Informe final* del Proyecto G023
Diversidad morfológica y genética de xoconochtli *Stenocereus stellatus* (Pfeiffer) Riccob. (Cactaceae): conocimiento, uso y estrategias para su conservación

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Resumen:

En este proyecto se realizarán estudios etnobotánicos entre los diferentes grupos étnicos del valle de Tehuacán, el Valle de Oaxaca y la Montaña de Guerrero, con el fin de detallar aspectos de uso y manejo y selección artificial en diferentes condiciones ambientales y culturales. Se seleccionarán muestras de poblaciones silvestres, cultivadas y otras formas de manejo, se marcarán los individuos comprendidos en cada muestra y se analizarán caracteres morfológicos, especialmente aquellos con significado taxonómico, aquellos con valor adaptativo a distintas condiciones ambientales y aquellos favorecidos por la selección artificial. Se utilizarán métodos estadísticos de análisis multivariado para comparar poblaciones y analizar sus similitudes y diferencias de acuerdo con sus condiciones ambientales y las condiciones de manejo a las que se encuentran sujetas. Se pretende comparar los patrones de diversidad genotípica dentro y entre las poblaciones en cuestión, comparar estos patrones con los patrones de diversidad fenotípica, analizar relaciones de parentesco entre los individuos de las distintas poblaciones y contar con una muestra de diversidad genética para utilizarse en programas de conservación.

INFORME FINAL

DIVERSIDAD MORFOLOGICA Y GENETICA DEL XOCONOCHTLI *Stenocereus stellatus* (Pfeiffer) Riccob. (CACTACEAE): CONOCIMIENTO, USO Y ESTRATEGIAS PARA SU CONSERVACION

Número de referencia: G023

Area: CONOCIMIENTO ECOLOGICO Y GENETICO

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CONTENIDO

PRESENTACION

El presente documento muