leaf projection (absolute cover), (5) mean number of plant individuals per farming system (relative abundance), (6) mean perpendicular leaf projection per farming system (relative cover).

The relation between weed utility and distribution was analyzed by means of Spearman’s correlation coefficients between the quantitative characters described above for all weed species found in Santa María Tecomavaca. In addition, a χ^2-test was realized with data from the dominant weed flora as found in Blanckaert *et al.* (2007). All analyses were performed using SPSS for Windows software, version 11.0 (SPSS Inc., 2001).

RESULTS AND DISCUSSION

This paper, which focused on the effect of incipient management on weed distribution in agricultural fields, complements the results of Blanckaert *et al.* (2007), who investigated the effect of agricultural management associated with the use of fertilizers and herbicides. The weed flora of Santa María Tecomavaca consisted of 161 species, belonging to 40 botanic families and 103 genera (Blanckaert *et al.*, 2007). A complete list of all weed species found may be consulted in Appendix 1. Of them, 91.9% presented one or more uses, with fodder being the most important one, followed by medicinal, edible and ornamental uses, or agro-ecological benefits (soil improver or mulch). Of the fodder plants, only 3.5% received some kind of incipient management, whereas 29% of the otherwise used weeds received incipient management by the farmers (Blanckaert *et al.*, 2007).

In general, the spatial distribution of weeds in the agricultural fields of Santa María Tecomavaca was very variable (Blanckaert *et al.*, 2007). Weed richness, however, diminished along a gradient of agricultural management intensity represented by the sequence of cropping systems milpa – lime – papaya –melon, which was associated with irrigation volume per hectare, contracted work forces per hectare and monetary investment for herbicides and fertilizers per hectare (Blanckaert *et al.*, 2007) (Figure 2).

Weed management appeared to be balanced between agricultural and non-agricultural management forms. Farmers in Santa María Tecomavaca eliminated or controlled weeds which were known to damage crops or whose presence complicated farming activities (Blanckaert *et al.*, 2007). However, they were also interested in the usefulness of the weeds growing on their fields, even when they were not economically important plants. The interest in these useful non-crop resources, and therefore also the incipient management forms they received, was linked with various factors. As such, for example, various farmers tolerated useful weeds when they were found at the border of the fields, when growing under a fruit tree, or when the crop had already reached a stage in which it was resistant against competition with weeds. Sometimes, when natural abundance of the weed of interest was low, some farmers weeded around them to stimulate their growth (protection), and some even allowed them to produce seeds to secure future populations (promotion). However, the number of farmers in Santa María Tecomavaca practicing promotion of useful weeds in their fields was very limited (Blanckaert *et al.*, 2007). It was expected that the effect of incipient management in the fields of Santa María Tecomavaca would be expressed by a differential proportion of useful weeds in the studied cropping systems. However, this remained almost constant in the four studied cropping systems (Figure 2), indicating that the effects of weed control were stronger than those of incipient management.

There was a significant positive correlation between the number of uses of a weed and the number of incipient management forms it received (Table 1; $r = 0.346$, $P < 0.001$). There were also positive associations between the number of uses and the number of different farming systems in which it was found (Table 1; $r = 0.245$, $P < 0.05$) and absolute frequency (Table 1; $r = 0.209$, $P < 0.05$). As such, more useful weeds tended to receive more incipient management forms, grew in more different farming systems and were found in more fields than their less useful counterparts. However, the associations mentioned above were weak and only registered for frequency values, not for abundance or cover values. Hence, incipient management of useful weeds in Santa María Tecomavaca weakly influenced their presence in agricultural fields, but did not influence their abundance or cover. Although Blanckaert *et al.* (2007) did not find significant differences in weed flora between different farming systems, each system tended to be dominated by different weed species (Table 2). Also the presence of these dominant weed species was not ruled by utility ($\chi^2 = 10.61$; $\alpha = 0.001$).

Weeds are able to disperse large quantities of seeds for their reproduction (Begon *et al.*, 1996). In consequence, they easily colonize agricultural fields and their natural abundance renders artificial propagation by man generally unnecessary. As such, although the use of weeds was important in Santa María Tecomavaca, there was no human-directed propagation (promotion) in its agricultural fields. In fact, when a culturally important useful weed was temporarily scarce, the villagers of Santa María Tecomavaca tried to increase its availability, not in the agricultural fields, but rather in their homegardens close to the dwelling, by means of transplantation, tolerance, protection or the cultivation of seeds previously collected from the fields or the natural vegetation. Examples of weeds in this situation are: ‘Papaloquelite’ (*Porophyllum ruderale* var. *macrocephalum* (DC.) Cronquist: Asteraceae), ‘Epazote’ or Mexican tea (*Chenopodium ambrosioides* L.: Chenopodiaceae), ‘Topoya’ or ‘Hierba del cáncer’ (*Tournefortia densiflora* M. Martens and Galeotti: Boraginaceae), ‘Quiebraplatos’ or ‘Campanita’ (*Ipomoea purpurea* (L.) Roth: Convolvulaceae), and ‘Hierba del chepíl’ (*Crotalaria longirostrata* Hook. and Am.: Fabaceae), amongst others.

In conclusion, in the study area of this work, the interaction between farmers and weeds was rather complex and involved various factors, both agricultural and non-agricultural. The lack of promotion of useful weeds explained how weed distribution within agricultural fields was not related with weed utility. As such, it seemed that weed distribution was directed mainly by practices of weed control (dominated by herbicides), and not by the activities of farmers associated with weed utility in their fields.

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Table 1. Spearman’s correlation coefficient between parameters of weed utility and distribution.

	Uses	Man	Farm	F	A	C	MILa	MILc	LIMa	LIMc	PAPa	PAPc	MELa
Man	0.346**												
Farm	0.245*	0.076											
F	0.209*	0.084	0.911**										
A	0.124	0.031	0.398**	0.488**									
C	0.147	0.101	0.503**	0.572**	0.875**								
MILa	0.195	0.034	0.757**	0.738**	0.523**	0.603**							
MILc	0.087	0.041	0.539**	0.485**	0.252*	0.321**	0.599**						
LIMa	0.161	0.080	0.717**	0.681**	0.286**	0.377**	0.531**	0.446**					
LIMc	0.183	-0.051	0.486**	0.435**	0.197	0.217*	0.334**	0.388**	0.662**				
PAPa	0.185	0.047	0.739**	0.685**	0.342**	0.397**	0.554**	0.450**	0.870**	0.594**			
PAPc	0.069	0.045	0.334**	0.289**	0.099	0.204	0.200	0.379**	0.384**	0.282**	0.405**		
MELa	0.209*	0.075	0.580**	0.513**	0.284**	0.317**	0.393**	0.252*	0.337**	0.293**	0.461**	0.193	
MELc	0.137	0.128	0.489**	0.438**	0.158	0.213*	0.328**	0.394**	0.424**	0.330**	0.492**	0.284**	0.672**

*Underlined results are significant (**P < 0.01; *P < 0.05; n = 92); Uses = number of uses, Man = number of incipient management forms, Farm = number of different farming systems in which the species is found, F, A and C = absolute frequency, abundance and cover of each species,* MIL_a *and* MIL_c*,* LIM_a *and* LIM_c*,* PAP_a *and* PAP_c*,* MEL_a *and* MEL_c *= relative abundance and cover per species in each farming system (MIL = milpa, LIM = Mexican lime orchard, PAP = papaya orchard, MEL = melon).*

Table 2. Uses of dominant weeds in each farming system

	FARMING SYSTEM			
USE	MILPA	LIME	PAPAYA	MELON
FODDER	14	12	7	1
MEDICINAL	3	4	1	1
EDIBLE	1	1	1	0
ORNAMENTAL	4	0	0	0
OTHER	3	4	0	0
	25	21	9	2

Appendix 1. Weed list from Santa María Tecomavaca

Family and Species	Local Name	Use	Detail	Part Used	Prepara-tion	Manage-ment
Acanthaceae						
Elytraria imbricata (Vahl) Pers.	hierba de sombra	F	-	1	1	0
Ruellia hirsuto-glandulosa (Oerst.) Hemsl.	-	F	-	1	1	0
Ruellia nudiflora (Engelm. & A.Gray) Urb.	acahuite	F	-	1	1	0
Tetramerium nervosum Nees	-	F	-	1	1	0
Aizoaceae						
Trianthema portulacastrum L.	verdolaga cimarrón/verdolaga cimarrona	F M	- diabetes (combined with *Lippia graveolens*)	1 1	1 13	0* 0*
Amaranthaceae						
Achyranthes aspera L.	costilla de ratón	F	-	1	1	0
Amaranthus hybridus L.	quelite/quintonil	F E	- -	1 2	1 3/5	0*/3/4 0*/3/4
Amaranthus sp.	-	-	-	-	-	0
Gomphrena decumbens Jacq.	borlita/perla/rosa seca	F	-	1	1	0*/3
**Iresine discolor* Greenm.	-	F	-	1	1	0
Iresine sp.	enredadera	E	prepared as flower when maize is scarce	3	3+7+4	0
Apiaceae						
Hydrocotyle verticillata Thunb.	lirio silvestre	F	-	1	1	0
Apocynaceae						
Vallesia glabra (Cav.) Link	chinto borrego	F E	- -	1 4	1 1	0 0
Asteraceae						
Bidens bigelovii A.Gray	hierba de tizón/aceitillo	F	seeds are toxic	1	1	0
Bidens odorata Cav.	-	F	-	1	1	0
Blumea viscosa (Mill.) V.M. Badillo	abrojo	F	-	1	1	0/3
Flaveria trinervia (Spreng.) C.Mohr	hierba de sapo	F M	- diabetes inflammation	1 2 2	1 8 10	0 0/3 0/3
**Florestina simplicifolia* B.L. Turner	-	F	-	1	1	0
Melampodium longifolium Cerv.	-	F	-	1	1	0
Parthenium hysterophorus L.	hierba de la hormiga	M	dengue/ant bite/stomach ache	1	8	0*
Porophyllum punctatum (Mill.) S.F.Blake	pápaloquelite macho	L	around animal corral	1	1	0/3
Porophyllum ruderale var. *macrocephalum* (DC.) Cronquist	pápaloquelite/pápalo	E/S	-	2	1	0*/3/4/6
Sanvitalia procumbens Lam.	manzanilla	F	-	1	1	0
Sonchus asper (L.) Hill	lechuga/lechuguilla/diente de león	F E	- -	1 2	1 1/3	0* 0*
Sonchus oleraceus L.	lechuga/lechuguilla/diente de león	F E	- -	1 2	1 1/3	0* 0*
Taraxacum officinale Weber ex F.H. Wigg.	lechuga/lechuguilla/diente de león	F E	- -	1 2	1 1	0* 0*
Tithonia tubiformis (Jacq.) Cass.	acahual/girasol montes/girasol silvestre	F/O	-	1	1	0*/3
Viguiera dentata (Cav.) Spreng.	chimalacate	F M A	- intestinal inflammation -	1 2 1	1 9 1	0*/3 0*/3 0*
Xanthium strumarium L.	chayotillo	F	-	1	1	0*
Zinnia peruviana (L.) L.	gallito/gallito del monte/gallito cimarrón/gallo silvestre/flor de maravillas	F/O	-	1	1	0*
Boraginaceae						
Cordia curassavica (Jacq.) Roem. & Schult.	escobillo	F	-	1	1	0
Cordia stellata Greenm.	-	-	-	-	-	0
Heliotropium angiospermum Murray	hierba de alacrán	M	scorpion sting	1	8	0*
Heliotropium curassavicum L.	-	F	-	1	1	0

Family and Species	Local Name	Use	Detail	Part Used	Prepara-tion	Manage-ment
Heliotropium foliosissimum J.F. Macbr.	-	F	-	1	1	0
Tournefortia densiflora M. Martens & Galeotti	topoya/hierba del cáncer/hachinole*	M	gastritis/cancer/kidney ailment labour	1 2	8 8/11	0*/3/4 0*/3/4
Brassicaceae						
Lepidium virginicum L.	-	F	-	1	1	0
Capparaceae						
Cleome tenuis subsp. *humilis* (Rose) H.H. Iltis	-	F	-	1	1	0
Cleome viscosa L.	-	F	-	1	1	0
Caryophyllaceae						
Arenaria sp.	-	Sin	-	-	-	0
Chenopodiaceae						
Chenopodium ambrosioides L.	Epazote/Epazote blanco/Epazote colorado/Epazote morado	E M S	- anthelmintic/improve memory (child) -	2 1 2	3/4/5 8 3/4/5	0*/3/4/5/6 0*/3/4/5/6 0*/3/4/5/6
Commelinaceae						
Commelina diffusa Burm. f.	hierba de pollo/chamiso/barquito	O	-	1	1	0*
Convolvulaceae						
Ipomoea leptotoma Torr.	enredadera	F	-	1	1	0
Ipomoea purpurea (L.) Roth.	quiebraplatos/bejuco/campanita/manto/enredadera	F O	- -	1 1	1 1	0* 0*/3/4/6
Ipomoea suffulta (Kunth) G. Don	bejuco/la campana/manto	F/O	-	1	1	0
Merremia dissecta (Jacq.) Hallier f.	hierba de araña	M	skin infections/irritations caused by spiders	2	6+10	0*/3/4
Merremia quinquefolia (L.) Hallier f.	enredadera	F	-	1	1	0
Cucurbitaceae						
Cucumis anguria L.	sandiita del monte	E	-	4	1	0*
Cyperaceae						
Cyperus esculentus L.	pionía/coquillo/cebollín	F M	- depression (child)/stomach ache/heart disease	1 5	1 2+8	0* 0*
Cyperus flavescens L.	pasto	F	-	1	1	0
Euphorbiaceae						
Acalypha arvensis Poepp. & Endl.	-	F/B	-	1	1	0
Acalypha ostryaefolia Riddell	chaguoquelite	M	indigestion (child)	1	11	0
Chamaesyce berteroana (Balb. ex Spreng.) Millsp.	golondrina roja/hierba lechosa	M	measles/chickenpox/smallpox wounds/splinter removal	1 6	11 1	0*/3 0*/3
Chamaesyce cumbrae (Boiss.) Millsp.	golondrina chica/golondrina/hierba lechosa	M	measles/chickenpox cough wounds	1 1 6	11 8 1	0* 0* 0*
Chamaesyce hypericifolia (L.) Millsp.	golondrina mediana	F	-	1	1	0
Chamaesyce hyssopifolia (L.) Small	golondrina mediana	F	-	1	1	0
Chamaesyce sp.	golondrina chica/golondrina/hierba lechosa	M	measles/chickenpox cough wounds	1 1 6	11 8 1	0* 0* 0*
Croton sp.	-	-	-	-	-	0
Euphorbia dentata Michx.	golondrina hoja ancha/golondrina/hierba lechosa	F M	- wounds	1 6	1 1	0* 0*
Euphorbia heterophylla L.	golondrina hoja ancha/golondrina/hierba lechosa	F M	- wounds	1 6	1 1	0* 0*
Euphorbia hirta L.	golondrina roja/hierba lechosa	M	measles/chickenpox/smallpox wounds/splinter removal	1 6	11 1	0*/3 0*/3
Euphorbia sp.	golondrina	-	-	-	-	0
Manihot sp.	-	-	-	-	-	0
Ricinus communis L.	higuerilla	M D	Stomach ache and indigestion (child)/fever Hair lotion	2 3	5 6	0* 0*
Fabaceae						
Coursetia caribaea (Jacq.) Lavin	-	F	-	1	1	0

Family and Species	Local Name	Use	Detail	Part Used	Prepara-tion	Manage-ment
Crotalaria incana L.	-	F	-	1	1	0
Crotalaria longirostrata Hook. & Arn.	hierba de chepíl/chepíl/chipilo	F E	- -	1 2	1 3	0 0/3/4/6
Desmodium nitidum M. Martens & Galeotti	-	F	-	1	1	0
Desmodium procumbens var. *longipes* (Schindl.) B.G. Schub.	-	F	-	1	1	0
Desmodium procumbens var. *transversum* (B.L. Rob. & Greenm.) B.G. Schub.	-	F	-	1	1	0
Desmodium tortuosum (Sw.) DC.	-	F	-	1	1	0
Desmodium sp.	enredadera	-		-	-	0
Indigofera suffruticosa Mill.	añil	D	colour cloths blue	1	2+14	0*
Medicago polymorpha L.	trébol montés	F	-	1	1	0
Painteria sp.	-	-	-	-	-	0
Rhynchosia minima (L.) DC.	-	F	-	1	1	0
Tephrosia cinerea (L.) Pers.	-	F	-	1	1	0
Gentianaceae						
Eustoma exaltatum (L.) Salisb. ex G. Don	-	F	-	1	1	0
Loasaceae						
Mentzelia aspera L.	amor seco/hierba pegajosa	F/B	-	1	1	0*/3
Malvaceae						
Abelmoschus esculentus (L.) Moench	angú	E/O	-	1	1	0/3
Abutilon ellipticum Schltdl.	chahuiscle	F	-	1	1	0
Abutilon mollicomum (Willd.) Sweet	-	F	-	1	1	0
Abutilon mucronatum J.E. Fryxell	hierba pegajosa/tronadora	F T	- children pop leaves in their hands	1 2	1 1	0* 0*
Abutilon percaudatum Hochr.	-	F	-	1	1	0
Abutilon sp.	-	-	-	-	-	0
Anoda crenatiflora Ortega	-	F	-	1	1	0
Anoda cristata (L.) Schltdl.	-	F E	-	1 3	1 1	0 0
Herissantia crispa (L.) Brizicky	-	F	-	1	1	0
Malva sp.	-	-	-	-	-	0
Malvastrum americanum (L.) Torr.	-	F	-	1	1	0
Malvastrum bicuspidatum subsp. *oaxacanum* Rose ex S.R. Hill	-	F	-	1	1	0
Rhynchosida physocalix Fryxell	-	F	-	1	1	0
Sida glabra Mill.	-	F/A D	- broom	1 7	1 2	0 0
**Sida pueblensis* Fryxell	hierba de botón	F	-	1	1	0
Sida rhombifolia L.	-	F D	- broom	1 7	1 2	0 0
Mimosaceae						
Desmanthus virgatus (L.) Willd.	huajito de ratón/huajito silvestre/huajito de monte/tepehuaje	E	-	3/4	1	0*
Nyctaginaceae						
Allionia incarnata L.	-	F	-	1	1	0
Boerhavia coccinea Mill.	-	F	-	1	1	0
Boerhavia erecta L.	nube/hierba de nube/nube del campo	O	-	1	1	0*
Boerhavia procumbens Lam.	-	F	-	1	1	0
Oxalidaceae						
Oxalis frutescens subsp. *angustifolia* (Kunth) Lourteig	-	F	-	1	1	0

FAMILY AND SPECIES	LOCAL NAME	USE	DETAIL	PART USED	PREPARA-TION	MANAGE-MENT
Papaveraceae						
Argemone ochroleuca Sweet	chicalote	M	eye infection	6	1	0*
			kidney ailment	1	8	0*
Passifloraceae						
Passiflora foetida L.	granadilla/granadita	E	-	4	1	0*
	pachona/pasionaria	M	ear ache	2	7	0*
		O	-	1	1	0*
Pedaliaceae						
Martynia annua L.	torito	M	cancer/diabetes	1	8	0
Phytolaccaceae						
Rivina humilis L.	hierba de la víbora	F	-	1	1	0*
		E	-	4	1	0*
Plumbaginaceae						
Plumbago scandens L.	negrito/aretito	M	acne/wounds	2	7	0*
		T	girls stick flowers to earlobes as if earrings	8	1	0*
Poaceae						
Arthraxon hispidus (Thunb.) Makino	pasto	F	-	1	1	0
Cenchrus ciliaris L.	pasto	F	-	1	1	0
Cenchrus incertus M.A. Curtis	pasto/cola de zorra	F	-	1	1	0
Cenchrus longispinus (Hack.) Fernald	pasto/abrojo/huisapole	F	-	1	1	0
Chloris gayana Kunth	pasto chino	F	-	1	1	0
Chloris virgata Sw.	pasto/pasto de escobita	F	-	1	1	0
Chloris sp.	pasto	F	-	1	1	0
Dactyloctenium aegyptium (L.) Willd.	pasto	F	-	1	1	0
Digitaria bicornis (Lam.) Roem. & Schult.	pasto	F	-	1	1	0
Digitaria insularis (L.) Fedde	pasto	F	-	1	1	0
Echinochloa colonum L.	pasto	F	-	1	1	0
Eragrostis barrelieri Daveau	pasto	F	-	1	1	0
Eragrostis cilianensis (All.) Vignolo ex Janch.	pasto/pasto espiga	F	-	1	1	0
Eragrostis intermedia A. Hitchc.	pasto	F	-	1	1	0
Lasiacis divaricata (L.) Hitchc.	carricillo	C	fence	7	1/2	0
Muhlenbergia sp.	pasto	F	-	1	1	0
Panicum hirsutum Sw.	pasto	F	-	1	1	0
Panicum sp.	pasto luis	F	-	1	1	0
Rhynchelytrum repens (Willd.) C.E. Hubb.	pasto/pasto guineo/pasto terciopelo	F	-	1	1	0
Setaria grisebachii E.Fourn.	cola de zorra	F	-	1	1	0
Setaria liebmannii E.Fourn.	cola de zorra	F	-	1	1	0
Sorghum bicolor (L.) Moench	pasto forrajera/sorgo	F	-	1	1	0/3/6
Sorghum halepense (L.) Pers.	pasto luis	F	-	1	1	0
Urochloa fusca (Sw.) B.F.Hansen & Wunderlin	pasto	F	-	1	1	0
Vulpia myuros (L.) C.C. Gmel.	pasto	F	-	1	1	0
Portulacaceae						
Portulaca oleracea L.	verdolaga	E	-	1/2	3	0*
Primulaceae						
Samolus ebracteatus var. *cuneatus* (Small) Henrickson	hierba de espanto	M	against fear	7	1	0
Samolus sp.		-	-	-	-	0
Rubiaceae						
Crusea calcicola Greenm.	-	F	-	1	1	0
Scrophulariaceae						
Capraria biflora L.	escobillo	F	-	1	1	0*
		D	broom	7	2	0*

FAMILY AND SPECIES	LOCAL NAME	USE	DETAIL	PART USED	PREPARA-TION	MANAGE-MENT
Solanaceae						
Datura discolor Greenm.	tlapa/toloache/quiebraplato	M	wounds or bruises/acne hallucinogenic tranquilizer	1/2 4 2	1/10 8 15	0* 0* 0*
Datura inoxia Mill.	tlapa/toloache/quiebraplato	M	wounds or bruises/acne hallucinogenic tranquilizer	1/2 4 2	1/10 8 15	0* 0* 0*
Datura stramonium L.	tlapa/toloache/quiebraplato	M	wounds or bruises/acne hallucinogenic tranquilizer	1/2 4 2	1/10 8 15	0* 0* 0*
Nicotiana glauca Graham	-	F	-	1	1	0
Physalis cinerascens (Dunal) Hitchc.	tomatillo/tomatillo silvestre/tomatillo cimarrón/totomache/miltomate/jaltomate	M T	against anger attacks (child) -	2 4	1 1	0* 0*
Solanum adscendens Sendtn.	-	F	-	1	1	0
Solanum americanum Mill.	hierba mora	E M	- bile kidney stones facial dermatitis	1 1 2 2	3/5 8 8 10	0*/3 0*/3 0*/3 0*/3
Solanum elaeagnifolium Cav.	-	F	-	1	1	0
Solanum erianthum D. Don	hoja de manteca	D	wash dishes	2	1	0*/3
Solanum lanceolatum Cav.	coyotomate/mocachane*/ estrella de mar/shumá**	M	inflammation during pregnancy/after labour/relaxing steam bath	1	11	0*
Solanum rostratum Dunal	pata de cabra	F	-	1	1	0*
Solanum tridynamum Dunal	berenjenilla/hierba de la berenjilla/berenjena/berenjena cimarrona	F	-	1	1	0*
Sterculiaceae						
Melochia pyramidata L.	tapaculo cimarrón	F	-	1	1	0
Melochia tomentosa L.	-	F	-	1	1	0*
Waltheria americana L.	tapacola/taparabo/tapaculo/ hierba pachona	F M	- diarrhoea/stomach ache	1 1	1 8	0*/3 0*/3
Tiliaceae						
Corchorus siliquosus L.	-	-	-	-	-	0
Ulmaceae						
Celtis caudata Planch.	espina blanca	-	-	-	-	0
Verbenaceae						
Bouchea prismatica (L.) Kuntze	-	F	-	1	1	0
Lantana camara L.	-	O	-	1	1	0*
Lantana hirta Graham	orégano de monte/orégano cimarrón/orégano silvestre	F	-	1	1	0
Lippia graveolens Kunth	orégano	F M S	- hang over/stomach ache -	1 2 2	1 1/8 1/2	0* 0* 0*
Phyla nodiflora (L.) Greene	-	F	-	1	1	0
Priva mexicana (L.) Pers.	-	F	-	1	1	0
Violaceae						
Hybanthus oppositifolius (L.) Taub.	-	F	-	1	1	0
Zygophyllaceae						
Kallstroemia hirsutissima Vail	abrojo/abrojo blanco	F M	- kidney ailments	1 1	1 8	0 0

Endemic. **Local Name: Spanish, *Náhuatl, **Mazateco. **Use**: F = fodder, E = edible, M = medicinal, O = ornamental, D = domestic, C = construction material, T = toy, L = living fence, S = spice, A = soil ameliorant, B = beneficial crop interaction. **Part used**: 1 = total plant, 2 = leaf, 3 = seed, 4 = fruit, 5 = root, 6 = exudate, 7 = stem, 8 = flower. **Preparation**: 1 = fresh/without preparation, 2 = dry, 3 = boiled, 4 = toasted, 5 = fried, 6 = ground dry, 7 = macerated, 8 = infusion, 9 = lubricated, 10 = unguent, 11 = hot water bath, 12 = steam bath, 13 = mixed, 14 = soaked, 15 = massage. **Management Forms**: 0 =controlled weed without incipient management, 0* =controlled weed and growing in natural vegetation, 3 = tolerated, 4 = protected, 5 = fomented, 6 = cultivated.*

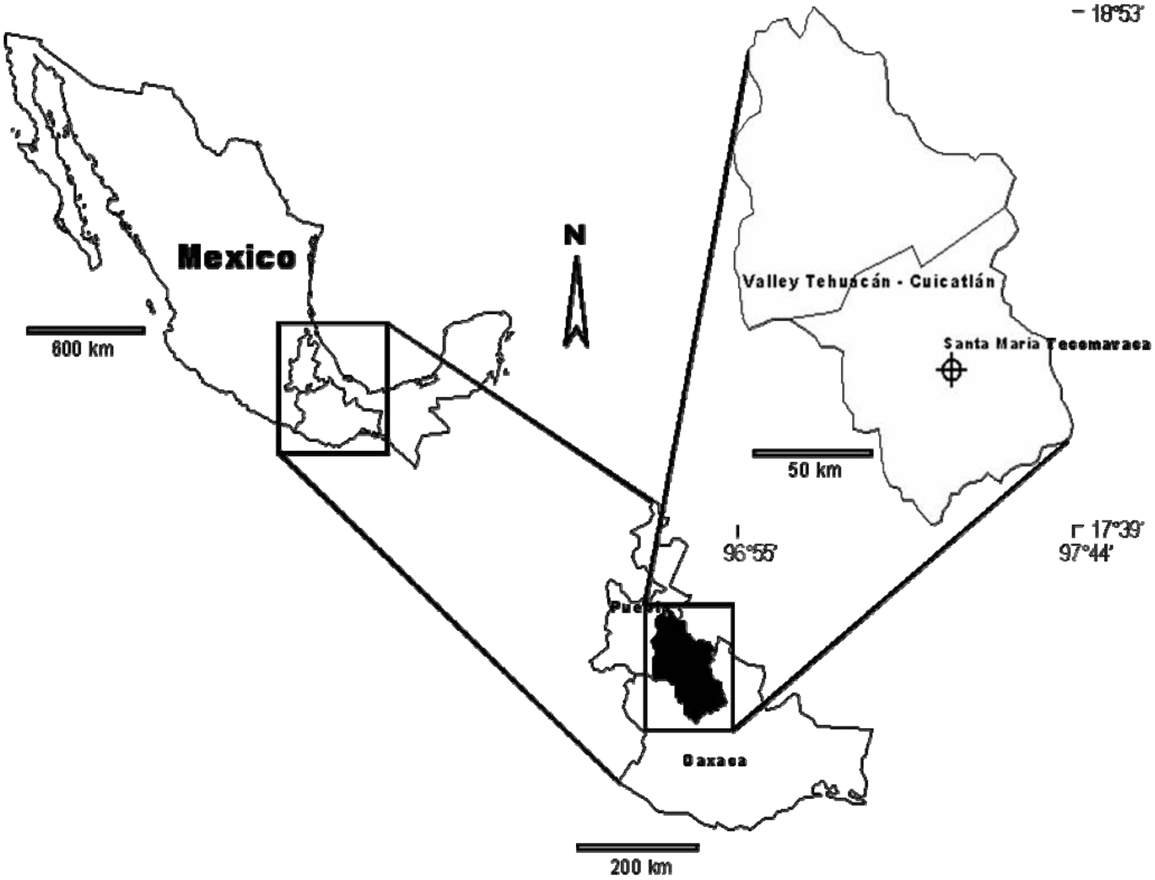

Figure 1. The rural community of Santa María Tecomavaca within the Tehuacán-Cuicatlán Biosphere Reserve.

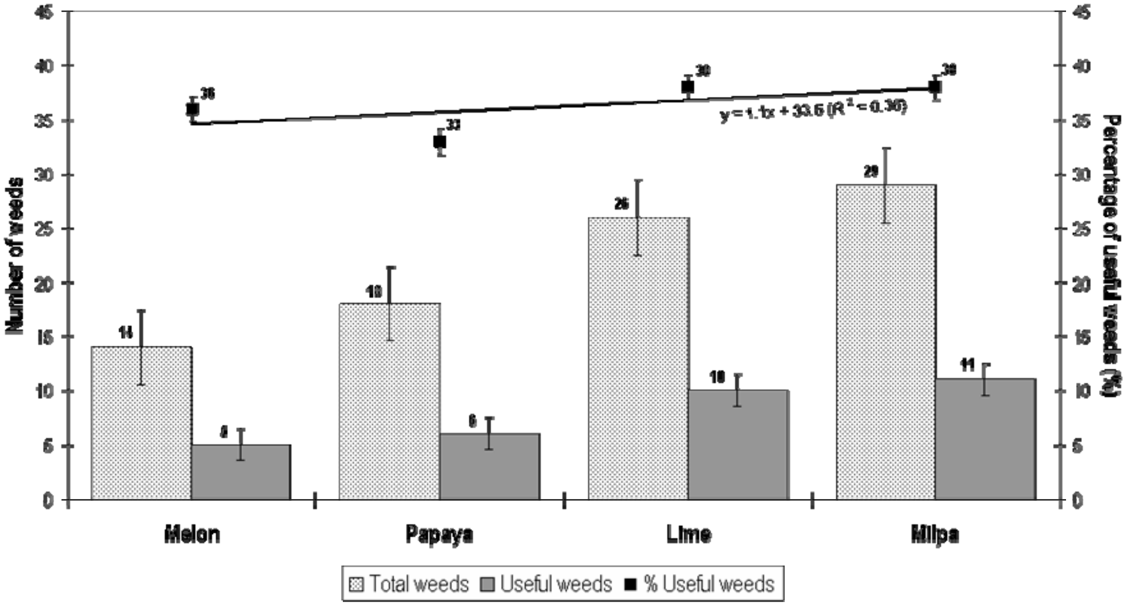

Figure 2. Total richness of weeds, richness of useful weeds and the percentage of useful weeds for each farming system in Santa María Tecomavaca.

Capítulo III

Herbicidas Facilitan la Invasión de Arvenses Exóticas en la Reserva de la Biosfera Tehuacán-Cuicatlán

Blanckaert, I., Vancraeynest K., Swennen R.L., Espinosa-García F.J., Piñero D., Lira-Saade R.
Herbicides encourage weed invasion in the semi-arid Tehuacán-Cuicatlán Biosphere Reserve, Mexico.

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RESUMEN

En México, aproximadamente el 22% de todas las malezas son de origen exótico o no nativo. Sin embargo, poco se sabe con respecto a su distribución local y a su diversidad en regiones rurales, y en particular, en sus áreas protegidas. Este trabajo documenta 124 arvenses nativas (85%) y 22 arvenses exóticas (15%) en la comunidad rural de Santa María Tecomavaca, ubicada dentro de la Reserva de la Biosfera Tehuacán-Cuicatlán, México. Se identifican las 19 malezas más problemáticas, de las cuales seis son de origen exótico y se discute el impacto de la invasión de arvenses exóticas. Los habitantes utilizan y manejan las plantas arvenses sin tomar en cuenta su origen. Así, los campesinos probablemente no apoyarán programas de control de malezas exóticas en el futuro sin que exista su substitución por otras nativas. La investigación detallada de cuatro sistemas agrícolas con diferentes niveles de aplicación de herbicidas y fertilizantes indica que el uso de herbicidas beneficia la riqueza de arvenses exóticas. En particular, el uso de herbicidas no selectivos y sistémicos parece afectar más a las arvenses nativas que a las exóticas. En consecuencia, cualquier programa de control a larga escala debería de tomar en cuenta este hecho. Este es el primer reporte sobre la invasión de arvenses exóticas y la susceptibilidad futura de la agricultura regional en la Reserva de la Biosfera Tehuacán-Cuicatlán.

Herbicides encourage weed invasion in the semi-arid Tehuacán-Cuicatlán Biosphere Reserve, Mexico.

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Herbicides encourage weed invasion in the semi-arid Tehuacán-Cuicatlán Biosphere Reserve, Mexico.

Abstract

In Mexico, approximately 22% of all weeds are exotic or non-indigenous. However, little is known about their local distribution and diversity in rural regions, and in particular, in its protected areas. This paper documents 124 native weeds (85%) and 22 exotic weeds (15%) in the rural community of Santa María Tecomavaca, situated within the Tehuacán-Cuicatlán Biosphere Reserve, Mexico. The 19 most problematic weeds are highlighted, of which six are exotics, and the impact of weed invasion is discussed. Villagers use and manage weedy plants irrespective of their origin. Hence, farmers will possibly not support future exotic weed eradication programs unless adequate substitutions are found from native plants. A detailed survey in four farming systems with different intensive use of herbicides and fertilizers indicates that herbicide use stimulates exotic weed richness. In particular, the use of non-selective systemic herbicides seems to affect native weeds more than exotics. Therefore, large-scale control programs need to apply them with care. This is the first report about weed invasion and future invasion susceptibility of the regional agriculture in the Tehuacán-Cuicatlán Biosphere Reserve.

Key words

agrochemical product application, exotic weeds, native weeds, traditional farming, sustainable weed management, useful non-crop resources

Introduction

Since the apparition of Elton's work (Elton, 1958), the impact of plant invasions has drawn the attention of scientists worldwide (Pyšek et al., 2004), and they are considered the second most important cause of biodiversity loss in the world. In Mexico, however, there is still little information about this phenomenon (Rzedowski, 1990; Espinosa-García, 2003; Espinosa-García et al., 2004a, b; Villaseñor and Espinosa-García, 2004). The country's extraordinary native biodiversity of approximately 23 000 species (Villaseñor, 2003) situates it among the five most diverse countries of the world. In addition, its elevated level of plant endemism highlights the need to evaluate present and future environmental and socio-economic impacts from invading organisms.

Weeds, in particular, possess the potential to behave as invaders (Hawkins, 1996; Espinosa-García et al., 2004b; Pyšek et al., 2004) because of their natural association with man-disturbed habitats (Baker, 1965; Harlan and de Wet, 1965). The Mexican territory beholds 2814 weed species (Villaseñor and Espinosa-García, 2004), representing 12.3% of its total vascular flora (Villaseñor, 2003). Of these weeds, 618 (22%) were introduced (Espinosa-García, 2003; Espinosa-García et al., 2004a; Villaseñor and Espinosa-García, 2004). In 1992, a list of the most problematic weeds in northern and central Mexico was produced (De Ita et al., 1992), more than half of which are exotic. However, at present, there is no accurate information about the magnitude, distribution and diversity of problematic alien weeds in many agricultural regions in Mexico and especially in its protected areas (Espinosa-García, 2003; Espinosa-García et al., 2004a).

Weeds are generally considered as noxious plants that merely need to be eradicated (Baker, 1965). They interfere with crop growth, complicate harvest or affect human and animal health (Richardson et al., 2000; Espinosa-García, 2003; Pyšek et al., 2004). However, the native Mexican weed diversity has been and is still a fundamental key stone of the country's rich agro-biodiversity. Weeds can protect soils against erosion, high soil temperatures or nutrient leaching. Also, they satisfy various needs such as animal fodder, food, spice and medicine and have ornamental, religious and ceremonial uses as well. Even though these weedy non-crop resources are primarily consumed at home, occasional sells at the local market strengthen the local subsistence economy (Bye and Linares, 1983; Bye, 1993; Espinosa-García and Díaz-Pérez, 1996; Vieyra-Odilón and Vibrans, 2001; Blanckaert et al., 2004; Prance and Nesbitt, 2005; Paredes-Flores, 2006; Blanckaert et al., 2007; Paredes-Flores et al., in press).

The success of many exotic weeds is the result of their deliberate introduction as potential useful plants (Rejmánek, 2005). In consequence, increased inoculum pressure (sensu Williamson, 1996) and human management towards better growth and reproduction of the introduced plants has facilitated their establishment and naturalization. Thus weeds, both native and exotic, can be harmful plants as well as useful, and as such, before any appropriate weed control programs can be designed and applied, it is absolutely necessary to understand the balance between weed noxiousness and use and management patterns (Espinosa-García, 2003).

Intensification of agricultural management generally results in diminished weed diversity (Swift et al., 1996; Marshall et al., 2001; Stoate et al., 2001). Elton's resistance hypothesis (Elton, 1958) predicts that less diverse plant communities are more susceptible for invasion by alien species, postulating a negative correlation between the number of native and exotic plants. At present, however, this prediction is under intense scrutiny because several experimental and non-experimental surveys at different scale levels (from small-scale plots to countries) have produced contradictory results, including negative (e.g. Kennedy et al., 2002), non-existent or weakly positive (Stohlgren et al., 2003) to positive correlations between native and exotic flora (Lonsdale, 1999; Stohlgren et al., 2003). In Mexico, most recently, Espinosa-García et al. (2004a) separated native weeds from non-weeds, considering that most alien species first grow in disturbed areas (Rejmánek, 1989; Hobbs, 2000; Rodgers III and Parker, 2003), precisely the conditions were also native weeds prosper, and found a negative correlation between native and exotic weeds with a multiple regression approach. In consequence, one expects more introduced weeds in crop production systems that are more intensified. Although modern-day agriculture is characterized by the increasing use of fertilizers and herbicides, not many studies dedicate their efforts towards the influence of those products on the invasion of exotic weeds. Today's most attention-drawing issue in plant invasion ecology is to predict and identify future problematic invaders (Mack et al., 2000; Espinosa-García, 2003). Hence the understanding on how agrochemicals affect invader weeds establishment is needed to define the future invasion susceptibility of the Mexican regional agriculture.

The goals of this paper are twofold: (1) to list the native and introduced weed flora and document its utility and management; and (2) to analyze weed distribution in different farming systems along an intensity gradient of agrochemicals (fertilizers and herbicides) in the rural community of Santa María Tecomavaca, situated within the Tehuacán-Cuicatlán Biosphere Reserve, Mexico.

Materials and methods

The Tehuacán-Cuicatlán Biosphere Reserve, a semi-arid region located in the states of Puebla and Oaxaca, is considered one of the most diverse and culturally important regions in Mexico (Dávila et al., 2002). Given the coexistence of diverse agricultural activities and biological conservation efforts within this protected area, there is a pressing need for the accurate evaluation of current alien weeds. The rural community of Santa María Tecomavaca has 1813 inhabitants (INEGI, 2000) and is situated in the southeast part of the Tehuacán-Cuicatlán Biosphere Reserve (17°57’48”N and 97°00’26”W; elevation 612 m above sea level), district of Teotitlán de Flores Magón, Oaxaca State, Mexico (Figure 1). Inhabitants are mestizo with Mazatec backgrounds.

The local climate is semi-arid with a mean annual temperature between 18 °C and 22 °C. Rain falls intensely and over a short three-week period during summer (July – September) with mean annual precipitations between 600 and 800 mm (INEGI, 2005), leaving the rest of the year dry (INEGI, 2005). The dominant vegetation in the region is thorn scrub forest, with species like *Pachycereus marginatus* (DC.) Britton and Rose, *Cephalocereus columna-trajani* (Karw. ex Pfeiff.) K. Schum., *Mitrocereus fulviceps* (F.A.C. Weber ex K. Schum.) Backeb. ex Bravo, *Plumeria rubra* L., *Bursera morelensis* Ramirez, *B. schlechtendalii* Engl., *B. aptera* Ramirez and *Acacia angustissima* (Mill.) Kuntze, among others (Grupo Mesofilo, 2001).

The cultivated area of Santa María Tecomavaca comprises numerous small-scale and highly diverse farming systems such as multi-species production like milpa (combining maize with squashes and often also beans), extensive fruit orchards of lime or papaya trees as well as intensive short-cycle melon fields. There is an irrigation infrastructure with two main water channels; one brings water from the “Rio Salado”-river which contains high salt levels (river-fed irrigation) and the other gathers fresh water from the adjacent mountain range (rain-fed irrigation). Also farm animals like cows, donkeys, horses and goats form an integral part of these crop production systems. Farmers apply several agrochemical products in their fields to increase productivity and/or to facilitate agricultural management. The most used fertilizers are: urea (46% N), NPK 17-17-17, ammonium phosphate (NP 18-46-0), ammonium sulphate (20.6% N), phosphate-nitrate (NP 20-20-0) and micro-elements (Fe, Mn, Cu, Zn, B, Mo) (Vancraeynest, 2005). Additionally, organic fertilizers such as animal manure is spread out manually, having collected it previously from the corral or family homegarden, or, more naturally, by allowing animals to graze freely on the harvested fields. Herbicides are used principally to prevent competition with the standing or future crop, to control plagues and/or diseases, and to maintain the field easily accessible. The most used herbicides are: Paraquat (contact herbicide) and Glyphosate and 2,4-D (systemic herbicides) (Vancraeynest, 2005). The investigated area measured approximately 36 km^2 and included 7 milpa (average field area 0.96 ha; 4-month cycle), 8 lime (average field area 1.19 ha; 12-month cycle), 6 papaya (average field area 1.38 ha; 14-month cycle) and 7 melon fields (average field area 2.82 ha; 3-month cycle).

Blanckaert et al. (2007) reported a total of 161 weed species in Santa María Tecomavaca in four different farming systems (milpa, lime, papaya and melon). The total list of weeds can be obtained with the first author. Weed management in this work considers not just control or eradication of weeds. It also includes all human interventions towards a weed associated with its utility for food, medicine, or as fodder plants, amongst others, including the simple preservation to the conscious stimulation of the desired plant (population) from the moment the decision is made not to eradicate it (Alcorn, 1981; Casas et al., 1997; Blanckaert et al., 2007). Therefore, weed management was categorized in five main groups (Alcorn, 1981; Casas et al., 1997; Blanckaert et al., 2007): (1) no management or control (i.e. no attention from the farmer and eradicated when needed), (2) tolerated/spared (i.e. not removed by the farmer), (3) protected (i.e. receiving special care from the farmer, for example, eliminating competing weeds around the plant(s) of interest), (4) promoted (i.e. (un)consciously propagated by the farmer) and (5) cultivated (i.e. deliberately sown or planted by the farmer).

The alien weeds of Santa María Tecomavaca were identified by using different taxonomic means (i.e. monographs, flora) including the list of alien plants for Mexico by Villaseñor and Espinosa-García (2004). Classification of native and introduced weeds was according to Pyšek et al. (2004) and Richardson et al. (2000) (Table 1), and applied as follows: (1) casual aliens (occur in only one federal state of Mexico), (2) naturalized plants (appear in more than one federal state but less than ten) and (3) invasive plants (appear in ten or more Mexican federal states). The term ‘transformer’ (Richardson et al., 2000; Pysek et al., 2004) was not applied, as no information was available to document this in Mexico.

Weed utility data (number of uses and management forms), as well as weed presence, abundance, and cover in four different agricultural systems (milpa, lime, papaya and melon), and information concerning the use of agrochemicals (herbicides and fertilizers), were taken from Vancraeynest (2005) and Blanckaert et al. (2007). Fodder plants included only weeds that were specifically managed by the farmer for that purpose. In order to uniformly represent application of agrochemicals in all four farming systems studied in

Santa María Tecomavaca, the amounts of herbicides and fertilizers used were standardized as liters per month per hectare and bags per month per hectare, respectively.

Influence of agrochemicals on exotic weed proportions was assessed by means of χ^2 tests for frequency data and a Multiple Forward Stepwise Regression Model. Dependent variables were proportion of exotic richness per field (PER = number of exotic weed spp./total number of weed spp.), proportion of exotic abundance per field (PEA = abundance of exotic weed spp./total abundance of weed spp.) and proportion of exotic cover per field (PEC = cover of exotic weed spp./total cover of weed spp.) and independent variables were herbicide use and fertilizer use. All tests were executed with SPSS for Windows software, version 11.0 (SPSS Inc., 2001).

Results

Of the 161 species reported in Santa María Tecomavaca by Blanckaert et al. (2007), the origin was determined for 91% (146 spp.). The provenance of 15 weeds could not be determined due to lack of information available.

Weed flora of Santa María Tecomavaca comprised 124 weeds native to Mesoamerica (85%) and 22 exotic weeds (15%) (Table 2). Most exotic weeds (20 spp.; 91%) came from the Old World (comprising Europe, Africa and Asia). Only two species came from elsewhere (Australia and South America). No casual alien weed was found in Santa María Tecomavaca. Eight of the exotics (36%) were naturalized, while 14 species (64%) were identified as invasive (Table 2). Of the 19 weeds identified by local farmers as most perturbing for the local agriculture (Vancraeynest, 2005; Blanckaert et al., 2007), six (31.6%) were exotic species.

Usefulness of native and exotic weeds and their management

The people of Santa María Tecomavaca amply use their non-crop resources without distinguishing between native or introduced weeds. Almost half of the native weeds (56 spp.; 45%), as well as 32% of the alien weeds (7 spp.) had one or more uses. Even though the proportion of useful alien weeds is lower than the proportion of useful native weeds, this difference is not significant ($\chi^2 = 1.36$; df = 1; P<1) (Table 4). Similarly, there was no significant difference in the number of uses ($\chi^2 = 0.48$; df = 2; P<1) (Table 4). It was observed, however, that native weeds presented ten different uses, while alien weeds only had four, indicating that the usefulness of the native weed flora has been more intensively explored by the local people.

The population of Santa María Tecomavaca expressed their interest for weeds in several ways, particularly for edible, medicinal or ornamental purposes (Blanckaert et al., 2007). Approximately 14.2% of all useful weeds received some kind of management. No significant differences were found between the management of native and exotic weeds, neither in the proportion of managed plants nor in the number of management forms ($\chi^2 = 2.04$; df = 1; P<0.2, y $\chi^2 = 4.46$; df = 2; P<0.2, respectively) (Table 4).

Effect of agrochemicals on the presence of native and introduced weeds

The characteristics of the four studied farming systems show an intensity gradient in the use of agrochemicals (herbicides and fertilizers). The lime orchards receive the lowest amounts of agrochemicals. Milpa fields and papaya orchards receive more, but the highest inputs are in the short-cycle melon monocultures (Grupo Mesofilo, 2001; Vancraeynest, 2005; Blanckaert et al., 2007) (Figure 2). Agrochemicals are fairly easy to obtain in the village.

However, the willingness to apply agrochemicals varies strongly between farmers (Figure 3). Factors that influence local decision-making are: its costs, its impact upon the crop, health effects on weed-eating farm animals and the indigenous plant name knowledge of the local weed flora (Vancraeynest, 2005; Blanckaert et al., 2007).

Simple correlations (Pearson's coefficient) revealed a significant positive relation between herbicide use and the proportion of exotic weed richness (PER) (Table 5). Also the Multiple Forward Stepwise Regression Model significantly confirmed this relation ($R^2 = 0.31$; Table 6). Nevertheless**,** no significant model could be generated to represent the behavior of exotic abundance (PEA) or exotic cover (PEC). In summary, these results suggest that, of the two kinds of agrochemical products analyzed in this work, only the use of herbicides causes a direct and significant elevation in the number of exotic weeds. In particular, systemic herbicides (Glyphosate and 2,4-D) seem to play a more important part in this relationship than the contact herbicide Paraquat (Pearson's coefficient $r=0.91$ ($P<0.01$) and $r=0.58$, ($P<0.01$), respectively).

The richness graph (Figure 4A) indicates how particularly the number of native weeds diminishes, while introduced weed numbers remain relatively stable with increased herbicide use. One may suggest that this effect is due to the selective action of the 2,4-D herbicide against dicotyledonous weeds in favor of monocots (e.g. alien grasses). However, our survey included only one farmer applying 2,4-D herbicide on his fields. As such, it seems that native weed diversity is affected by the elevated use of the non-selective systemic herbicide Glyphosate.

Figure 4B indicates that exotic weed abundance is higher than native weed abundance, whereas their cover is again lower than the native weed cover (Figure 4C). This is explained by the dominance of Poaceae (Table 2) in exotic weed diversity, which have small leaves and reproduce fast.

Discussion

Weed flora of Santa María Tecomavaca comprises 85% (124 spp.) native species and 15% (22 spp.) introduced species. As such, despite evidence of invasion, the general weed flora of the semi-arid rural community is still dominated by native weeds. This confirms the former observations of Vibrans (1998) that weed communities in Mexican agriculture have most likely evolved in the Mesoamerican region and are generally not dominated by immigrant species of the Old World. The proportion of native and introduced weeds found in Santa María Tecomavaca confirm the report of Espinosa-García et al. (2004a), with 1549 weeds for the whole federal state of Oaxaca, of which 1331 (86%) are native and 218 (14%) are alien.

Interestingly enough, our data (15%) are also similar to the national proportions of exotic weeds (22%). Hence, invasion reaches one of the floristically most diverse states of the Mexican Republic, and as the study zone forms part of a Biosphere Reserve, this warrants our attention. For example, the native weed flora of Santa María Tecomavaca holds three endemic species of the Oaxaca and Puebla states: *Iresine discolor* Greenm. (Amaranthaceae), *Florestina simplicifolia* B.L. Turner (Asteraceae) and *Sida pueblensis* Fryxell (Malvaceae) (Méndez-Larios et al., 2004; Blanckaert et al., 2007). These three species have disappeared from the most intensive farming system of Santa María Tecomavaca (melon monoculture), whereas two are still found within the more traditional polyculture milpa farming system.

For more than 14 000 years, the inhabitants of the Tehuacán-Cuicatlán region have attained an extraordinary relationship with their natural environment (MacNeish, 1967, 1992). Our small-scale study describes 124 useful native weeds, suggesting that the real number of useful weeds in the whole valley is high (a previous estimate by Casas et al. (2001) calculated 117 species) and which confirms the report of Dávila et al. (2002). On the other hand, exotic weeds are also used by the local habitants. However, the discordant time-span of apprehension towards native and exotic weeds is reflected in the differential intensity of their uses and management forms.

Among other things, our data discloses the need to perform additional small scale invasion studies in Mexico. Even though such surveys evaluate only the local and small-scale impact of introduced weed flora, they are one of the essential pieces complementing the giant jigsaw of future invasive weed control in Mexico. However, the above-mentioned suggestions will only be valuable if the utility of exotic species is also considered, as otherwise farmers might not support eradication without an alternative resource. The cultivation of a weedy kind of the exotic *Sorghum bicolor* grass as a fodder plant is similar to the case of *Cenchrus ciliaris* in the Sonora Desert reported by Espinosa-García (2003). All this indicates that the presence of alien weeds is a complex issue and that any management plan addressing this problem must take into account that some exotic plants may already have been adopted in daily agricultural practice. The future control of such species will be complicated without first evaluating possible native fodder weeds that are able to substitute it.

This paper also highlights the well-documented effect of increasing herbicide use on weed flora diversity, resulting in diminishing weed richness, abundance and cover (Swift et al., 1996; Marshall et al., 2001; Stoate et al., 2001). Herbicide use is differential according to the farming system. Many farmers do not use herbicides, or prefer to combine herbicides with manual weeding (machete or hoe). Vancraeynest (2005) describes that weed residuals are generally left on the fields as green manure and postulates that trade-off between fast-but-expensive chemical weeding and time-consuming-but-cheap manual weeding seems to be regulated by field dimensions. He states that small fields are easily cleaned by hand without chemical aids, but in larger fields manual and chemical weeding is combined, or only chemical weeding is done. Our data confirm this as the largest fields in Santa María Tecomavaca are generally cultivated with melon monoculture or papaya trees, while lime orchards and milpa fields have smaller average surfaces. Indeed, both melon and papaya fields use the highest amounts of herbicides.

The multiple regression model indicates that the use of herbicides directly causes a reduction in the proportion of native weeds in the general weed flora. In particular, it was noted that native weeds are more sensitive to the use of non-selective systemic herbicides like Paraquat and Glyphosate than exotic weeds. As such, we consider that the use of those kinds of herbicides significantly disturbs the equilibrium between the native weeds and invaders. In Santa María Tecomavaca, no strong effect of native weeds was found on the presence, abundance or cover of exotic weeds. It seems that, in human-dominated ecosystems, native weeds richness does not significantly limit invasion of exotic weeds. This tendency is alarming for the weed flora within the Tehuacán-Cuicatlán Biosphere Reserve. Even though native weed diversity is still much higher than exotic weed diversity, the continued use of non-selective systemic herbicides in the future may drastically change this proportion, facilitating the establishment of exotic weeds in the future, causing increased weeding problems.

The local farmers in Santa María Tecomavaca are already familiar with selective plant management practices (Blanckaert et al., 2007), and this awareness should facilitate the incorporation of effective weed control measures against aggressive exotic weed species. However, they should receive more accurate information about the influence of different types of herbicides on native and exotic weed diversity and their effect on the establishment of highly persistent and exotic weed species (Espinosa-García, 2003). In general, Mexico must be encouraged to transform international regulations like the Cartagena Protocol and the Stockholm Convention as well as its own Mexican Official Norms into transparent legislation leading to adequate prevention and control programs that are able to reach the farmers in the rural communities.

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Table 1
Invasion terminology, modified from Pyšek et al. (2004) and Richardson et al. (2000)

Terminology	Definition
NATIVE plant *(Syn: indigenous)*	ORIGINATED IN A GIVEN REGION WITHOUT HUMAN INVOLVEMENT, AND BELONGS TO THE LOCAL FLORA *In this paper:* Originated in Mesoamérica
INTRODUCED plant *(Syn: alien, exotic, non-native, non-indigenous)*	TRANSPORTED FROM ONE REGION INTO ANOTHER (DIFFERENT FROM THE ORIGIN) BY HUMAN ACTIVITY *In this paper:* Transported from the Old World, Australia or South America to Mesoamérica
CASUAL ALIEN	INTRODUCED PLANT REPRODUCING OCCASIONALLY BUT NOT ABLE TO ESTABLISH IN SELF-REPLACING POPULATIONS WITHOUT DIRECT HUMAN INTERVENTION *In this paper:* Introduced plant appearing in only one Mexican Federal State
NATURALIZED plant *(Syn: established)*	INTRODUCED PLANT ESTABLISHED IN SELF-REPLACING POPULATIONS FOR AT LEAST 10 YEARS WITHOUT DIRECT HUMAN INTERVENTION *In this paper:* Introduced plant appearing in >1 and <10 Mexican Federal States
INVASIVE plant	NATURALIZED PLANTS ABLE TO DISPERSE >100 M AWAY FROM PARENTAL PLANTS AFTER LESS THAN 50 YEARS. *In this paper:* Introduced plant appearing in >10 Mexican Federal States

Table 2
Exotic weeds in Santa María Tecomavaca

Family & Species	Origin*	Invasion Status (*sensu* Richardson et al., 2000)
Amaranthaceae		
Achyranthes aspera L.	Old World	Naturalized
Asteraceae		
Sonchus asper (L.) Hill	Old World	Naturalized
Sonchus oleraceus L.	Old World	Invasive
Taraxacum officinale Weber ex F.H.Wigg.	Old World	Invasive
Cucurbitaceae		
Cucumis anguria L.	Old World	Naturalized
Cyperaceae		
Cyperus esculentus L.	Old World	Invasive
Euphorbiaceae		
Ricinus communis L.	Old World	Invasive
Fabaceae		
Medicago polymorpha L.	Old World	Naturalized
Poaceae		
Arthraxon hispidus (Thunb.) Makino	Old World	Naturalized
Cenchrus ciliaris L.	Old World	Invasive
Chloris gayana Kunth	Old World	Invasive
Chloris virgata Sw.	Old World	Invasive
Dactyloctenium aegyptium (L.) Willd.	Old World	Naturalized
Digitaria bicornis (Lam.) Roem. and Schult.	Australia	Naturalized
Echinochloa colonum L.	Old World	Invasive
Eragrostis barrelieri Daveau	Old World	Invasive
Eragrostis cilianensis (All.) Vignolo ex Janch.	Old World	Invasive
Rhynchelytrum repens (Willd.) C.E.Hubb.	Old World	Invasive
Sorghum bicolor (L.) Moench	Old World	Invasive
Sorghum halepense (L.) Pers.	Old World	Invasive
Vulpia myuros (L.) C.C. Gmel.	Old World	Naturalized
Solanaceae		
Nicotiana glauca Graham	South America	Invasive

*Old World (comprises Europe, Africa and Asia)

Table 3
Problematic weeds in Santa María Tecomavaca

EXOTIC WEEDS	Use	Management*	Crop**
Asteraceae			
Sonchus oleraceus L.	Edible	-	Papaya
Cyperaceae			
Cyperus esculentus L.	Medicinal	-	Melon
Poaceae			
Chloris virgata Sw.	-	-	Lime
Echinochloa colonum L.	-	-	Papaya
Rhynchelytrum repens (Willd.) C.E. Hubb.	-	-	Lime
Sorghum bicolor (L.) Moench	Fodder	Tol/Cul	Papaya

NATIVE WEEDS	Use	Management*	Crop**
Amaranthaceae			
Amaranthus hybridus L.	Fodder/Edible	Tol/Pro	Milpa
Asteraceae			
Xanthium strumarium L.	-	-	Papaya
Viguiera dentata (Cav.) Spreng	Fodder/Medicinal/Soil improver	Tol	Lime
Convolvulaceae			
Ipomoea leptotoma Torr.	-	-	Milpa
Ipomoea purpurea (L.) Roth.	Ornamental	Tol/Pro/Cul	Milpa
Merremia quinquefolia (L.) Hallier f.	-	-	Milpa
Loasaceae			
Mentzelia aspera L.	Fodder/Beneficial crop interaction	Tol	Milpa
Malvaceae			
Abutilon mucronatum J.E. Fryxell	Toy	-	Lime
Sida glabra Mill.	Soil improver/Domestic	-	Milpa
Poaceae			
Cenchrus incertus M.A. Curtis	-	-	Lime
Cenchrus longispinus (Hack.) Fernald	-	-	Papaya
Solanaceae			
Solanum rostratum Dunal	-	-	Milpa
Zygophyllaceae			
Kallstroemia hirsutissima Vail	Medicinal	-	Milpa

* Management (Tol=tolerated, Pro=protected, Cul=cultivated)
** Crop (crop production system where weed is dominant)

Table 4
Uses and management forms of native and exotic weeds in Santa María Tecomavaca

	Native weeds (124 spp.)	Exotic weeds (22 spp.)
USEFULNESS		
Useful plants	56 *(45%)*	7 *(32%)*
- with 1 use	43	6
- with 2 uses	10	1
- with >2 uses	3	0
Number of uses	10	4
WEED MANAGEMENT		
Managed plants	20 *(16%)*	1 *(5%)*
- with 1 management form	13	0
- with 2 management forms	3	1
- with >2 management forms	4	0
Number of management forms	4	2

Table 5
Simple correlations (Pearson's coefficient) between herbicide use, fertilizer use, proportion of exotic richness (PER), proportion of exotic abundance (PEA) and proportion of exotic cover (PEC).

	Herbicides	Fertilizers	PER	PEA
Fertilizers	0.487*			
PER	0.554*	0.271		
PEA	0.095	-0.099	0.305	
PEC	0.087	-0.090	0.247	0.931*

$*P<0.0125, \ n = 28$

Table 6
Multiple Forward Stepwise Regression Model summary

	BETA	B	S.E. B	t	P
Constant		0.109	0.019	5.672	0.0001
Herbicides	0.554	0.081	0.024	3.390	0.002

$R = 0.554; R^2 = 0.307; R^2 \text{ adjusted} = 0.280; F_{1,26} = 11.492; P<0.002; S.E. = 0.0743$

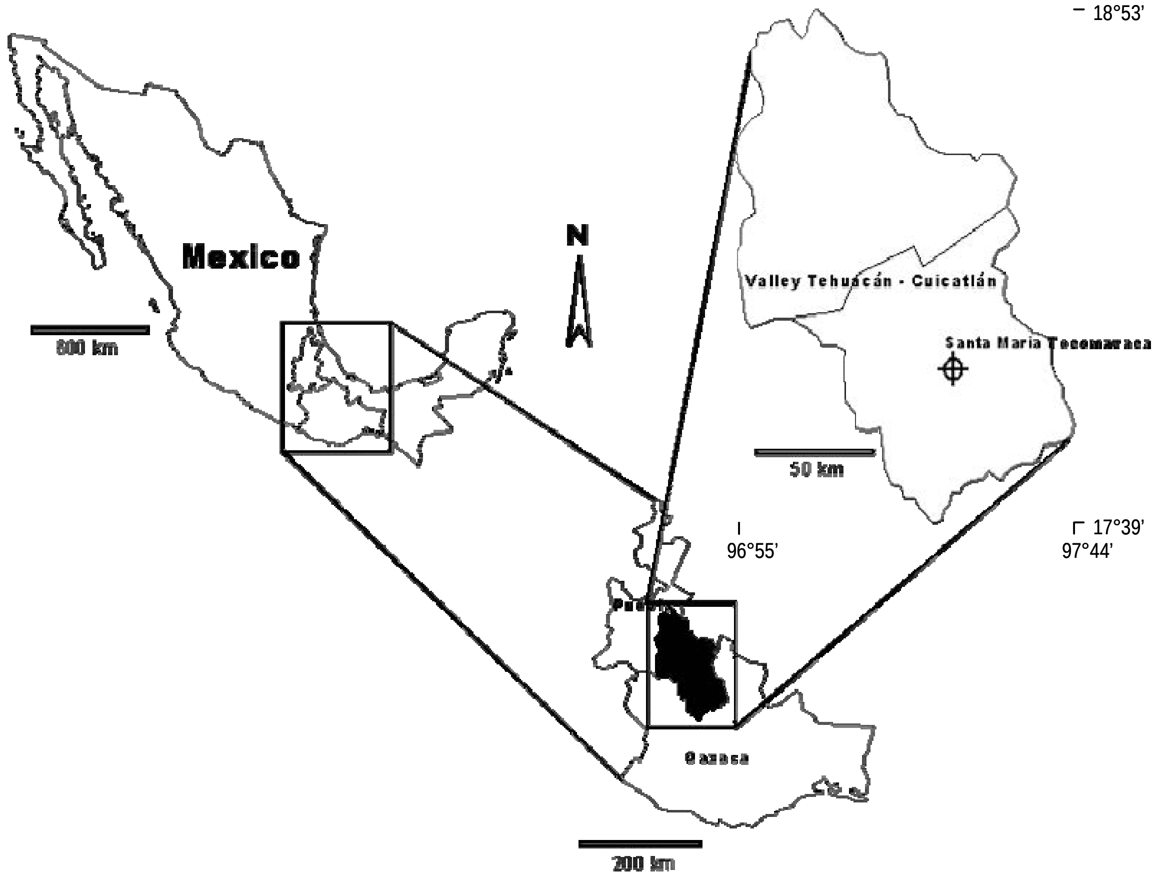

Figure 1
Location of Santa María Tecomavaca in the Oaxaca State, Mexico

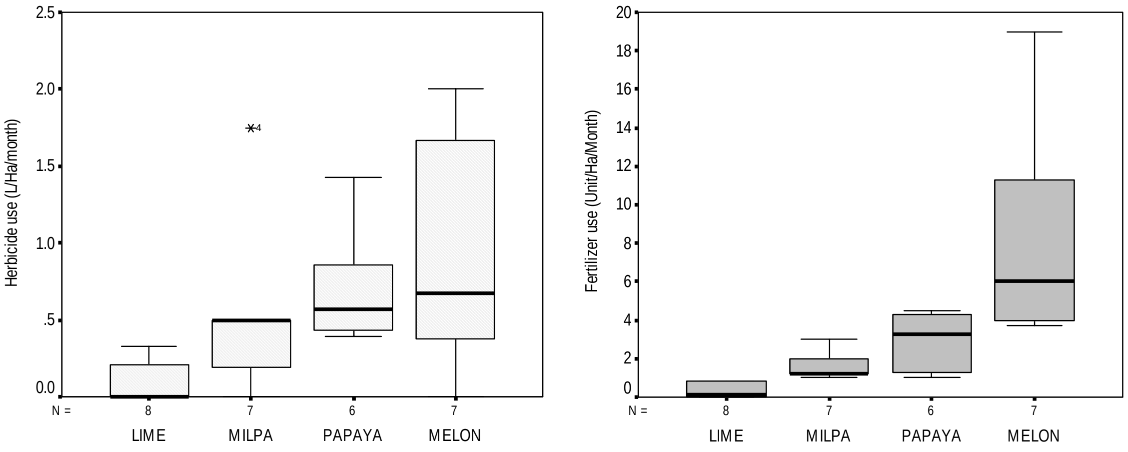

Figure 2
Herbicide and fertilizer use in the four studied farming systems in Santa María Tecomavaca; (Unit = one bag of fertilizer; bold line indicates median, box corresponds with quartile range and whistles indicate extremes)

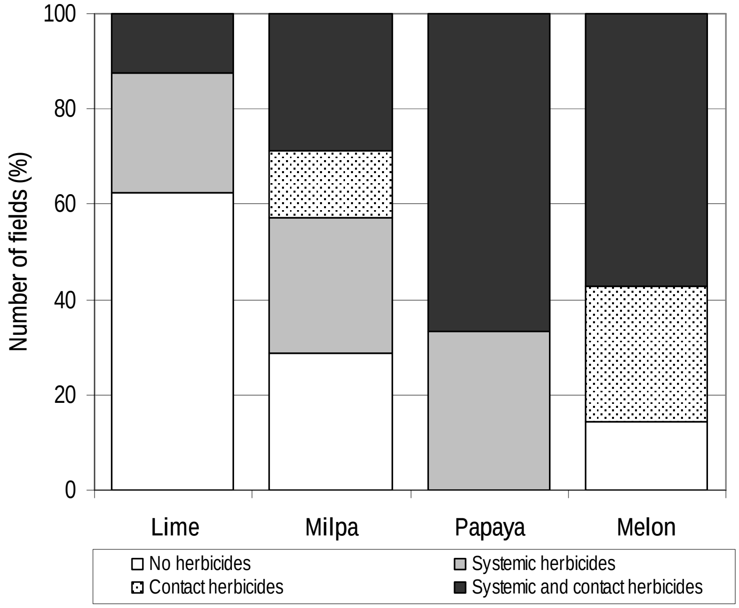

Figure 3
Herbicide use depending on the farming system

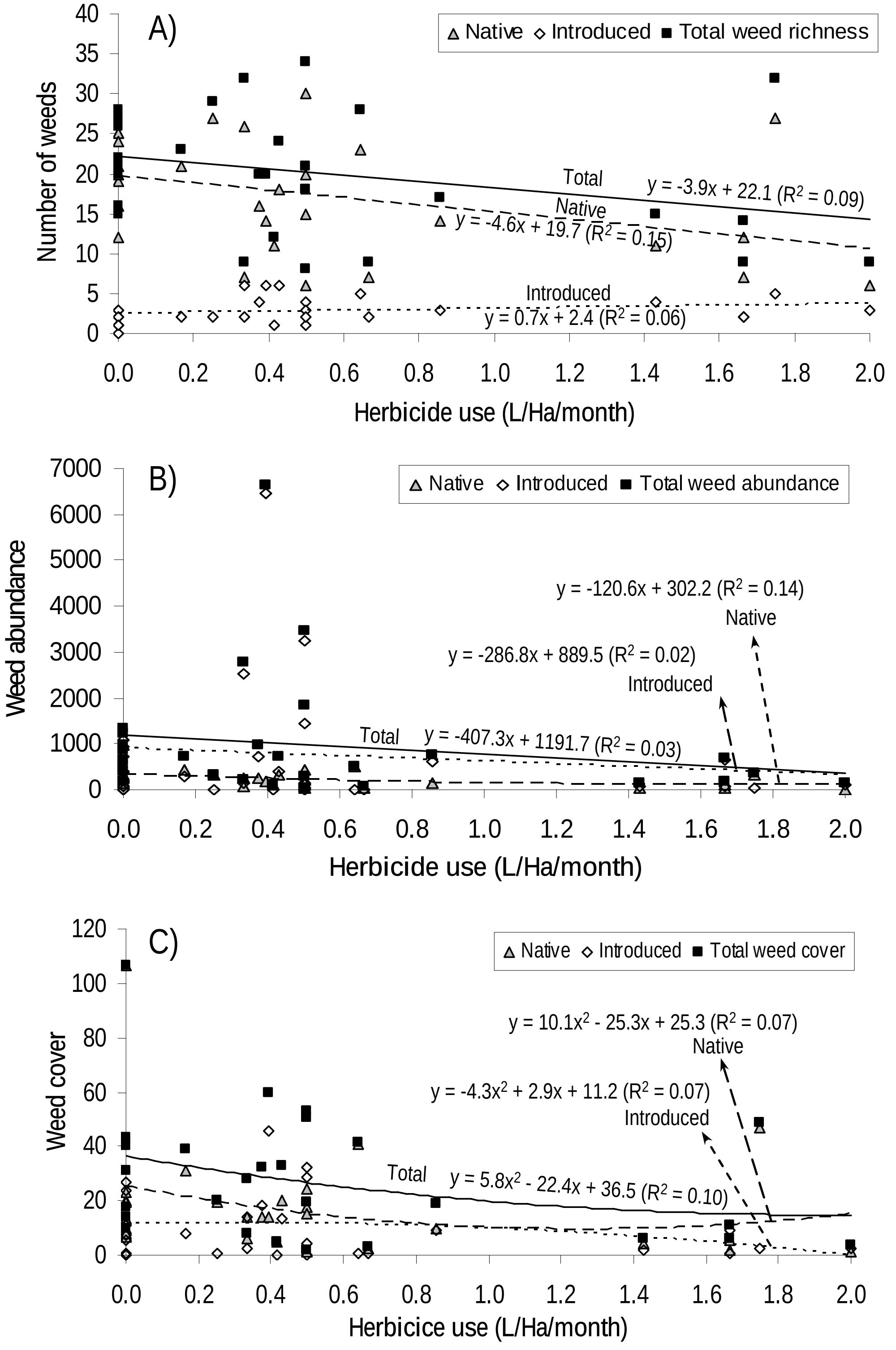

Figure 4
Effect of herbicide use on A) presence, B) abundance and C) cover of native and introduced weeds in Santa María Tecomavaca

Epazote
Chenopodium ambrosioides

Capítulo IV

Indicios de Domesticación Incipiente de Dos Arvenses Comestibles en México Semiárido: Evidencias Etnobotánicas, Morfológicas, Fitoquímicas y Moleculares

Blanckaert, I., Paredes-Flores M., Espinosa-García F.J., Piñero D., Lira-Saade R.
Incipient domestication of two edible weeds in semi-arid Mexico: evidence from ethnobotanical, morphological, phytochemical and molecular data.

Economic Botany (xxxx) xx: xx-xx
En revisión

RESUMEN

Existen pocos estudios que investiguen las etapas iniciales de domesticación para plantas arvenses subutilizadas. En este trabajo, se analizaron evidencias etnobotánicas, morfológicas, fitoquímicas y genéticas para determinar las diferencias entre las poblaciones manejadas y sin manejo de dos especies mexicanas de plantas arvenses: Epazote (Chenopodium ambrosioides L.) y Papaloquelite (Porophyllum ruderale var. macrocephalum (DC.) Cronquist) que crecen en Santa María Tecomavaca, Oaxaca, una localidad de la Reserva de la Biósfera Tehuacán-Cuicatlán. Las evidencias revelaron la existencia de variantes morfológicas asociadas a un gradiente de intensidad de manejo para el Epazote y no para el Papaloquelite. Esta variación está asociada a aparentes preferencias de sabor relacionadas con la disminución de sustancias de defensa química. Estos resultados, además, fueron congruentes con la variación genética encontrada para las mismas variantes. En resumen, aunque el Epazote es un cultivo menor, los resultados derivados de las cuatro fuentes de evidencia analizadas (diferenciación cultural, gigantismo, reducción de defensa química y herencia de caracteres adquiridos), sugieren que actualmente, al menos en la zona de estudio, está bajo un proceso de domesticación incipiente.

Incipient domestication of two edible weeds in semi-arid Mexico: evidence from ethnobotanical, morphological, phytochemical and molecular data.

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Abstract

Few studies have investigated the initial stages of domestication for underutilized weedy vegetables or condiments. We combined ethnobotanical, morphological, phytochemical and genetic evidence to determine differences between managed and unmanaged populations of two Mexican edible weeds: Epazote (*Chenopodium ambrosioides* L.) and Papaloquelite (*Porophyllum ruderale var. macrocephalum* (DC.) Cronquist) in Santa María Tecomavaca, Oaxaca, a community within the Tehuacán-Cuicatlán Biosphere Reserve. The results revealed the existence of morphological variants associated with a gradient of management intensity for Epazote. This variation involved improved palatability correlated with the reduction of chemical defence substances. Most remarkably, these results were congruent with the genetic variation in the same variants. In conclusion, although Epazote is considered a 'minor' crop, the results from the four sources of evidence (cultural differentiation patterns, gigantism, reduction in chemical defences and inheritance of adaptive traits) suggest a current incipient domestication process, at least within the study zone.

Resumen

Existen pocos estudios que investiguen las etapas iniciales de domesticación para plantas arvenses comestibles subutilizadas. En este trabajo, se analizaron evidencias etnobotánicas, morfológicas, fitoquímicas y genéticas para determinar diferencias entre poblaciones manejadas y sin manejo de dos especies mexicanas de plantas arvenses: Epazote (*Chenopodium ambrosioides* L.) y Papaloquelite (*Porophyllum ruderale var. macrocephalum* (DC.) Cronquist) que crecen en Santa María Tecomavaca, Oaxaca, una localidad de la Reserva de la Biósfera Tehuacán-Cuicatlán. Las evidencias revelaron la existencia de variantes morfológicas asociadas con un gradiente de intensidad de manejo para el Epazote. Esta variación está asociada con preferencias de sabor relacionadas con la disminución de sustancias de defensa química. Estos resultados, además, fueron congruentes con la variación genética encontrada para las mismas variantes. En resumen, aunque el Epazote es un cultivo menor, los resultados derivados de las cuatro fuentes de evidencia analizadas (diferenciación cultural, gigantismo, reducción de defensa química y herencia de caracteres adquiridos), sugieren que actualmente al menos en la zona de estudio está bajo un proceso de domesticación incipiente.

Key words

Chenopodium ambrosioides; Epazote; Papaloquelite; Porophyllum ruderale var. macrocephalum; Tehuacán-Cuicatlán Biosphere Reserve; underutilized food crops

Introduction

Ever since the beginning of agriculture, humans have selected, cultivated and harvested plants in different ways around the world. This has resulted in a continuous array of intermediate phases between wild, weedy, cultivated and domesticated plants, depending on the degree of their relationship with man. The process of domestication is gradual, continuous and multidirectional (Bye 1993; Hernández-Xolocotzi 1993, Rindos 1984). Hence, unraveling its complex pathway is not an easy task, and in particular few studies have analyzed the differences between unmanaged and managed populations in the first stages of the domestication process (Sultan 1995).

Weeds, in particular, are generally unwanted (Harlan and deWet 1965), but in Mexico, for example, traditional farmers tolerate the presence of certain useful weedy herbs among their crops (Chacón and Gliessman 1982). Moreover, they tend to tolerate, protect or promote these plants during agricultural activities (Davis and Bye 1982; Hernández-Xolocotzi 1993), while others transplant or inclusive cultivate them in their family homegarden (Blanckaert, et al. 2004). Various studies describe this symbiotic relationship between people and useful weeds and present evidence for the initial phases of plant domestication (*Lepidium virginicum* L. (Bye 1979), *Ibervillea millspaughii* (Cogn.) J. Jeffrey, *Melothria pendula* L. (Lira and Casas 1998), *Jaltomata procumbens* (Cav.) J.L. Gentry (Davis and Bye 1982), *Porophyllum ruderale* var. *macrocephalum* (DC.) Cronquist (Vázquez Rojas 1991), *Solanum nigrescens* M. Martens and Galeotti, *Phytolacca icosandra* L., *Chenopodium berlandieri* Moq. (Bye 1993), *Amaranthus* spp. (Mapes, Basurto and Bye 1997), *Anoda cristata* (L.) Schl. (Bye 1993; Rendón and Núñez-Farfán 2001), *Proboscidea* *louisianica* (Mill.) Thell. subsp. *fragans* (Lindl.) Bretting (Paredes-Flores 2006), amongst others).

Undoubtedly, the role of seeds and fruits is extremely important in the subsistence of both modern and ancient societies, but vegetables or minor crops seem to receive less credit than they deserve (IPGRI 2002). In different parts of the world, non-commercial edible greens bring variety to the traditional basic diet since thousands of years, providing otherwise absent vitamins and nutrients (Bye 1981; Ertug 1997; Picó and Nuez 2000) or condiments that preserve food (Sherman and Billing 1999). Additionally, although these edible greens are generally harvested for own consumption, occasional surplus is often sold on the local market, strengthening family subsistence (Vieyra-Odilón and Vibrans 2001). However, most studies on incipient domestication focus on plants whose used parts are related with the reproductive system (fruits and seeds), overlooking species with edible leaves, stems, roots, petioles or other vegetative structures used as food or condiments.

From an evolutionary viewpoint, edible vegetables – which by definition lack defense mechanisms - can only be domesticated after people had already begun protecting plants within the agroecosystem (Vavilov 1926). At present, three different models try to explain the domestication of herbaceous vegetables (Rindos 1984:145-150) postulating different degrees of physiological, morphological and phytochemical changes indicators for the domestication process. However, despite the possible routes to domestication of herbaceous vegetables, it remains difficult to predict their evolutionary pathway under human management. Each species has a unique biology and morphology and responds differently to selective forces. In fact, each event of plant domestication should be considered individually.

The aim of this work was to identify possible indicators of incipient domestication of two edible, aromatic greens (*Porophyllum ruderale* var. *macrocephalum*: Asteraceae and *Chenopodium ambrosioides*: Chenopodiaceae) in Santa María Tecomavaca, a small village in rural, semi-arid Mexico where useful weeds have been studied previously (Blanckaert, et al. 2007). The species studied here were selected because they have been used since Pre-Hispanic times (Lozoya and Lozoya 1982:31-44; Picó and Nuez 2000), they grow both in the natural vegetation and within human-disturbed habitats, they receive different forms of human manipulations with various degrees of intensity, and local people recognized different variants which receive different appreciations (Blanckaert, et al. 2007). First, the intensity and directions of artificial selection in the study zone were determined, followed by experimental cultivation under fixed conditions to determine changes in morphology and phytochemistry, and last, by analyzing inheritance of possible effects in managed and unmanaged populations.

Botanical description of the studied plant species

Porophyllum ruderale var. *macrocephalum* (DC.) Cronquist (Asteraceae, Tageteae tribe, subsection Tagetinae) is native to the desert highlands of Mesoamerica (Johnson 1969; Strother 1977) and distributed from the southeast of the United States of America to Peru and Brazil. Several *Porophyllum* spp. are know as “Papaloquelite”, derived from the indigenous Náhuatl language (“papalo”=butterfly, “quilitl”=edible herb; Bretting and Hernández 1982). In Mexico, it is a common weed and its raw edible stems and leaves have been used as condiments and in folk medicine for more than 500 years (Bretting and Hernández 1982; Picó and Nuez 2000). At present, they are still cultivated commercially in south-central Mexico (Vázquez Rojas 1991). Botanically, it is described as follows: monoecious, annual, herbaceous, erect, slightly green-bluish; stem branched in the superior part, striate; leaves simple, opposite or alternate, thin, ovate to obovate, rarely lanceolate or oblanceolate; sinuate with a gland in each sinus and one on the apex; leaf surface with or without glands; apex rounded, base generally rounded, sometimes attenuate; heads solitary, terminal; peduncles erect, clavate; phyllaries 5, green-purple, with two lines of linear glands, apex obtuse, rarely acuminate; flowers perfect, actinomorphic; corolla puberulent, purple to olive green, tube narrow, infundibuliform; pappus straw-coloured to brown; bristles scabrous; achenes hispid (Johnson 1969). It is a diploid species with chromosome number 2n = 22 (Strother 1983).

Chenopodium ambrosioides L. (Chenopodiaceae, Chenopodieae tribe, Ambrina section), also known as *Teloxys ambrosioides* (L.) Webster., is commonly classified under the *Chenopodium* genus, although it has recently been grouped within the *Dysphania* genus (Mosyakin and Clemants 2002). The *Chenopodium* genus comprises several useful species, used as food, condiment and/or medicine. Some domesticates are the European *C. album* (Fat hen; Nesbitt 2005) and *C. bonus-henricus* L. (Good King Henry; Gröll 2001), the Mexican *C. berlandieri* ssp. *nutalliae* Saff. (Huauzontle; Wilson and Heiser 1979), and the Andean *C. quinoa* Willd. (Quinoa; Wilson 1990). *Chenopodium ambrosioides* is native to the Mesoamerican region, and has been utilized in its traditional cuisine and in folk medicine since prehispanic times (Lozoya and Lozoya 1982:31-44; Picó and Nuez 2000). The active component responsible for the anthelmintic properties of Epazote oil has been identified as ascaridole (Gupta, et al. 2002; MacDonald, et al. 2004; Pino, et al. 2003). At present, it is still commercially cultivated in northern and central Mexico, where it is commonly known as “Epazote”, a term with Náhuatl origin (“epátl”=skunk, "zotli"=herb) (Lozoya and Lozoya 1982:31-44). It is also cultivated in other parts of the world. Botanically, this species is described as an annual or perennial herbaceous plant, erect or ascending, strongly odorous, glandular; stem simple or branched; leaves petiolate, oblong and lanceolate, sub-entire or sinuate-dentate; inflorescences spicate with numerous flowers in manner of pyramidal panicle, with or without intermittent leaves; perianth glandular, surrounding the fruit; pericarp thin, easily released, glandular; seed horizontal or vertical with obtuse margin, black, shiny and smooth (Lozoya and Lozoya 1982:31-44). It is a diploid species with chromosome number 2n = 32 (Schwarzová 1993).

Materials and methods

Mexico lies within one of the world's most important centres of plant domestication (Bye 1993; Hernández-Xolocotzi 1993), and, in particular, the Tehuacán-Cuicatlán Biosphere Reserve, a semi-arid valley in central Mexico, is considered one of its most diverse and culturally important regions (Dávila, et al. 2002; MacNeish 1992). At present, more than 800 plant species are used by the locals (Casas, et al. 2001; Paredes-Flores, Lira and Dávila n.d.) and several works document different levels of interactions between local inhabitants and their surrounding natural resources (Avendaño, et al. 2006, Blanckaert, et al. 2004; Paredes-Flores, Lira and Dávila n.d.; Rodríguez-Arévalo, et al. 2006).

This study was elaborated in Santa María Tecomavaca, a rural community within the Tehuacán-Cuicatlán Biosphere Reserve (1813 inhabitants (INEGI 2000), 17°57'48''N and 97°00'26''W, elevation 612 m above sea level). Inhabitants are mestizo with Mazatec backgrounds. The semi-arid climate presents mean annual temperatures between 18°C and

22°C, and intense rain fall over a short three-week period during summer between 600 and 800 mm (INEGI 2005), leaving the rest of the year dry. The dominant vegetation in the region is thorn scrub forest (Grupo Mesofilo 2001), with *Pachycereus marginatus* (DC.) Britton and Rose, *Cephalocereus columna-trajani* (Karw. ex Pfeiff.) K. Schum. and *Bursera morelensis* Ramirez, amongst others. Agriculture consists of numerous small-scale and diverse farming systems, supported by an irrigation infrastructure, both river- and rain-fed.

Ethnobotany

Following the guidelines of participative observation (Alexiades 1996) free and semi-structured interviews were conducted, collecting information of the informants (personal dates, socio-economic situation), as well as local names, uses, plant parts used, manner of preparation, plant variants recognized and management forms for *C. ambrosioides* and *P. ruderale* var. *macrocephalum*. In this work, incipient management considered all human manipulations of the plant of interest, from simple preservation to conscious stimulation (Alcorn 1981; Blanckaert, et al. 2007, Casas, et al. 1997). Three groups were defined: (A) not managed or wild, (B) incipient management, including (1) tolerated/spared = allowed to grow by the farmer, or (2) protected = allowed to grow and receiving special care from the farmer, and (C) intense management, including (1) promoted = (un)consciously propagated by the farmer, or (2) cultivated = deliberately sown or planted by the farmer.

Experimental cultivation

Seeds from all variants (two variants per species were recognized by informants) and under all management forms were collected from different plant populations (natural vegetation, homegardens and agricultural fields). The investigated area measured approximately 36 km^2. Due to low abundance of the investigated species, seeds were collected by hand from all available mature individuals in each population. Collected seeds were conserved in paper bags under stable environmental conditions. Prior to cultivation, seed germination capacity was determined according to the standards regulated by the International Seed Testing Association (ISTA 1976:16-22).

The experimental plot was a five-repeated random block design. Treatments consisted of two factors: (A) variant and (B) management form. Each species had five treatments: (1) coloured variant + wild, (2) coloured variant + incipient management, (3) white variant + wild, (4) white variant + incipient management and (5) white variant + intense management. Treatments were assigned at random.

In September 2004, seeds were sown in black plastic germination bags filled with local soil substrate and under homogeneous conditions in Santa María Tecomavaca. For each treatment, 100 bags were prepared, totalling 500 bags per species. In each germination bag, five to ten seeds were placed 1 cm deep and irrigated manually. After germination, seedlings were thinned and weeded. A fence was constructed against predation from iguanas (*Iguana iguana* and *Ctenosaura pectinata*) and birds. Insecticide (Foley©) was applied regularly around and inside the cultivated area against leaf-cutting ants (*Atta mexicana*) and crickets (Gryllidae), while salt traps protected against slugs. Cultivation started in September 2004, and ended in December 2004.

Morphology

Non-destructive morphology measurements were performed on one randomly labelled plant in each quadrant (five plants per treatment). For *P. ruderale* var. *macrocephalum*, they included plant height, total leaf cover, stem colour, stem thickness, number of leaves, leaf width, leaf length, number of glands per leaf lamina, number of glands per leaf margin, petiole length, number of inflorescences, inflorescence width, inflorescence length, peduncle length, viable (black) fruits per inflorescence, empty (white) fruits per inflorescence, fruit length, seed length, seed width and seed thickness. For *C. ambrosioides*, measurements were: plant height, total leaf cover, stem colour, stem thickness, stem trichomes, trichome density, internode distance, leaf width, leaf length, number of teeth, tooth length and tooth width. All metric measurements were done with a digital calliper. Afterwards, the measured plants were harvested, bagged individually and dried to obtain dry weight of each plant part. In total, 32 morphological characters for *P. ruderale* var. *macrocephalum* (all continuous) and 20 for *C. ambrosioides* (17 continuous and 3 categorical) were measured.

Phytochemistry

Fresh material (500g coming from at least 20 plants) was collected for each treatment, sealed in plastic bags and transported on ice to the phytochemistry laboratory in the F.E.S.-Iztacala, U.N.A.M. Essential oils were extracted by means of steam distillation and the components were identified and quantified through gas chromatography/mass spectrometry.

Genetics

From five plants per treatment of *C. ambrosioides*, ten mature and undamaged leaves were harvested and freeze-dried in liquid nitrogen. Also leaf material from ten offspring seedlings (two per treatment) was included. Total genomic DNA was extracted according to the procedures described by Doyle (1991). Based on sequence simplicity, multiple amplification and polymorphisms, five microsatellite primer sequences were selected from the library published by Mason et al. (2005): QCA026, QCA051, QCA058, QCA065 and QCA076. All amplifications were performed with a touchdown amplification protocol as described in Maughan et al. (2004), with minor modifications. PCR products were separated with 6% polyacrylamide gel electrophoresis, run in 0.5x TBE. PCR products were visualized by silver staining and stored dry.

Statistics

Morphology data were analysed by SAHN Cluster Analysis and Principal Component Analysis (PCA) to identify patterns, followed by Discriminant Function Analysis (DF) and Multivariate Analysis of Variance (MANOVA) to determine significant effects. All data matrixes were standardized. Cluster analysis was performed with correlation coefficient and UPGMA method. Essential oil composition was analysed by Kruskal-Wallis tests. PCR band patterns were codified as presence/absence (code 1 and 0, respectively) and analysed by SAHN Cluster Analysis. All analysis were performed using the statistical software packages of NTSYSpc, version 2.0 (SAHN Cluster and PCA), SPSS for Windows, version 11.0 (DF and Kruskal-Wallis) and STATISTICA for Windows, version 5.1 (MANOVA) (Rohlf 1997, SPSS Inc. 2001, Statsoft Inc. 1998).

Results

Tracking down artificial selection

PAPALOQUELITE (*Porophyllum ruderale* var. *macrocephalum*)

In Santa María Tecomavaca, the name "Papaloquelite" or "Pápalo" was used for two distinct *Porophyllum* species: *P. ruderale* var. *macrocephalum* and *P. punctatum* (Mill.) S.F. Blake, of which only the first species was edible. All informants (100%) acknowledged the direct consumption of its fresh leaves, whereas some also mentioned its use in certain dishes (3 informants; 8%). One informant mentioned its benefits as a fodder plant and another informant its application in traditional medicine against respiratory problems.

Two variants of edible Papaloquelite were identified. The first variant received the names: "blanco" (white), "verde" (green), "criollo" (creole), "delgado" (thin) or "hembra" (female). The other variant was known as: "colorado" (reddish), "rojo" (red), "morado" (purple), "rosado" (reddish to pink) and "grueso" (thick). Informants identified Papaloquelite variants mainly by colour (40%), colour + smell/taste + habitat (27%), colour and leaf dimensions (12%), leaf dimensions + habitat (7%), colour + habitat (7%) and leaf dimensions (7%). Notwithstanding, the authors often had difficulties to identify these variations in the field (pers. obs.). Of all interviewees, only 40% recognized both variants. Of them, 47% preferred to consume the white variant (better taste, less pungent), while 20% claimed to like the coloured variant better, and 33% had no preference at all. On the other hand, however, the remaining 60% of the informants recognized only one kind of Papaloquelite and some of these persons even claimed that the above-mentioned variants are the product of small-scale differential environmental conditions, such as exposition to direct sunlight or particular soil conditions.

Approximately 70% of the informants grew Papaloquelite in their homegarden and/or agricultural fields. Most people claimed to grow the white variant (67%), but, as was suggested by the arguable identification of Papaloquelite variants described above, 33% of the informants did not know which kind they grew. Most Papaloquelite plants (71%) grew spontaneously in the homegarden or field, while others were sown (18%) or transplanted (11%). The first seeds were generally collected from the natural vegetation (60%), but sometimes bought (20%) or gifted from friends or family (20%). Not one informant eliminated seedlings or plants from a less preferred variant in order to favour the preferred one. Many informants (64%) took special care of the Papaloquelite plants in their homegardens, by watering, weeding and fencing against free-roaming animals. No chemical control against leaf-cutting ants (*Atta mexicana*) was needed. In Santa María Tecomavaca, maintaining subsequent generations of Papaloquelite plants in the homegarden is not an easy task as this plant quickly dehydrates after flowering. As such, many informants eliminated these inedible remains before seeds were able to mature. However, others (50%) did allow their plants to produce and shed seeds. They often also made sure to prepare an appropriate seedbed under the plants and often shook mature plants to stimulate seed fall, followed by irrigation and weeding around the newly emerged seedlings.

Although Papaloquelite is broadly recognized as an edible herb used as a condiment, approximately 18% of the informants did not like its typical taste and did not consume it. Half of the informants (52%) consumed its leaves occasionally, whereas 30% of the informants expressed the importance of this plant in their personal basic alimentation, consuming it once or twice a week, or even daily.

EPAZOTE (*Chenopodium ambrosioides*)

In Santa María Tecomavaca, the name "Epazote" was used for *Chenopodium ambrosioides*. All informants (100%) acknowledged the consumption of its leaves, whereas 78% also recognized its medicinal use against intestinal worms (tea), scorpion stings (ground with salt), pain (tea), and haemorrhoids (local application). Occasionally, it was mentioned that the daily consumption of Epazote improves the memory of children.

Two Epazote variants were recognized. One was known as: "blanco" (white) or "verde" (green). The other was called: "colorado" (reddish), "rojo" (red), "morado" (purple) or "oloroso" (odorous). Epazote variants were distinguished by colour + smell/taste (63%), colour (20%), smell/taste (9%), colour + smell/taste + leaf dimensions (4%), colour + leaf dimension (2%) and colour + smell/taste + leaf dimension and number + seed number (2%). In contrast with Papaloquelite, the authors were able to distinguish the above-mentioned variations in colour, smell/taste and leaf dimensions in the field (pers. obs.). Also, almost all informants (94%) acknowledged the existence of both Epazote variants. The majority of them (87%) preferred to consume white Epazote, whereas 13% claimed not to have any specific preference and consumed both.

Approximately 90% of the informants grew Epazote plants in their homegarden or agricultural field, of which 73% grew only the white one, 24% had both kinds and 2% claimed to have only coloured Epazote. Half of the informants (52%) said that the plants came to grow spontaneously in their homegarden/field, while 45% specifically sowed the first plants and 5% first transplanted a mature plant. Most often, first seed were gifted from family or friends (86%), or bought on the market (14%). Almost one third of the informants (27%) indicated that they eliminate the coloured Epazote from their garden, in favour of the white one, while 73% denied such activity.

All informants with Epazote plants in their homegarden took special care of the plants, mostly through irrigation in combination with weeding, fencing against free-roaming animals and chemical control against leaf-cutting ants (*Atta mexicana*). Unlike annual Papaloquelite, Epazote does not dry out after flowering. In consequence, its leaves remain edible and most homegarden owners allow their Epazote plants to produce seeds. They occasionally shake the plants to stimulate seed fall, followed by pruning to allow fast germination. Finally, the seedbed is then irrigated and new seedlings are protected by weeding.

Just like Papaloquelite, Epazote is widely recognized as an edible herb and applied as a spice. However, its flavour was more appreciated by the villagers. All informants consumed its leaves once or twice a week or even daily and not one informant disliked its scent.

Artificial selection: 1. morphological evidence

Human artificial selection may be directed towards specific morphology changes in the plant parts of interest (Rindos 1984). However, for *P. ruderale* var. *macrocephalum*, the SAHN Cluster and PCA graph did not show clear patterns (data not shown). In contrast, distinct results were obtained for *C. ambrosioides*. The Cluster Analysis (r = 0.86) clearly divided the Epazote accessions in three main groups (Figure 1). The first group (I) contained all red variants and the white variants under incipient management; the second group (II) contained the wild white variants and the third group (III) contained the white variants under intense management.

These groupings were confirmed by PCA and MANOVA (Figure 2 and Table 1). The first, second and third principal axis explained 55.6%, 18.6% and 14.0% respectively of the total variation among Epazote accessions. The first principal component separated two groups: (I) all red variants and the white variants under incipient management, and (II+III) wild and intensely managed white variants. This separation was based upon characters related to leaf form and dimension (leaf length: $F_{4,20} = 21.26$, $P<0.001$ and tooth number: $F_{4,20} = 240.03$, $P<0.001$), trichome number/cm stem ($F_{4,20} = 33.55$, $P<0.001$), plant height ($F_{4,20} = 3.93$, $P<0.05$) and parenchyma colour (Table 1). As such, the (II+III) group (wild and intensely managed white Epazote) had higher plants with larger leaves which presented more teeth, while stems had more trichomes and greener parenchyma inside. The second principal component seemed to separate the first group (I) into two subgroups: (I_1) all the red variants, and (I_2) the white variants under incipient management. However, no significant quantitative characteristics were found responsible for this separation besides stem colour (factor loading 0.66). As such, the (I) group remained complete, with the red and white Epazote having a red and more reddish-greenish stem, respectively. The third principal component separated the second group (II+III) into two subgroups under different human management intensity: (II) wild white Epazote and (III) intensely managed white Epazote. This separation was based upon characters related with leaf dimensions (leaf width: $F_{4,20} = 7.54$, $P<0.001$; tooth length: $F_{4,20} = 21.15$, $P<0.001$ and tooth width: $F_{4,20} = 46.66$, $P<0.001$)

(Table 1). As such, the intensely managed white Epazote had broader leaves with larger and broader teeth than the wild white Epazote.

In conclusion, the combined effect of the three first components separated the same three main groups among the Epazote accessions as the cluster analysis: (I) all the red variants, both wild and under incipient management, together with the white variants under incipient management, (II) the wild white variants and (III) the intensely managed white variants. The Discriminant Function Analysis confirmed these results by indicating significantly different groups (Wilks' Lambda = 0.000 (P<0.001) and the three first functions explained 99.9% of variation). Figure 3 illustrates the leaf morphology of a wild red Epazote and the cultivated white variant.

Although the three Epazote groups are morphologically distinct, our measurements of Epazote plant height, leaf length and leaf width fall within the values reported previously for this species in several Floras (Table 2). However, the leaf length of all the wild and cultivated Epazote plants (except one) was found larger (13.3-16.0 cm) than the most extreme value reported before (12 cm).

Artificial selection: 2. Phytochemical evidence

Human artificial selection for edible aromatic plants is generally directed towards better flavour and odour, which is caused by a diminution in the concentration of strong scented components in the essential oil (Rindos 1984). However, in all accessions of *P. ruderale* var. *macrocephalum*, approximately 90% of the essential oil consisted of D-limonene, a terpene characterized by a strong smell of oranges and used in the food industry, cleaning products, as paint stripper and botanical insecticide. Additionally, small fractions of βphellandrene, β-myrcene and ocimene were found, all having a strong scent as well. No significant differences were found among accessions. There is no evidence that the composition of the essential oil of the different morphs of *P. ruderale* var. *macrocephalum* is influenced by human management.

In contrast, the components responsible for flavour and odour in the essential oil of *C. ambrosioides* were: *p*-cymene, α-terpinolene, 2-carene, δ-3-carene, *d*-limonene, thymol, ascaridole, pulegone and farnesyl acetone. The studied accessions of Epazote show variations in the concentration of these nine components (Figure 4 and Table 3). Most importantly, there is a strong reduction of compound concentration towards the white cultivated Epazote. However, data limitations prevented us to determine the significance of this effect. Ascaridole, a toxic compound to humans (MacDonald et al. 2004), was not detectable in the white cultivated epazote and in the white variant under incipient management, but it was clearly present in the other variants. All Epazote accessions belonged to the same chemotype dominated by 2-carene, p-cymene and α-terpinolene and not to the more common described ascaridole-chemotype (Gupta, et al. 2002; Pino, Marbot and Real 2003).

Artificial selection: 3. Genetic evidence

Differentiation among populations may be induced by environmental differences and not only by human selection pressures (Rendón and Núñez-Farfán 2001). Also, artificial selection has no evolutionary power if induced changes are not passed on to the next generations and fixed in the genetic code. We sought genetic differences in variants of *C.*

ambrosioides only, as *P. ruderale* var. *macrocephalum* did not show significant morphological or phytochemical variants.

All five selected microsatellite markers amplified successfully with *C. ambrosioides* DNA, and polymorphisms were detected with one marker (QCA076). The most remarkable result derived of this source of evidence was that Cluster Analysis (Figure 5) distinguished similar groupings as in the morphology assessment. Thus, group 1 includes wild white Epazote; group 2 is formed by intensely managed white Epazote, while group 3 contains all red Epazote and the white Epazote under incipient management. Interestingly, these results were also unaltered in seedlings from the next generation, for only one white Epazote accession under intense management was wrongly classified (Figure 5).

Discussion

This study evaluated four sources of evidence for present-day artificial selection pressures on two aromatic, edible Mexican weeds used as vegetables since Prehispanic times in the context of incipient domestication. A schematic overview of the results obtained from these sources of evidence is shown in Table 4, and will form the base of the following discussion.

The local nomenclature in Santa María Tecomavaca for *Chenopodium ambrosioides* (Epazote) and *Porophyllum ruderale* var. *macrocephalum* (Papaloquelite or Pápalo) was similar to terms found in previous reports on plant resources from Tehuacán-Cuicatlán and some other regions (Blanckaert, et al. 2004; Bretting and Hernández 1982; Calderón de Rzedowski and Rzedowski 2001:119; Correll, et al. 1979:533; Lozoya and Lozoya 1982:31; Pino, Marbot and Real 2003; Picó and Nuez 2000; Standley and Steyermark 1946:140; Vázquez Rojas 1991). However, the detailed cultural descriptions presented in this paper illustrated more thoroughly the interests of the local inhabitants and postulated the biological characters that may or may not present future changes through selection pressures executed in the study zone.

Although consumption of *P. ruderale* var. *macrocephalum* (Papaloquelite) was culturally adopted within the whole study area, the existence of differentially appreciated Papaloquelite variants was not generally agreed upon and based mainly on morphology and not so much on taste or smell. Even though *P. ruderale* var. *macrocephalum* was cultivated within homegardens, there were no significant morphological or phytochemical changes between supposed Papaloquelite variants from the study zone. This result, confirms the data obtained by Vázquez Rojas (1991) for the same species in another region of Mexico (state of Guerrero). Moreover, the essential oil composition of Papaloquelite was similar to previous studies, with limonene as its dominant compound (Barbosa Bezerra, Andrade-Neto and Mendes de Freitas 2002; Guillet, Bélanger and Arnason 1998). To our knowledge, there are no reports of different chemotypes for this species.

The uses of *C. ambrosioides* (edible and medicinal) were widely acknowledged in the studied community and its taste was broadly appreciated by the villagers. Nevertheless, in contrast with Papaloquelite, the two Epazote variants were clearly recognized in the community, and local identification was based on morphology, taste and smell. Moreover, there was a strong preference for the consumption of one variant (white Epazote), whereas, to a less extent, the coloured Epazote was considered more effective when used for medical applications than the white one. Indeed, the red Epazote variants from our study presented small amounts of ascaridole, the well known antihelminthic component of Epazote (Gupta, et al. 2002; MacDonald, et al. 2004; Pino, et al. 2003). On the other hand, the white cultivated and under incipient management did not show detectable amounts of ascaridole. Taking into accaount that ascaridole is toxic to humans (MacDonald, et al. 2004) and cattle (Espinosa-García and Díaz-Pérez 1996), this may be the result of artificial selection towards low toxicity.

Although white Epazote is the preferred variant, many people prefer to secure the availability of any kind of Epazote to prevent times of scarcity. In fact, the multiple cropping of a wide variety of domesticates and local landraces together with useful weeds and wild plants within orchards or homegardens is a tradition with a large cultural history in the whole Mesoamerican region, which does not only make the best possible use of the available soil and space (Blanckaert, et al. 2004; Hawkes 1983), but also lowers the risk of complete harvest loss and anticipates future needs (Baskin 1997).

On the other hand, the differential preference for the Epazote variants was reflected in the way the local inhabitants managed these plants. Almost one third of the informants actively eliminated the less preferred (red) variant from their homegarden, resulting in a positive selection for the white Epazote variant in the homegardens of Santa María Tecomavaca. Also, only the white Epazote variant was found under cultivation, while red Epazote was found tolerated and protected but never promoted or cultivated. These different management intensities for the Epazote variants were reflected in their morphology. All red variants were morphologically identical, independent from management intensity (wild, tolerated or protected). The wild and cultivated white Epazote plants were morphologically distinct from the red variants and have significantly larger leaves. A small group of tolerated/protected (incipient management) white Epazote plants were morphologically similar to the red plants, presenting only slightly greener stems and slightly broader leaves.

The possibility exists that this group is the result of hybridization between red and white variants as they coexist in the same habitat and undergo incipient management forms like tolerance and protection, which imply weaker directive selection forces than cultivation. In conclusion, human management has selected for three morphologically distinct groups, a wild group without management, an intermediate tolerated/protected group, and a cultivated group under intense management.

Even though we found significantly different Epazote morphs, almost all phenotypic changes reported in this paper still fall within the natural limits of plasticity as reported in many floristic works. Only leaf length, which is a significant feature in the identification of cultivated white Epazote, had larger values than any former report. This illustrates the urgent need for a detailed taxonomic revision of *C. ambrosioides*, taking into account the morphological differences that may result from human selection in the context of plant domestication. Considering the large history of human-plant interactions in Mesoamerica, and the native origin of this species in the region, *C. ambrosioides* would be an excellent candidate to realize a complete review within its whole distribution area.

The phytochemical evidence is relatively congruent with the ethnobotanical and morphological evidence presented above. Even though all Epazote accessions belonged to the same chemotype dominated by 2-carene, *p*-cymene and α-terpinolene, the concentration of strong scented compounds varied among the accessions. In particular, there is a strong decrease in the white cultivated Epazote. Although we were unable to determine significant effects, these results confirm that the white cultivated variant has a softer scent and a more pleasant taste and showed no ascaridole. Repeated measurements are needed to determine the power of this effect, while time-dependent samples may document variability caused by seasonality.

Perhaps the most notable of all results presented in this paper, is the similarity between the former and the genetic evidence found with microsatellite markers, for the three morphological groups of Epazote described above coincide with allelic differences found in a non-coding region amplified with the QCA076 marker. The identification of the biological characters that are related with these variable genomic regions was beyond the scope of this paper. However, the fact that they coincide with morphological groupings and considering that the detected polymorphisms were conserved within the subsequent progenies, there is sufficient evidence to conclude that these particular characteristics are being fixed in the Epazote population of Santa María Tecomavaca.

The observations described in this paper for *C. ambrosioides* related with local nomenclature, incipient management forms and morphological and phytochemical changes have been described for other non-domesticates used as vegetables: (1) higher biomass, like in *Brassica campestris* (Bye 1979), *Anoda cristata* (Rendón and Núñez-Farfán 2001) and *Amaranthus* spp. (Mapes, Basurto and Bye 1997), (2) gigantism, like in *Proboscidea louisianica* subsp. *fragans* (Paredes-Flores, 2006), (3) less pungent substances, like in *Solanum nigrescens*, *Phytolacca icosandra* and *Chenopodium berlandieri* (Bye 1993) and (4) different colour patterns, like in *Phytolacca icosandra* (Bye 1993). Unfortunately, most of the former studies were not able to detect significant differences or associate them with incipient management forms. Also, few tried to correlate the observed morphological and/or phytochemical variance with genetic markers, like we did for *C. ambrosioides*. Such associations are indispensable to determine the adaptive effect of artificial selection on the available phenotypic variance.

The results described in this paper for *C. ambrosioides* allowed us to try and fit this species in one of the proposed models for vegetable domestication. Rindos (1984) postulated that many plants valued for their vegetative parts were originally domesticated as seed plants. Indeed, in the 19th century, *C. ambrosioides* was cultivated as an oil-seed crop for the harvest of "*Chenopodium* oil" (MacDonald, et al. 2004), which contained high levels of the potent anthelmintic ascaridole, the main compound against several forms of intestinal parasites (Gupta, et al. 2002). However, toxicity problems collapsed this industry before *C. ambrosioides* was considered a domesticated species and it seems therefore unlikely that the pathway of Epazote domestication began by the exploitation of its seeds. On the other hand, neither did *C. ambrosioides* show the typical life cycle separation into vegetative and reproductive generations, as postulated under the *Brassica campestris* model (Rindos 1984). Its leaves continued to be consumed after anthesis was reached. In conclusion, the evolution of Epazote seemed to fit the model of simple colonization within the agro-ecology, which does not induce striking modification of seed dispersal methods (Rindos 1984), but may be associated with gigantism and reduction of chemical defences. This confirmed that – contrary to the criteria described by Hawkes (1983) - the loss of natural dispersion mechanisms to facilitate seed harvest should not be defined as an indicator for the domestication of weedy plants with vegetative used plant parts.

However, we also found morphological changes that did not fit any domestication model described before, like more trichomes on the cultivated Epazote kind in comparison with the less preferred red Epazote plants, which was contrary to the general hypothesis of loss of physical deterrents (Rindos 1984). However, the explanation of this phenomenon was beyond the scope of the work presented here. In summary, the overall results of this paper suggested that the current models for vegetable domestication are still far from satisfactory and that more studies on edible herbs under the initial stages of domestication are needed to fine-tune our knowledge on this interesting part of plant evolution.

The outcome of human selection depends on genetic variation and phenotypic plasticity (Taylor and Aarssen 1988). If a plant species is able to respond to selection (natural or artificial) by producing different phenotypes, it may evolve towards adaptation in the context of domestication. *Chenopodiom ambrosioides* appears to be a successful weedy crop under cultivation, which is currently undergoing a process of incipient domestication. The people of Santa María Tecomavaca have selected for Epazote individuals with different morphological and phytochemical characters, and these differences are correlated with genetic markers. However, it needs to be reminded that *C. ambrosioides*, just like other managed species, continues to evolve and that its future domestication depends on economic, social and cultural conditions, both in time and space.

Papaloquelite variants recognized by the local inhabitants of Santa María Tecomavaca are most likely the result of phenotypic plasticity induced by environmental conditions of the habitat. As these differences disappear when cultivated under homogeneous conditions, human selection for improved Papaloquelite variants has not yet been able to fix the desirable changes, not morphologically neither physiologically, which makes evolutionary adaptation unlikely. On top of this, the unidirectional selection is weakened by the confusing identification of variants and unclear personal preferences. Moreover, the lack of domesticates in the *Porophyllum* genus may indicate that the species of this genus do not possess the necessary aptitude to become domesticated. This observation seems to place the members of the *Porophyllum* genus within the group of species lacking the necessary adaptive complexes for domestication (sensu Hawkes 1983), rendering its evolution under artificial selection difficult. However, our results and the work by Vázquez Rojas (1991) do not exclude the possibility that *P. ruderale* var. *macrocephalum* may one day become the weedy crop humans have selected for during centuries.

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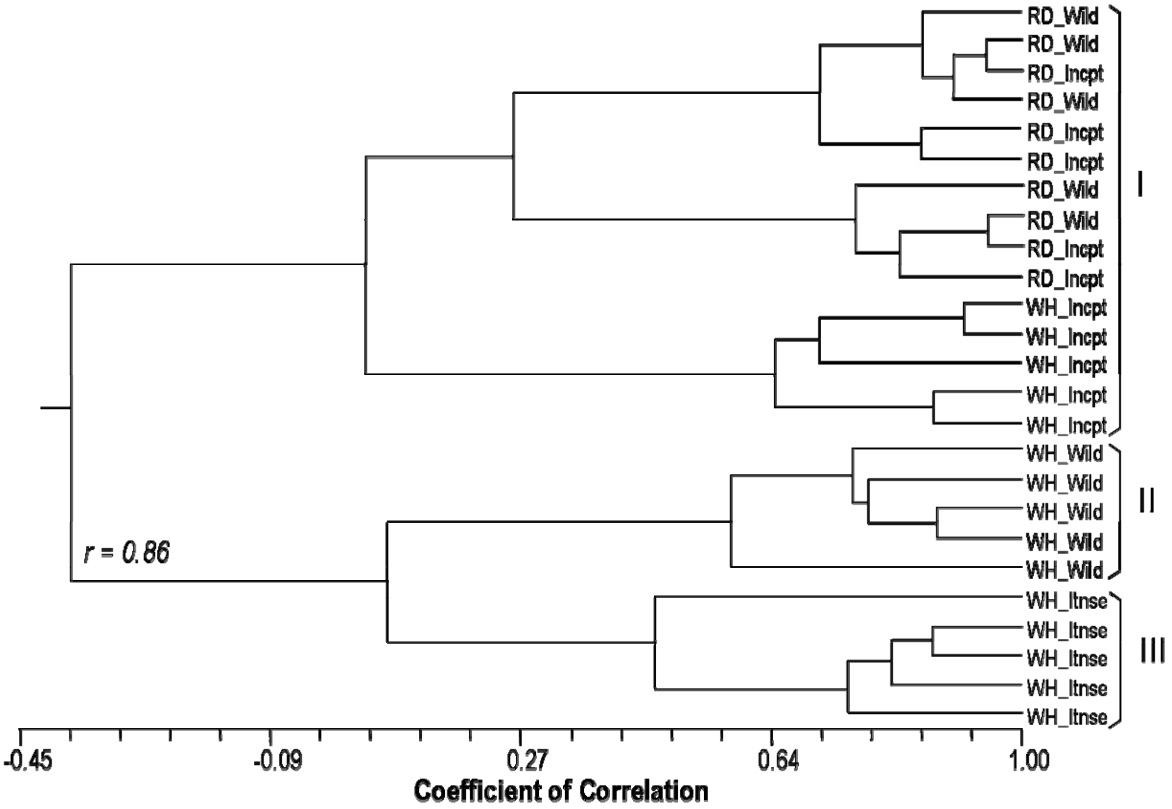


Legend: I, II and II are grouping symbols. RD_Wild = wild red variant, RD_Incpt = red variant under incipient management, WH_Wild = wild white variant, WH_Incpt = white variant under incipient management, WH_Itnse = white variant under intense management

Figure 1.

SAHN Cluster of Epazote (*C. ambrosioides*) morphology data (20 characters).

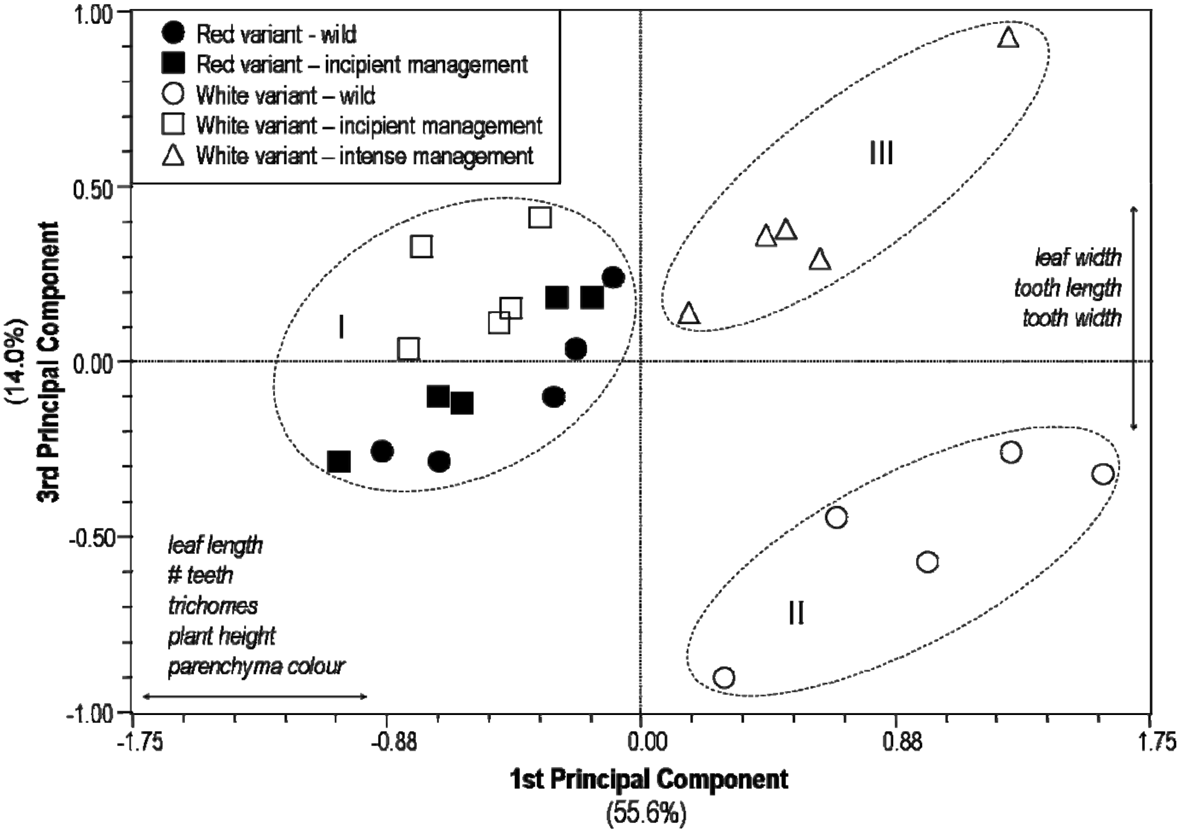


Figure 2.

Principal Component Analysis (PCA) of Epazote (*C. ambrosioides*) morphological data (20 characters). Arrows indicate significant effects with P<0.001 (except plant height: P<0.05).

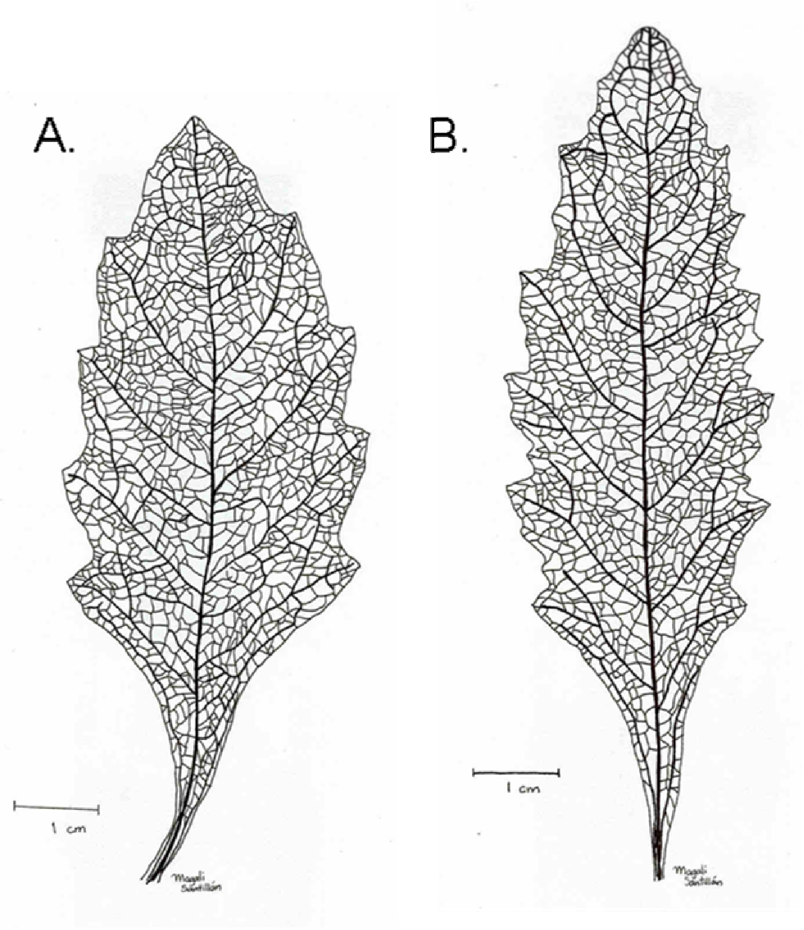
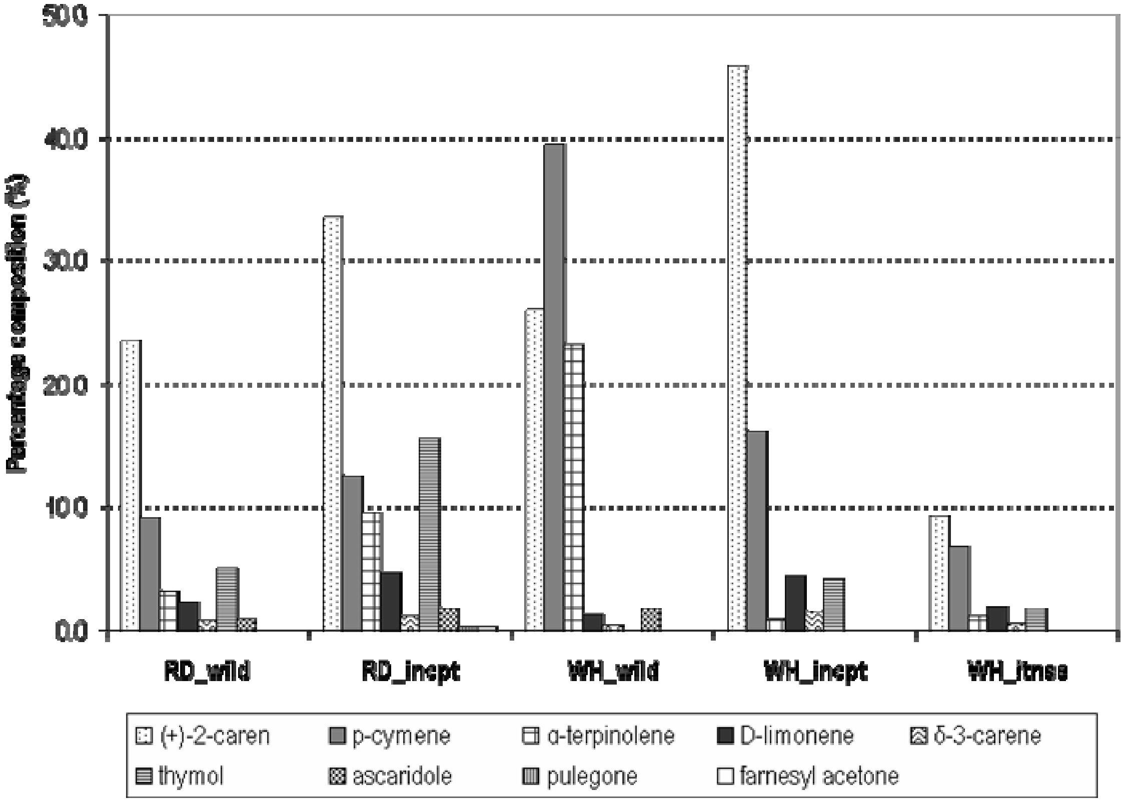


Figure 3.

Leaf morphology of (A) wild red Epazote and (B) cultivated white Epazote.



Legend: RD_Wild = wild red variant, RD_Incpt = red variant under incipient management, WH_Wild = wild white variant, WH_Incpt = white variant under incipient management, WH_Itnse = white variant under intense management

Figure 4.

Olorous components of essential oil of *C. ambrosioides*.

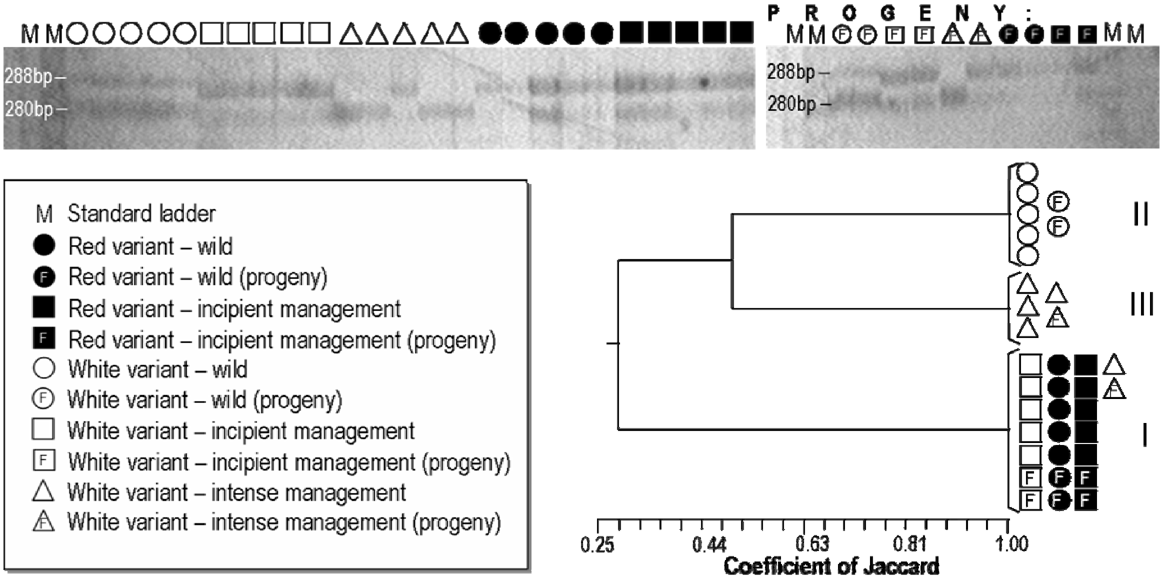


Figure 5.

Polymorphisms detected by the QCA076 microsatellite marker in *Chenopodium ambrosioides*.

Table 1.

Significant effects of Epazote (*C. ambrosioides*) morphology (MANOVA).

Variable	Mean effect	Mean error	$F_{4,20}$	P
Trichomes/ cm stem	289.84	8.64	33.55	0.000***
Leaf width	58.64	7.77	7.54	0.000***
Leaf length	2,119.74	99.72	21.26	0.000***
Number of teeth	357.54	1.49	240.03	0.000***
Tooth length	2.64	0.13	21.15	0.000***
Tooth width	44.34	0.95	46.66	0.000***
Plant height	417.93	106.41	3.93	0.016*
Stem width	1.50	0.85	1.77	0.175
Stem thickness	1.34	0.58	2.32	0.093
Dry weight stem	2.77	1.43	1.93	0.144
Dry weight roots	0.17	0.11	1.56	0.222
Dry weight greens	5.65	0.88	6.39	0.002**
Dry weight total plant	18.18	5.68	3.20	0.035*

*significant at 0.05 level, **significant at 0.01 level, ***significant at 0.001 level

Table 2.

Measurements reported in several Floras for *Chenopodium ambrosioides*. (Note: we measured leaves destined for consumption. As such, our lower limits are not directly comparable with lower limits in the Floras).

	Plant height [m]	Leaf length [cm]	Leaf width [cm]	Petiole length [mm]
Santa María Tecomavaca (this study)	*0.59–1.09*	*9.7–16*	*3.6–5.5*	–
Flora Medicinal de México[1]	0.40–1	3–10	1–5	–
Flora del Valle de México[2]	0.40–1	3–10	1–5	–
Flora of North America[3]	0.30–1 (–1.50)	2 – 8 (–12)	0.5–4 (–5.5)	–18.0
Manual of the Vascular Plants of Texas[4]	0.30–1	2–12	1.5–5.5	–
Flora of Guatemala[5]	–1	3–10	1.5–5.5	–
Flora de Nicaragua[6]	0.25–1 (–1.50)	1.7–7 (–12.5)	0.5–2.5 (–5.5)	–

[1]Lozoya and Lozoya (1982:31-44); [2]Calderón de Rzedowski and Rzedowski (2001); [3]Flora of North America Editorial Committee (2003); [4]Correll et al. (1979); [5]Standley and Steyermark (1946); [6]Stevens et al. (2000)

Table 3.

Percentage composition of the essential oil of *C. ambrosioides*. (The last column presents minimum and maximum concentrations found in the five accessions studied in this paper.)

Component	RT*	min - max %
(E)-2-hexenal	4.34	0.0 – 0.4
(+)-2-carene	7.62	9.3 – 45.8
p-cymene	7.82	6.7 – 39.4
D-limonene	7.92	1.3 – 4.7
δ-3-carene	8.67	0.4 – 1.5
nonanal	9.81	0.7 – 4.0
2-ethyl-cyclohexanone	10.46	0.0 – 1.0
pulegone	12.55	0.0 – 0.3
α-terpinolene	13.54	0.9 – 23.2
2-methyl-5-(1-methyl ethyl)-2-cyclohexen-1-one	13.67	0.0 – 0.2
thymol	14.94	0.0 – 15.5
ascaridole	15.32	0.0 – 1.8
2-methyl-2-buteonic acid	18.37	0.0 – 0.7
1-methyl-3-(1-methyl ethyl)-cyclohexene	18.55	0.0 – 0.6
2-pentadecanone	27.75	0.0 – 0.5
(E)-2-tetradecene	28.43	0.0 – 9.9
cyclotetradecane	28.44	0.0 – 12.5
farnesyl acetone	29.02	0.0 – 0.3
cyclohexadecane	30.61	3.6 – 47.4
phosphonic acid	30.76	0.0 – 0.7
phytol	30.84	1.1 – 17.1

** RT = Retention Time*

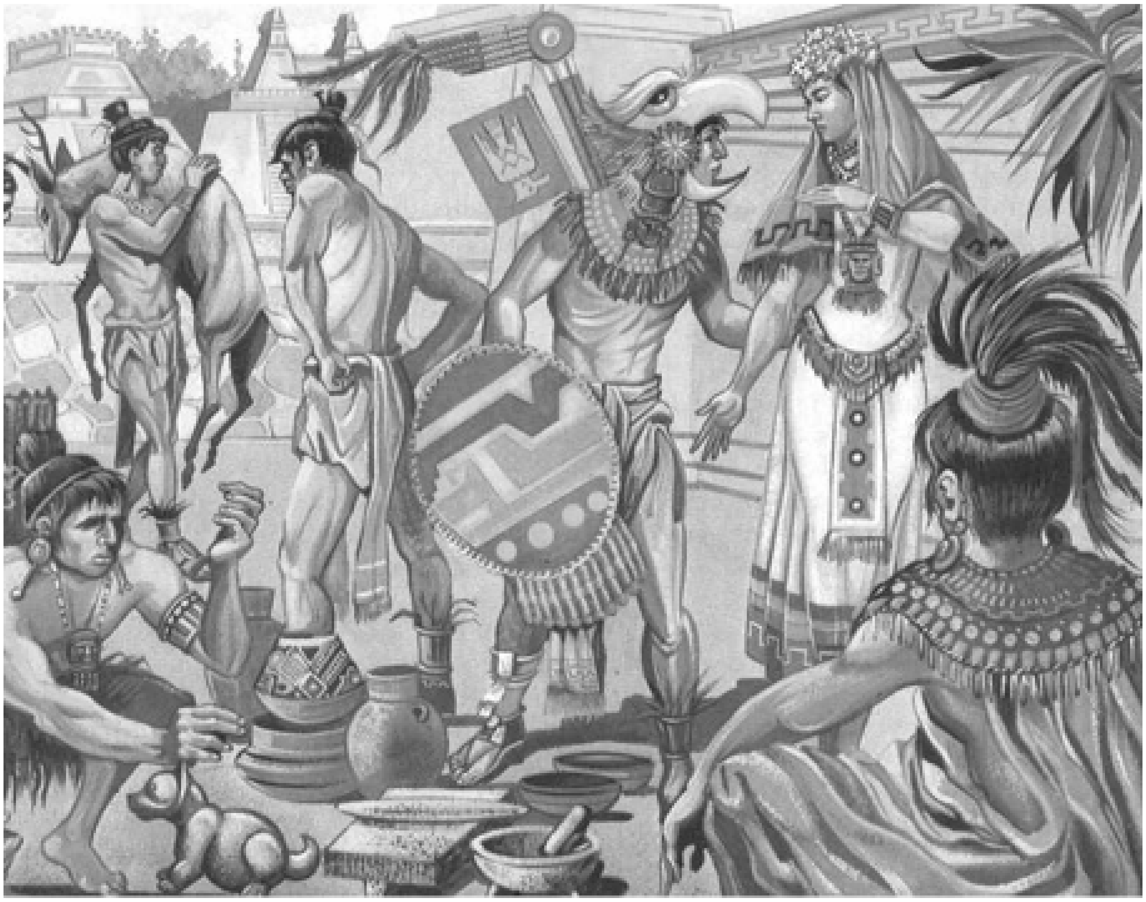
Table 4.

Indicators for incipient domestication of *P. ruderale* var. *macrocephalum* and *C. ambrosioides*.

INDICATOR	*P. ruderale* var. *macrocephalum*	*C. ambrosioides*
1. Common knowledge and Cultural practice*		
1. General knowledge of plant use(s)	✦✦✦✦	✦✦✦✦
2. Recognition of variants	✦✦	✦✦✦✦
3. Variants distinguished by morphology	✦✦✦✦	✦✦✦✦
4. Variants distinguished by taste and/or smell	✦	✦✦✦
5. Preference for one specific variant	✦✦	✦✦✦✦
6. General taste appreciation	✦✦✦✦	✦✦✦✦
7. Grow species in homegarden	✦✦✦	✦✦✦✦
8. Positive selection for one specific variant	-	✦✦
2. Morphological evidence		
1. Increment in total biomass	no	yes
2. Gigantism in used plant part(s)	no	yes
3. Gigantism in other plant parts	no	no
4. Significant differences	no	yes
3. Phytochemical evidence		
1. Differential composition of essential oil	no	yes
2. Difference related with human management	no	yes
3. Significant differences	-	-
4. Genetic evidence		
1. Polymorphisms	-	yes
2. Variance related with common knowledge	-	yes
3. Variance related with cultural practice	-	yes
4. Variance related with morphological evidence	-	yes
5. Variance related with phytochemical evidence	-	yes

**Symbols represent the proportion of informants with a positive testimony associated with each factor:*

✦ = 0-25%, ✦✦ = 26-50%, ✦✦✦ = 51-75%, ✦✦✦✦ = 76-100



Discusión General y Conclusiones

DISCUSIÓN GENERAL Y CONCLUSIONES

En este trabajo se intentó comprobar la validez de dos hipótesis generales a través de una serie de hipótesis particulares. De estas hipótesis, una se relaciona con la influencia del manejo humano tradicional o incipiente en la riqueza, abundancia y distribución de la flora arvense presente en varios sistemas agrícolas de Santa María Tecomavaca, Oaxaca, y la otra con la posible evolución a través de la domesticación incipiente de algunas de las especies que la constituyen (H_1 y H_2 en Tabla 1). Ambas hipótesis, por una parte, apoyan la idea de que el manejo tradicional se enfoca a la conservación e incluso a la promoción de las plantas que son útiles (Bye, 1981; Chacón & Gliessman, 1982; Alcorn, 1984; Casas et al., 1994; Caballero, 1995; Casas et al., 2001). Por otra parte, dichas hipótesis son contrarias a las más aceptadas que implican que las plantas que coexisten con los cultivos son siempre nocivas para la agricultura y a las cuales comúnmente denominan malezas (Harlan, 1929; Baker, 1965; Harlan & deWet, 1965; Baker, 1967, 1972, 1974).

Como se resume en la Tabla 1, las dos hipótesis generales fueron parcial o totalmente corroboradas en el trabajo. La flora arvense encontrada en los terrenos agrícolas de Santa María Tecomavaca consiste en 161 especies, pertenecientes a 40 familias y 103 géneros de Angiospermas e incluyen tres especies endémicas de la región: *Iresine discolor* Greenm. (Amaranthaceae), *Florestina simplicifolia* B.L. Turner (Asteraceae) y *Sida pueblensis* Fryxell (Malvaceae). Las familias mejor representadas en este estudio (Poaceae, Asteraceae y Malvaceae) coinciden con lo reportado por Dávila et al. (2002) para toda la Reserva de la Biosfera Tehuacán-Cuicatlán, dentro de la cual se encuentra la zona de estudio de este trabajo. Por otra parte, no obstante que el territorio de Santa María Tecomavaca representa solamente el 0.2% de la superficie del estado, dentro de sus límites crece el 14.5% de la diversidad total (1113 spp.) de malezas registradas para el estado de Oaxaca por Villaseñor & Espinosa-García (1998). Adicionalmente, solo la tercera parte de las arvenses (31.7%) es encontrada en la vegetación secundaria de la zona, lo cual refleja la alta restricción de hábitat que generalmente tienen estas plantas (Baker, 1974, deWet & Harlan, 1975).

En cuanto a la importancia que representa la flora arvense en Santa María Tecomavaca, los resultados obtenidos mostraron claramente dos hechos. Por una parte, se hizo evidente que los campesinos consideran que las plantas no domesticadas presentes en sus terrenos compiten con sus cultivos y dificultan las actividades agrícolas, lo cual coincide con la percepción negativa que se tiene comúnmente de estas plantas (Harlan, 1929; Baker, 1965; Harlan & deWet, 1965; Baker, 1967, 1972, 1974). Como consecuencia de ello, realizan varias actividades para su control, las cuales van desde el deshierbe con machete, hasta el control químico con herbicidas, tal como se ha reportado anteriormente para la misma comunidad (Grupo Mesófilo, 2001). Por otra parte, se encontró que las plantas arvenses en Santa María Tecomavaca también representan recursos de gran importancia para la subsistencia de la gente (91.9% de las arvenses presentan uno o más usos) y en este sentido corrobora lo que ha sido descrito en otro trabajos, tanto para la zona de estudio (Blanckaert, 2001; Casas et al., 2001; Paredes-Flores, 2001; Van Diest, 2002; ; Rosas-López, 2003; Paredes-Flores, 2006), como para otras regiones de México (Rzedowski, 1978; Bye, 1981; Chacón & Gliessman, 1982; Bye & Linares, 1983; Caballero, 1984; Viveros & Casas, 1985; Casas et al., 1994; Caballero, 1995; Espinosa-García & Díaz-Pérez, 1996; Vieyra-Odilón & Vibrans, 2001).

Tabla 1. Síntesis de las hipótesis trabajadas en la tesis y su aceptación o rechazo.

Manejo Humano y Distribución de la Flora Arvense General	H_1 La utilidad y las formas de manejo de las plantas arvenses determinan su distribución en los sistemas agrícolas, resultando en una mayor distribución de arvenses útiles y nativas en los sistemas agrícolas con menor uso de productos químicos.		Parcialmente Aceptada
	h_{1a} Las plantas arvenses tienen utilidad y están sujetas a diferentes formas de manejo incipiente en los diferentes sistemas de cultivo.	⇨	Aceptada
	h_{1b} Las diferencias en la distribución de las plantas arvenses dentro de diferentes sistemas de cultivo son atribuibles a su utilidad.	⇨	Rechazada
	h_{1c} Las plantas arvenses nativas tienen más utilidad que las arvenses introducidas y los sistemas agrícolas con mayor uso de productos químicos tienen una mayor abundancia y cobertura de arvenses introducidas que nativas.	⇨	Parcialmente Aceptada
Evolución en Dos Arvenses Elegidas	H_2 Las diferencias morfológicas, fitoquímicas y/o genéticas entre las plantas manejadas y silvestres indican que las poblaciones manejadas han sido sujetas a y/o están bajo un proceso de domesticación incipiente.		Aceptada (*C. ambrosioides*) Rechazada *(P. ruderale)*
	h_{2a} El grado de manejo influye gradualmente en las características morfológicas y/o fitoquímicas de las plantas arvenses.	⇨	Aceptada *(C. ambrosioides)* Rechazada *(P. ruderale)*
	h_{2b} Las poblaciones de una especie arvense sujetas a distintas formas de manejo son genéticamente diferentes entre sí.	⇨	Aceptada (*C. ambrosioides*)

Dentro de las plantas arvenses útiles de Santa María Tecomavaca, las empleadas como forraje destacan por su importante papel dentro de la agricultura de subsistencia de la zona. Estas plantas proporcionan alimento para la ganadería que forma parte integral del sistema agropecuario local, evitando así el gasto que representa el comprar alimento comercial e incrementando la sobrevivencia del ganado en tiempos de sequía, lo cual aumenta la seguridad financiera de las familias campesinas (Espinosa-García & Díaz-Pérez, 1996; Vieyra-Odilón & Vibrans, 2001). Por otra parte, algunas de las arvenses tienen aplicaciones en la medicina tradicional, la alimentación o la ornamentación de los espacios antropogénicas, así como también presentan beneficios agroecológicos, como por ejemplo el enriquecimiento del suelo o el establecimiento de una interrelación positiva entre arvense y cultivo. Todos estos datos confirman que la flora arvense no necesariamente representa un grupo de plantas dañinas, sino que también enriquece la dieta básica, proporciona herramientas para mantener y mejorar la salud humana y contribuye a fortalecer y garantizar la seguridad económica de las familias campesinas en esta zona semiárida.

El reflejo de la dualidad anteriormente señalada en cuanto a la percepción de la flora arvense por parte de la gente de Santa María Tecomavaca, también se observa en el manejo, pues los campesinos ejercen varias formas de presión sobre las arvenses. Así, estas plantas son eliminadas cuando se considera que son dañinas, mediante prácticas de control conocidas generalmente como "manejo agrícola" y entre las que se incluye el control químico con herbicidas (Auld et al., 1979; Cox & Atkins, 1979). Por otro lado, cuando son útiles, son toleradas, protegidas e incluso fomentadas o cultivadas con el fin de asegurar su disponibilidad dentro de los terrenos de cultivo y huertos familiares. En este trabajo, como en muchos otros (Alcorn, 1981; Chacón & Gliessman, 1982; Vázquez Rojas, 1991; Bye, 1993; Hernández-Xolocotzi, 1993; Casas et al., 1997; Lira & Casas, 1998; Blanckaert et al., 2004; Avendaño et al., 2006; Paredes-Flores, 2006; Rodríguez-Arévalo, 2006), estas acciones son reconocidas como "manejo incipiente", "manejo tradicional" o "manejo no-agrícola", para así diferenciarlas del manejo agrícola antes mencionado. El manejo incipiente forma parte integral de la manipulación selectiva de los bienes naturales que los campesinos tradicionales han desarrollado desde tiempos prehispánicos, asegurando así la utilización eficiente de los recursos naturales (Bye, 1993; Casas & Caballero, 1995; Challenger, 1998).

Todo lo anterior sugiere que el manejo que un campesino ejerce sobre las plantas arvenses, depende de su conocimiento sobre la utilidad/nocividad de estas plantas y no sólo del sistema de cultivo y la biología de las malezas, los cuales son los dos factores que generalmente se consideran en los trabajos enfocados hacía el control de malezas o manejo agrícola (Auld et al., 1979; Benech-Arnold & Sánchez, 1995; Norris, 1997; Thill & Mallory-Smith, 1997; Marshall et al., 2001). Esto ha sido documentado en otros trabajos (Alcorn, 1984; Boster, 1985; Espinosa-García & Díaz-Pérez, 1996), en donde, al igual que en este, se encontró que el conocimiento de los pobladores de Santa María Tecomavaca con respecto a la utilidad de las plantas arvenses aumenta con su edad y que las plantas arvenses con mayor utilidad reciben más formas de manejo incipiente por parte de los campesinos. La excepción a esta última tendencia es la de las arvenses que son exclusivamente forrajeras, cuya abundancia natural hace innecesario el estímulo humano.

Como resultado de las prácticas de control de malezas (en particular, el uso de herbicidas), la diversidad, abundancia y cobertura de arvenses en Santa María Tecomavaca disminuye a lo largo de un gradiente de intensidad de manejo agrícola (frutal de limón, policultivo de milpa con diferentes combinaciones de maíz, calabazas y frijoles, frutal de papaya y monocultivo de melón), lo cual confirma lo señalado al respecto por varios autores (Marshall et al., 2001; Stoate et al., 2001; Marshall et al., 2003). Al mismo tiempo, las tres especies endémicas reportadas para la zona, han desaparecido por completo de los campos de monocultivo en el Municipio de Santa María Tecomavaca. Por otra parte, la invasión de los organismos exóticos, considerada la segunda causa más importante de la pérdida de biodiversidad en el mundo, está relacionada con el uso de productos químicos. Así, en Santa María Tecomavaca, el uso de herbicidas no selectivos y sistémicos afecta severamente la riqueza de plantas arvenses nativas, favoreciendo el establecimiento de las arvenses exóticas, un fenómeno que no ha sido documentado claramente en la literatura. Aunque los habitantes de la zona utilizan y manejan plantas arvenses sin tomar en cuenta su origen y que la proporción de arvenses nativas es todavía mucho mayor que las arvenses exóticas, el uso cada vez más intenso de los herbicidas puede poner en peligro esta proporción, facilitando la invasión de las exóticas en el futuro. Hoy en día, las prácticas que caracterizan los policultivos tradicionales y los frutales extensivos son cada vez más frecuentemente sustituidas por técnicas industriales que utilizan también cada vez más fertilizantes, pesticidas y herbicidas (Challenger, 1998). Esta tendencia en el campo pone en peligro la agro-biodiversidad tan característica de la agricultura mexicana (Graham, 1993; Humphries, 1993; Casas & Caballero, 1995).

Aunque se conoce que el manejo agrícola genera una disminución de la diversidad de la flora arvense, el impacto del manejo tradicional incipiente sobre la distribución de las plantas arvenses útiles está menos entendido y no se encuentra mucha información al respecto en la literatura. En Santa María Tecomavaca, la proporción de plantas útiles en los diferentes sistemas de cultivo estudiados en este trabajo, se mantiene prácticamente constante y aunque las plantas arvenses con mayor utilidad crecen en más sistemas agrícolas y en más terrenos que sus contrapartes con menor utilidad, no son más abundantes ni presentan una cobertura mayor. Lo anterior indica que los pobladores de Santa María Tecomavaca toleran o protegen, pero no propagan intensamente las arvenses de interés humano en sus terrenos de cultivo. Por otra parte, se han registrado prácticas de fomento y cultivo de arvenses útiles dentro de los huertos familiares cercanos al hogar. Así, se confirma la importancia de los huertos familiares en la subsistencia familiar, como ya ha sido descrito en otros trabajos (Niñez, 1985; Cleveland & Soleri, 1987; Rico-Gray et al., 1991; High & Shackleton, 2000; Blanckaert, 2001; Méndez et al., 2001; Van Diest, 2002; Blanckaert et al., 2004). Toda la información discutida anteriormente, proporciona suficiente evidencia para poder parcialmente aceptar la primera hipótesis general (H_1) de este trabajo (Tabla 1), ya que, si bien la utilidad y las formas de manejo incipiente de las plantas arvenses no determinan su distribución en los sistemas agrícolas, se encontró una mayor distribución de arvenses útiles y nativas en los sistemas agrícolas con menor uso de productos químicos.

La hipótesis relacionada con la evolución bajo selección humana involucró a dos de las 161 arvenses registradas en la zona: Papaloquelite (*Porophyllum ruderale* var. *macrocephalum*: Asteraceae), y Epazote (*Chenopodium ambrosioides*: Chenopodiaceae). La selección de estas dos especies se llevó a cabo tomando en cuenta cuatro criterios: sus usos, la presencia de diferentes formas de manipulación humana, la presencia de poblaciones en hábitats naturales y antropogénicos, y la identificación de variantes por la gente local. Los resultados encontrados para estas dos especies revelaron tendencias contrastantes. En el Papaloquelite, este trabajo confirma los reportes previos (Vázquez Rojas, 1991; Guillet et al., 1998; Barbosa Bezerra et al., 2002), en el sentido de que no existe una clara diferenciación entre las variedades, mientras en el Epazote, este trabajo representa el primer registro en la literatura publicada de su evolución bajo la selección artificial en la literatura.

Así, aunque en Santa María Tecomavaca, los nombres locales para ambas especies estudiadas son similares a los reportados en otros estudios (Standley & Steyermark, 1946; Correll et al., 1979; Bretting & Hernández, 1982; Lozoya & Lozoya, 1982; Vázquez Rojas, 1991; Picó & Nuez, 2000; Calderón de Rzedowski & Rzedowski, 2001; Pino et al., 2003; Blanckaert et al., 2004), las descripciones detalladas de sus variantes morfológicas y nomenclatura en este trabajo sugiere que la selección artificial por parte de los pobladores de la zona para el Epazote es aparentemente mucho más intensa que para el Papaloquelite. Sus variantes (blanca y roja) son reconocidas en toda la comunidad, y los habitantes tienen una clara preferencia para el Epazote blanco, que tiene un olor más agradable y un sabor más suave que el Epazote rojo. No obstante esta preferencia, ambos tipos se consumen y los pobladores generalmente prefieren tener ambos disponibles en sus hogares. De hecho, la presencia de una amplia variedad de plantas domesticadas y razas locales en combinación con plantas arvenses y silvestres útiles dentro de un solar o huerto familiar, es una tradición con una larga historia cultural en la región de Mesoamérica. De esta manera, se eficientiza el espacio y el suelo disponible (Hawkes, 1983; Blanckaert et al., 2004), se disminuye el riesgo de una perdida total de la cosecha y se previenen futuras calamidades como plagas, entre otras (Baskin, 1997).

La preferencia por parte de los habitantes de Santa María Tecomavaca hacía el Epazote blanco, se encuentra reflejada en el manejo incipiente que se ejerce sobre esta planta. Existe una selección positiva a favor de la variante blanca en los huertos familiares del pueblo, en donde esta planta frecuentemente se encuentra bajo cultivo. En contraste, la variante menos preferida y denominada roja, se encuentra también en los huertos, pero es a veces eliminada a favor de la variante blanca y nunca es cultivada. Estas manipulaciones humanas se encuentran reflejadas en la morfología y fitoquímica de las variantes de Epazote. Los Epazotes rojos son morfológicamente muy similares, independientemente de la forma de manejo a la cual han estado sometidos (silvestres, tolerados o protegidos), y en conjunto, se encuentra un pequeño grupo de posibles híbridos entre rojos y blancos, con tallos ligeramente más verdes y hojas ligeramente más anchas. Por otro lado, los Epazotes blancos presentan, principalmente, hojas más largas que los rojos, lo cual indica un cambio morfológico en la parte utilizada de la planta. Además, los Epazotes blancos que son cultivados en los huertos familiares en Santa María Tecomavaca, presentan hojas más largas y anchas y niveles bajas en los componentes olorosos de su aceite esencial, resultando en un sabor y olor más agradable. Cabe mencionar que casi todas las diferencias morfológicas mencionadas en este trabajo para Epazote se encuentran dentro de los límites de plasticidad fenotípica reportados para esta especie en diferentes Floras (Standley & Steyermark, 1946; Correll et al., 1979; Lozoya & Lozoya, 1982; Stevens et al., 2000; Calderón de

Rzedowski & Rzedowski, 2001; Flora of North America Editorial Committee, 2003). Sin embargo, los valores para largo de hoja, medidos en la variante blanca (silvestre y cultivada), son más altos que los valores de cualquier otro reporte. Esto ilustra la necesidad de realizar una revisión taxonómica de Epazote y en particular, se deben de revisar las diferencias morfológicas que pueden ser el resultado de la selección humana. Considerando la larga historia cultural en la región Mesoamericana, *C. ambrosioides* sería una candidata excelente para realizar una revisión completa dentro de su área de distribución, en el contexto de un proceso de domesticación incipiente. Todo lo anterior indica que los pobladores de Santa María Tecomavaca, a través de los años, han seleccionado plantas de Epazote con un tallo más verde, hojas más grandes y un sabor y olor más agradable que sus contrapartes menos preferidos. Además, existe una congruencia extraordinaria entre las agrupaciones morfológicas de Epazote y las diferencias alélicas encontradas en una región no-codificante amplificada con un marcador microsatélite. La identificación de los caracteres biológicos asociados a la región variable se encuentra fuera del alcance de este trabajo. Sin embargo, el hecho de que coinciden con los grupos morfológicos asociados al manejo humano y que los polimorfismos detectados se mantienen en la generación subsiguiente, proporciona suficiente evidencia para concluir que estas características en particular están siendo fijadas en el código genético de las poblaciones de Epazote en Santa María Tecomavaca.

Las observaciones descritas en este trabajo para el Epazote, relacionadas con los cambios en la coloración, el aumento en la biomasa o el gigantismo de partes utilizados, así como la disminución de substancias de defensa química, son factores que han sido asociados anteriormente con la domesticación incipiente de otras plantas utilizadas como verduras (Bye, 1979, 1993; Mapes et al., 1997; Rendón & Núñez-Farfán, 2001; Paredes-Flores, 2006). Esto ubica el caso de Epazote dentro del modelo de domesticación a través de la simple colonización dentro del agrohábitat, lo cual no implica una modificación drástica de los modos de dispersión de semillas (Rindos, 1984), pero se asocia con el gigantismo y la reducción de defensas químicas, tal como lo hemos encontrado para el Epazote en la zona de estudio. No obstante, también encontramos diferencias que no encajan dentro de algún modelo de domesticación postulado anteriormente, como por ejemplo la presencia de tricomas en el tallo de plantas de Epazote cultivadas y preferidas por los habitantes locales, lo cual es contrario a la hipótesis de la pérdida de defensas físicas (Rindos, 1984). Así, es claro que los modelos actuales de la domesticación de plantas utilizadas como verduras todavía presentan algunos vacíos. Pocos estudios logran la detección de diferencias significativas, la asociación con el manejo humano o la correlación entre diferencias morfológicas y/o fitoquímicos con la variación genética como se ha hecho en este trabajo para *C. ambrosioides*. Por lo anterior, se considera que se necesitan más estudios sobre este tipo de domesticación de plantas, y en particular sobre las fases iniciales de este proceso, para poder entender mejor los mecanismos de esta parte fundamental de la evolución vegetal.

En conclusión, las diferencias morfológicas, fitoquímicas y genéticas entre las plantas manejadas y silvestres indican que el Epazote es una especie arvense exitosamente cultivada, la cual actualmente se encuentra bajo un proceso de domesticación incipiente. En cambio, el Papaloquelite no presenta diferencias asociadas a la selección humana, y se ubica dentro del grupo de especies que no presentan los complejos adaptativos (*sensu* Hawkes, 1983) para la domesticación, volviendo difícil su evolución bajo la selección artificial. Es importante recordar que el Epazote y el Papaloquelite, así como otras especies bajo manejo humano, continúan evolucionando constantemente y que su futura evolución bajo la domesticación depende de las condiciones sociales, económicas y culturales, tanto en el tiempo como en el espacio.

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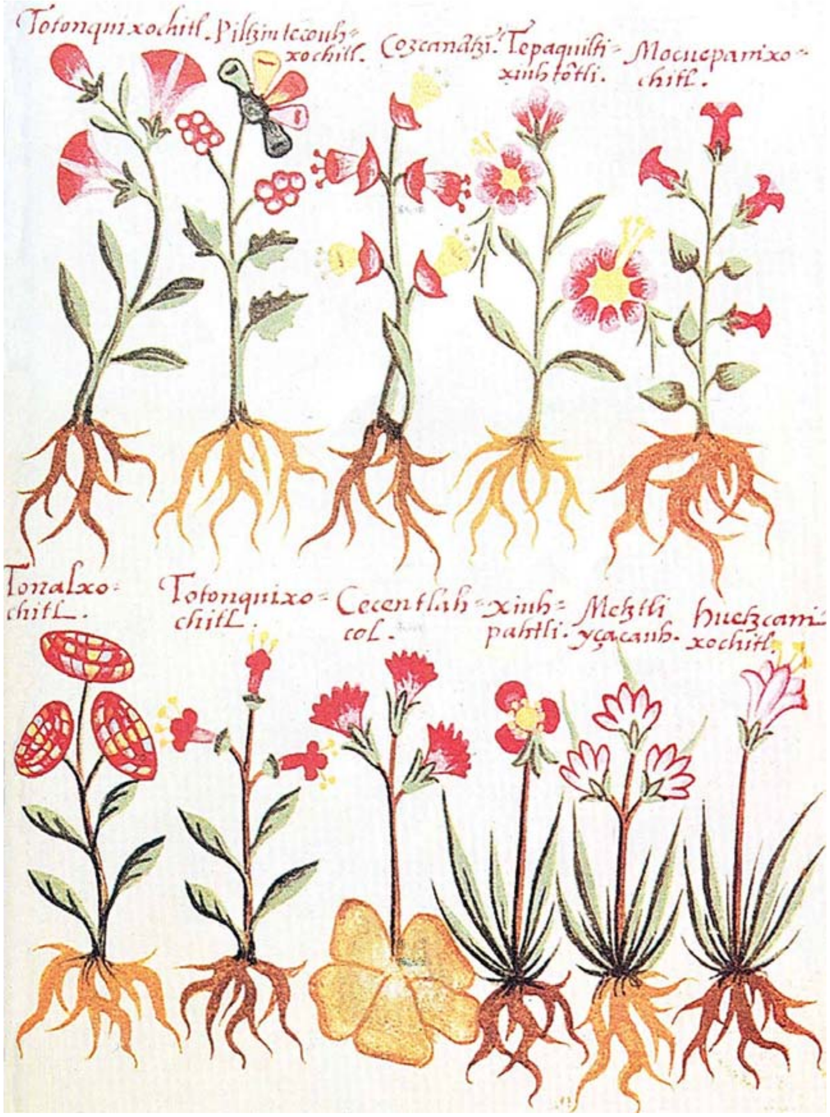
Totonquixochitl.
Pilzintecouh-xochitl.
Cozcauhtzi.
Tepaquilti-xiuhtotli.
Mocuepanixo-chitl.
Tonalxo-chitl.
Totonquixo-chitl.
Cecentlalh-col.
Xiuh-pahtli.
Metztli ycacauh.
Huehzcani-xochitl.

Apéndices

Apéndice A Parámetros de utilidad y distribución de las plantas arvenses

Usos=número de usos, Manejo=número de formas de manejo, Sistemas agrícolas=número de sistemas agrícolas en que fue registrado cada especie, Frec=frecuencia absoluta de cada especie, Abun=abundancia absoluta de cada especie, Cob=cobertura absoluta de cada especie, MILabunR=abundancia relativa de cada especie en Milpa, MILcobR=cobertura relativa de cada especie en Milpa, LIMabunR=abundancia relativa de cada especie en Limón, LIMcobR=cobertura relativa de cada especie en Limón, PAPabunR=abundancia relativa de cada especie en Papaya, PAPcobR=cobertura relativa de cada especie en Papaya, MELabunR=abundancia relativa de cada especie en Melón, MELcobR=cobertura relativa de cada especie en Melón .

Especie	Usos	Manejo	Sistemas agrícolas	Frec	Abun	Cob	MIL abunR	MIL cobR	LIM abunR	LIM cobR	PAP abunR	PAP cobR	MEL abunR	MEL cobR
Abutilon mucronatum J.E.Fryxell	2	0	4	13	8.58	0.78	0.65	0.73	17.71	28.17	0.32	0.07	0.83	3.94
Acalypha arvensis Poepp. & Endl.	2	0	4	23	46.26	3.14	8.66	10.82	0.87	0.61	19.67	18.45	6.40	8.14
Acalypha ostryaefolia Riddell	1	0	2	2	1.00	0.53	0.00	0.00	0.04	0.18	0.00	0.80	0.00	0.00
Amaranthus hybridus L.	2	2	4	17	9.89	1.20	1.65	4.38	0.63	1.45	2.70	4.70	5.60	9.92
Anoda crenatiflora Ortega	1	0	1	2	1.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Argemone ochroleuca Sweet	1	0	1	1	2.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	1.90	1.35
Bidens bigelovii A. Gray	1	0	3	5	36.50	4.24	12.10	12.70	0.40	0.34	0.50	0.51	0.00	0.00
Bidens odorata Cav.	1	0	1	2	1.50	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Boerhavia coccinea Mill.	1	0	1	3	5.33	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Boerhavia erecta L.	1	0	4	19	6.63	0.35	1.52	1.11	1.70	1.14	0.14	0.13	3.23	4.68
Cenchrus ciliaris L.	1	0	1	1	36.00	6.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cenchrus incertus M.A.Curtis	1	0	3	5	2.80	0.29	0.27	0.12	1.63	2.66	0.07	0.30	0.00	0.00
Cenchrus longispinus (Hack.) Fernald	1	0	3	7	9.00	0.57	2.32	1.18	1.62	1.56	1.28	3.06	0.00	0.00
Chamaesyce sp	1	0	4	10	19.60	0.97	0.31	3.02	0.00	0.00	0.00	0.00	0.00	0.00
Chamaesyce hypericifolia (L.) Millsp.	1	0	4	19	14.37	0.90	2.28	1.64	1.99	1.34	4.66	5.03	0.86	0.61
Chloris gayana Kunth	1	0	4	21	831.71	9.71	60.38	40.72	66.87	43.01	42.10	18.98	4.51	4.36
Chloris sp.	1	0	3	7	3.14	0.12	0.54	0.17	1.22	1.53	0.19	0.07	0.00	0.00
Cleome viscosa L.	1	0	1	1	1.00	0.02	0.10	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Commelina diffusa Burm.f.	1	0	4	8	2.88	0.18	0.88	1.33	0.62	0.30	0.43	0.36	1.80	1.81
Cordia curassavica (Jacq.) Roem. & Schult.	1	0	2	6	2.50	0.33	0.14	0.67	0.00	0.00	0.00	0.00	0.00	0.00
Coursetia caribaea (Jacq.) Lavin	1	0	1	1	1.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Crotalaria incana L.	1	0	3	6	4.00	0.33	0.23	0.38	0.00	0.00	0.00	0.00	0.29	0.72
Crusea calcicola Greenm.	1	0	2	4	39.00	3.42	7.48	6.32	0.00	0.00	0.00	0.00	0.00	0.00
Cucumis anguria L.	1	0	1	1	4.00	0.42	0.41	0.39	0.00	0.00	0.00	0.00	0.00	0.00
Cyperus flavescens L.	2	0	4	16	161.13	2.38	3.69	0.00	0.12	0.09	53.90	0.11	66.73	0.00
Datura stramonium L.	1	0	4	10	1.80	0.24	0.42	2.92	0.65	0.24	0.10	32.33	0.68	52.62
Desmanthus virgatus L.	1	0	4	14	8.14	0.43	0.31	0.40	13.94	1.22	0.10	0.03	1.83	12.28
Desmodium sp.	1	0	2	2	1.00	0.10	0.03	1.56	0.00	0.00	0.00	0.70	0.00	0.00
Digitaria bicornis (Lam.) Roem. & Schult.	1	0	2	5	12.00	0.98	1.45	0.00	0.00	0.02	0.00	0.00	0.00	0.00
Digitaria insularis (L.) Fedde	1	0	1	1	2.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Echinochloa colonum L.	1	0	3	6	28.33	2.77	0.70	6.63	0.09	0.00	12.06	7.36	0.00	0.00
Eragrostis barrelieri Daveau	1	0	1	1	9.00	0.63	0.00	0.00	0.00	0.00	0.00	0.00	15.00	0.00
Euphorbia dentata Michx.	2	0	4	16	12.25	0.87	2.33	0.00	0.29	0.00	0.94	0.00	0.26	6.82
Euphorbia sp.	1	0	1	1	3.00	0.20	0.64	9.00	2.26	0.26	3.61	1.76	3.33	1.03
Flaveria trinervia (Spreng.) C.Mohr	2	1	2	2	10.50	0.71	0.00	0.00	0.00	0.00	0.00	0.00	0.56	0.00
Florestina simplicifolia B.L.Turner	1	0	1	1	11.00	0.54	0.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gomphrena decumbens Jacq.	1	1	1	2	2.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Heliotropium angiospermum Murray	1	0	2	5	1.80	0.13	0.00	0.00	1.39	0.22	0.05	0.00	0.00	0.00

Especie	Usos	Manejo	Sistemas agrícolas	Frec	Abun	Cob	MIL abunR	MIL cobR	LIM abunR	LIM cobR	PAP abunR	PAP cobR	MEL abunR	MEL cobR
Heliotropium curassavicum L.	1	0	1	1	10.00	0.37	0.00	0.00	0.00	1.49	0.00	0.00	0.00	0.00
Heliotropium foliosissimum J.F.Macbr.	1	0	1	2	1.50	0.19	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.00
Herissantia crispa (L.) Brizicky	1	0	3	9	20.11	1.49	0.72	0.00	52.67	0.94	0.24	0.00	0.00	0.00
Indigofera suffruticosa Mill.	1	0	1	1	2.00	0.35	0.00	0.00	0.00	0.00	0.00	3.61	0.00	0.00
Ipomoea leptotoma Torr.	1	0	3	3	17.75	0.95	6.99	0.00	0.00	0.90	0.00	0.00	0.56	0.00
Ipomoea purpurea (L.) Roth.	2	3	4	19	12.89	2.04	3.13	1.23	1.00	0.00	0.87	0.05	0.26	0.82
Kallstroemia hirsutissima Vail	2	0	3	5	6.00	0.71	0.85	20.52	2.14	16.53	0.10	6.76	0.00	0.00
Lantana hirta Graham	1	0	1	2	2.50	0.46	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00
Lasiacis divaricata (L.) Hitchc.	1	0	1	1	14.00	0.28	0.00	0.00	0.00	3.12	0.00	0.00	0.00	0.00
Malvastrum americanum (L.) Torr.	1	0	4	19	12.53	0.82	1.15	0.00	7.95	0.00	1.69	0.07	1.10	0.00
Melampodium longifolium Cerv.	1	0	1	2	20.50	1.05	0.00	0.00	0.00	0.00	0.00	8.07	0.00	0.00
Melochia pyramidata L.	1	0	1	2	8.00	0.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mentzelia aspera L.	2	1	3	10	10.30	0.83	1.17	0.00	0.00	0.00	0.00	0.00	0.37	0.00
Merremia dissecta (Jacq.) Hallier f.	1	2	1	1	2.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Merremia quinquefolia (L.) Hallier f.	1	0	3	9	8.63	0.71	3.43	0.00	2.12	0.01	0.08	0.00	0.00	0.00
Muhlenbergia sp.	1	0	1	1	2.00	0.04	0.00	0.00	0.00	3.99	0.00	0.00	0.00	0.00
Painteria sp.	0	0	1	1	3.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Panicum hirsutum Sw.	1	0	3	17	9.59	0.51	1.01	0.00	0.00	0.00	0.00	0.00	16.66	0.00
Panicum sp.	1	0	2	4	2.75	0.17	0.39	1.75	0.00	0.00	0.00	29.53	0.00	0.00
Parthenium hysterophorus L.	1	0	3	6	15.83	0.56	0.05	0.00	0.00	0.00	0.00	6.28	3.33	0.00
Passiflora foetida L.	3	0	1	1	4.00	0.21	0.00	0.00	0.00	8.21	0.00	0.00	0.00	0.00
Physalis cinerascens (Dunal) Hitchc.	2	0	3	5	5.20	0.47	0.38	0.00	1.47	0.00	0.39	0.25	0.00	0.00
Plumbago scandens L.	2	0	1	1	15.00	0.59	0.00	0.00	0.00	0.00	0.00	0.84	0.00	0.00
Porophyllum ruderale var. *macrocephalum* (DC.) Cronquist	2	3	1	1	1.00	0.08	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rhynchelytrum repens (Willd.) C.E.Hubb.	1	0	3	4	14.50	0.82	3.23	0.16	7.61	0.00	0.10	0.00	0.00	0.00
Rhynchosia minima (L.) DC.	1	0	4	15	9.87	1.68	1.69	0.56	3.86	2.25	1.59	0.01	0.16	0.00
Rhynchosida physocalix Fryxell	1	0	1	1	3.00	0.08	0.00	0.00	0.00	0.00	0.00	32.85	0.00	0.00
Ricinus communis L.	2	0	4	6	1.00	0.12	0.27	0.00	0.02	0.10	0.33	0.00	1.20	0.00
Rivina humilis L.	2	0	1	1	3.00	0.14	0.00	0.00	0.00	0.00	0.00	0.78	0.00	0.00
Ruellia nudiflora (Engelm. & A.Gray) Urb.	1	0	2	4	8.00	0.32	0.00	0.00	0.19	0.17	2.38	0.00	0.00	0.00
Sanvitalia procumbens Lam.	1	0	2	11	39.45	1.61	4.18	0.00	0.00	0.00	0.00	0.90	0.00	0.00
Setaria grisebachii E.Fourn.	1	0	2	2	2.00	0.04	0.05	28.53	0.00	0.00	0.00	0.00	0.00	0.00
Setaria liebmanii E.Fourn.	1	0	1	1	2.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sida glabra Mill.	2	0	3	12	8.25	0.50	0.81	0.00	11.99	0.80	0.06	0.00	0.00	0.00
Sida pueblensis Fryxell	1	0	3	12	23.33	1.55	3.22	1.48	8.97	2.41	0.73	0.19	0.00	0.00
Sida rhombifolia L.	2	0	4	10	3.40	0.12	0.32	3.66	3.60	26.18	1.82	1.38	0.72	0.00
Solanum elaeagnifolium Cav.	1	0	1	2	58.50	2.61	0.00	0.00	0.00	0.00	0.00	0.00	34.34	1.02
Solanum erianthum D. Don	1	1	2	3	1.33	0.38	0.00	0.00	0.77	0.11	0.10	18.64	0.00	0.00
Solanum rostratum Dunal	1	0	4	6	8.00	0.42	1.96	0.00	0.04	0.00	15.15	0.00	0.46	44.84
Solanum tridynamum Dunal	1	0	1	2	2.50	0.29	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00
Sonchus asper (L.) Hill	2	0	1	1	1.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sonchus oleraceus L.	2	0	1	4	10.50	0.45	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Sorghum bicolor (L.) Moench	1	2	2	3	13.67	0.74	0.00	0.00	5.29	0.00	0.11	2.83	0.00	0.00
Sorghum halepense (L.) Pers.	1	0	1	1	1.00	0.19	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Taraxacum officinale Weber ex F.H.Wigg.	2	0	1	1	3.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tephrosia cinerea (L.) Pers.	1	0	2	5	19.80	1.65	0.11	0.77	0.00	0.00	0.00	0.00	0.00	0.00
Tetramerium nervosum Nees	1	0	3	3	4.67	0.52	0.27	0.00	0.00	0.00	0.00	0.15	0.18	0.00

Especie	Usos	Manejo	Sistemas agrícolas	Frec	Abun	Cob	MIL abunR	MIL cobR	LIM abunR	LIM cobR	PAP abunR	PAP cobR	MEL abunR	MEL cobR
Tithonia tubiformis (Jacq.) Cass.	2	1	2	5	15.00	1.12	2.39	0.67	0.00	0.00	0.00	0.00	0.00	0.00
Trianthema portulacastrum L.	2	0	4	14	15.07	1.65	10.89	5.40	0.65	1.82	0.98	0.00	9.85	0.00
Urochloa fasciculata Kunth	1	0	2	6	15.14	0.37	0.00	0.00	1.38	0.12	2.85	0.00	0.00	0.00
Viguiera dentata (Cav.) Spreng.	3	1	4	12	37.00	2.96	3.17	42.96	33.67	5.98	1.10	1.25	1.00	31.64
Waltheria americana L.	2	1	4	17	13.29	1.13	1.27	1.30	19.23	39.30	0.42	2.14	0.67	2.52
Xanthium strumarium L.	1	0	3	4	3.75	0.49	0.00	0.00	0.04	23.63	15.58	5.36	0.92	3.43
Zinnia peruviana (L.) L.	2	0	2	2	2.50	0.09	0.22	0.00	0.00	0.00	0.00	15.13	0.00	0.00

Apéndice B Mediciones morfológicos de *Porophyllum ruderale* var. *macrocephalum*

*1=cobertura planta [cm^2], 2=número hojas, 3=ancho hoja [mm],4=largo hoja [mm], 5=largo peciolo [mm], 6=ancho/largo hoja,7=ancho*largo hoja, 8=largo peciolo/largo hoja, 9=número glándulas en la márgen, 10=número glándulas en la lamina, 11=número total glándulas, 12=glándulas/mm^2, 13=número aquenios, 14=ancho aquenio [mm], 15=grosor aquenio [mm], 16=largo aquenio [mm], 17=largo pedúnculo [mm], 18=altura planta [cm], 19=grosor tallo [mm], 20=semillas viables/inflorescencia, 21=semillas vacías/inflorescencia, 22=número total semillas/inflorescencia, 23=largo fruto [mm], 24=largo vilano [mm], 25=largo semilla [mm], 26=ancho semilla [mm], 27=grosor semilla [mm], 28=peso seco hojas [g], 29=peso seco tallo [g], 30=peso seco raices [g], 31=peso seco inflorescencias [g], 32=peso seco planta total [g]*

	ROJO + SILVESTRE					ROJO + INCIPIENTE					BLANCO + SILVESTRE					BLANCO + INCIPIENTE					BLANCO + INTENSO				
	planta 1	planta 2	planta 3	planta 4	planta 5	planta 1	planta 2	planta 3	planta 4	planta 5	planta 1	planta 2	planta 3	planta 4	planta 5	planta 1	planta 2	planta 3	planta 4	planta 5	planta 1	planta 2	planta 3	planta 4	planta 5
1	169.0	224.0	195.0	196.0	189.0	240.0	210.0	255.0	225.0	143.0	255.8	143.0	224.8	162.5	232.5	182.0	144.0	144.0	288.0	272.0	225.0	255.0	289.0	255.0	252.0
2	51	54	57	42	50	74	63	66	54	68	62	53	56	45	54	57	36	53	59	83	45	53	57	55	50
3	35.65	36.51	37.32	38.86	37.26	42.37	39.66	36.80	39.45	37.40	42.74	40.18	42.72	35.07	40.89	36.56	38.77	40.34	41.75	45.45	40.17	45.45	39.28	45.68	40.60
4	42.78	47.28	45.41	46.09	43.72	52.54	47.53	45.11	49.10	45.69	52.16	48.65	51.87	41.94	50.29	42.98	46.10	50.48	51.47	56.91	44.55	53.70	50.48	53.71	50.10
5	30.05	30.54	27.98	31.69	27.01	36.21	33.87	36.10	33.44	31.80	31.99	25.96	28.92	27.60	33.88	30.52	25.90	30.24	31.92	36.12	29.59	35.62	32.95	34.19	29.50
6	0.84	0.77	0.82	0.84	0.85	0.81	0.84	0.82	0.80	0.82	0.82	0.83	0.83	0.84	0.82	0.85	0.84	0.80	0.81	0.80	0.90	0.85	0.78	0.85	0.81
7	1525.34	1727.01	1700.91	1794.85	1630.18	2227.35	1884.76	1659.10	1945.48	1714.33	2229.41	1962.46	2219.08	1479.27	2062.23	1572.88	1792.81	2037.72	2151.45	2593.61	1794.35	2449.89	1992.09	2458.24	2042.94
8	0.70	0.65	0.61	0.69	0.62	0.69	0.71	0.80	0.68	0.69	0.61	0.53	0.56	0.66	0.68	0.71	0.57	0.60	0.62	0.64	0.67	0.67	0.66	0.64	0.59
9	12	12	13	11	11	13	13	14	13	14	14	13	15	12	14	12	13	14	13	14	12	13	12	14	15
10	9	0	7	3	6	11	10	12	11	7	12	7	9	10	12	2	7	7	9	9	14	15	6	17	17
11	21	12	20	14	17	24	23	26	24	20	26	20	24	22	26	14	20	21	22	23	26	28	18	31	32
12	0.014	0.007	0.012	0.008	0.011	0.011	0.012	0.016	0.012	0.012	0.012	0.010	0.011	0.015	0.013	0.009	0.011	0.010	0.010	0.009	0.014	0.012	0.009	0.013	0.016
13	3	2	2	3	3	6	3	5	4	5	3	3	2	1	3	3	1	3	3	6	3	4	3	4	4
14	6.36	7.64	7.93	7.06	6.99	7.22	7.37	6.44	6.41	7.03	7.53	7.02	6.79	7.39	8.06	7.18	9.08	8.44	7.62	7.40	6.52	7.58	7.04	7.69	6.92
15	5.75	6.21	6.84	6.64	6.56	6.60	6.79	6.10	5.65	6.14	6.76	6.06	5.72	6.63	7.61	5.78	7.85	7.17	7.03	6.58	6.22	6.45	6.76	6.94	6.09
16	21.00	22.73	21.59	20.99	21.59	22.97	23.06	21.27	22.60	22.60	23.23	23.23	22.07	22.26	22.71	21.08	23.37	23.02	21.98	22.37	21.92	22.19	23.07	22.44	22.53
17	36.18	39.56	45.22	30.89	35.10	39.88	42.72	29.48	39.14	31.62	32.67	29.98	29.70	46.75	44.68	37.81	55.52	41.91	29.94	30.59	26.81	27.65	34.60	33.11	30.76
18	62.7	61.3	65.5	64.2	64.8	90.2	81.8	75.0	80.2	174.9	70.5	53.1	59.1	58.2	80.9	59.4	65.5	74.3	77.4	82.4	68.0	78.9	80.9	79.1	82.8
19	3.29	3.17	3.30	3.20	3.26	4.96	3.98	4.10	4.23	3.94	4.08	3.06	3.71	3.35	5.08	3.63	3.38	4.00	4.24	5.76	3.65	4.84	3.98	4.70	4.08
20	54	61	74	69	70	67	63	36	70	48	75	60	59	61	91	64	84	80	72	85	54	73	89	60	81
21	16	16	2	8	3	2	2	12	2	22	5	10	13	19	4	7	1	3	11	3	10	3	3	16	6
22	69	77	76	77	73	69	65	49	72	70	79	70	71	80	95	71	85	83	83	87	64	76	92	75	87
23	19.35	21.02	20.00	19.95	19.54	21.27	21.32	18.42	21.26	21.38	19.91	19.92	19.22	18.93	19.94	18.42	21.85	21.81	20.74	22.21	19.01	19.37	20.66	18.68	20.36
24	8.28	8.66	8.18	8.43	8.17	9.13	9.07	7.25	9.25	9.59	8.05	8.13	7.51	7.87	8.86	7.51	9.05	9.49	8.77	9.87	8.18	8.50	9.45	7.92	9.07
25	11.08	12.36	11.82	11.52	11.37	12.14	12.25	11.17	12.01	11.79	11.86	11.78	11.71	11.06	11.08	10.90	12.80	12.32	11.97	12.34	10.83	10.87	11.21	10.76	11.29
26	0.64	0.59	0.65	0.68	0.62	0.57	0.59	0.58	0.61	0.64	0.60	0.61	0.58	0.60	0.61	0.64	0.67	0.63	0.63	0.68	0.63	0.61	0.61	0.65	0.60
27	0.36	0.31	0.35	0.34	0.36	0.27	0.30	0.29	0.29	0.33	0.30	0.31	0.28	0.30	0.33	0.34	0.39	0.36	0.36	0.36	0.35	0.33	0.32	0.34	0.33
28	0.366	0.443	0.428	0.506	0.463	0.834	0.674	0.615	0.611	0.566	0.782	0.452	0.443	0.349	0.733	0.438	0.375	0.580	0.487	0.884	0.471	0.915	0.535	0.830	0.667
29	0.521	0.576	0.756	0.753	0.741	1.691	1.181	0.990	0.988	0.883	1.017	0.621	0.738	0.490	1.290	0.635	0.611	1.015	1.089	1.863	0.718	1.356	1.069	1.433	1.099

Table 1 (continued)

30	0.128	0.161	0.163	0.181	0.168	0.388	0.234	0.182	0.240	0.236	0.259	0.238	0.222	0.122	0.288	0.111	0.101	0.182	0.177	0.372	0.127	0.379	0.255	0.336	0.225
31	0.370	0.350	0.439	0.547	0.417	0.795	0.593	0.513	0.523	0.710	0.508	0.413	0.302	0.164	0.605	0.431	0.305	0.625	0.498	0.970	0.338	0.549	0.472	0.669	0.552
32	1.385	1.530	1.786	1.987	1.789	3.708	2.682	2.300	2.362	2.395	2.566	1.724	1.705	1.125	2.916	1.615	1.392	2.402	2.251	4.089	1.654	3.199	2.331	3.268	2.543

Apéndice C Mediciones morfológicos de *Chenopodium ambrosioides*

1=cobertura planta [cm^2], 2=color tallo [0=rojo, 1=blanco], 3=color parénquima [0=rojo, 1=blanco-rojizo, 3=blanco], 4=tricomas [0=no, 1=si], 5=número tricomas/cm tallo, 6=ancho hoja [mm], 7=largo hoja [mm], 8=ancho/largo hoja, 9=número de dientes, 10=largo diente [mm], 11=ancho diente [mm], 12=largo/ancho diente, 13=altura planta [cm], 14=ancho tallo [mm], 15=grosor tallo [mm], 16=peso seco tallo [g], 17=peso seco raices [g], 18=peso seco materia verde [g], 19=peso seco planta total [g], 20=peso seco materia verde/planta total [g].

	COLOURED + WILD					COLOURED + INCIPIENT					WHITE + WILD					WHITE + INCIPIENT					WHITE + INTENSE				
	plant 1	plant 2	plant 3	plant 4	plant 5	plant 1	plant 2	plant 3	plant 4	plant 5	plant 1	plant 2	plant 3	plant 4	plant 5	plant 1	plant 2	plant 3	plant 4	plant 5	plant 1	plant 2	plant 3	plant 4	plant 5
1	374	506	323	609	289	567	420	304	437	378	576	896	462	609	644	484	783	529	483	360	784	675	580	702	648
2	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	1	1	1	1	1	2	2	2	2	2
4	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1
5	0	0	0	0	0	0	0	0	0	0	18	16	5	11	19	0	0	0	0	0	19	12	11	14	14
6	39.36	40.09	38.63	41.95	37.96	41.67	39.94	37.69	42.58	38.02	41.15	41.80	36.34	40.06	41.59	44.46	45.74	42.92	42.06	41.62	55.28	48.30	42.53	44.42	47.78
7	107.61	107.23	102.97	111.70	99.92	114.22	104.60	97.44	120.21	107.48	142.58	160.04	118.59	139.49	156.59	114.32	118.03	119.03	114.16	109.82	159.74	148.92	133.22	159.46	149.05
8	0.37	0.37	0.37	0.38	0.38	0.36	0.38	0.39	0.36	0.35	0.29	0.26	0.31	0.29	0.27	0.39	0.39	0.36	0.37	0.38	0.35	0.32	0.32	0.28	0.32
9	10	10	10	11	11	10	9	10	10	8	28	32	29	28	30	11	10	10	11	11	22	18	19	19	18
10	3.86	3.67	3.76	3.96	3.59	4.03	3.79	3.50	4.03	3.63	3.04	3.70	3.19	3.14	3.55	3.78	3.68	3.70	3.82	3.19	6.22	4.53	5.32	4.95	4.99
11	13.45	13.59	13.26	14.96	13.56	14.49	14.80	13.11	17.14	15.73	9.11	7.63	6.78	7.40	7.98	14.91	15.01	15.39	15.08	13.34	14.32	12.36	13.32	14.25	13.82
12	0.29	0.28	0.28	0.27	0.27	0.28	0.26	0.27	0.24	0.24	0.34	0.50	0.49	0.44	0.45	0.26	0.25	0.25	0.25	0.24	0.46	0.38	0.41	0.36	0.37
13	80.0	85.5	81.8	98.8	66.7	88.7	75.8	59.4	92.8	83.7	93.9	105.9	88.8	88.9	109.3	69.1	81.6	70.2	77.7	72.3	106.5	88.8	78.9	93.5	86.6
14	5.82	6.56	5.04	6.14	5.04	6.52	4.94	4.44	6.03	5.59	6.00	6.94	4.66	6.57	8.68	5.33	5.44	5.88	5.32	4.96	7.87	6.54	5.46	6.48	5.88
15	5.73	5.60	4.72	6.08	4.54	5.84	4.78	4.35	5.61	4.80	5.53	6.63	4.41	6.44	7.28	4.70	5.36	5.35	5.15	4.53	7.39	6.14	5.22	5.75	5.82
16	3.6	4.3	1.3	4.3	1.2	3.6	1.9	0.8	3.2	2.0	2.8	3.5	1.8	4.1	5.4	1.2	2.3	1.3	1.6	1.2	4.5	2.4	1.4	2.3	1.9
17	1.3	1.3	0.3	1.1	0.4	1.4	0.6	0.4	1.0	0.8	0.8	0.8	0.6	0.9	1.0	0.2	0.5	0.6	0.7	0.4	1.0	0.5	0.2	0.6	0.5
18	2.8	2.6	1.3	2.7	0.9	2.4	1.6	0.6	2.5	1.6	2.9	3.3	2.2	4.7	5.7	0.3	1.1	1.2	1.2	0.4	3.4	1.5	1.0	1.8	1.6
19	7.7	8.2	2.9	8.1	2.5	7.4	4.1	1.8	6.7	4.4	6.5	7.6	4.6	9.7	12.1	1.7	3.9	3.1	3.5	2.0	8.9	4.4	2.6	4.7	4.0
20	0.36	0.32	0.45	0.33	0.36	0.32	0.39	0.33	0.37	0.36	0.45	0.43	0.48	0.48	0.47	0.18	0.28	0.39	0.34	0.20	0.38	0.34	0.38	0.38	0.40

Xochiquétzal
Diosa de las Flores

Láminas Fotográficas

El pueblo de Santa María Tecomavaca (vista desde el camino hacia Buena Vista).

El Río Salado, que proporciona agua para el riego de Santa María Tecomavaca.

Entrevista con pobladores de Santa María Tecomavaca en un campo de Limón con Maíz.

Un campo de Limón con un canal de riego proviniendo del Río Salado.

Muestreo mediante la Línea de Canfield en un campo de Papaya.

Aplicación de una herbicida de contacto en un campo de Melón.

Llenar bolsas para el cultivo experimental de Epazote y Papaloquelite con Don Miguel.

Cultivo experimental de Epazote y Papaloquelite con protección contra depredadores.

Plántulas de Epazote (arriba izq.) y Papaloquelite (arriba der.); fumigación (abajo izq.); ¡Visita inesperada! (abajo der.).

Inflorescencias de Papaloquelite.

Epazote en el huerto familiar: blanco (izq.) y rojo (der.).

Coloración en el tallo de Epazote: blanco (izq.) y rojo (der.).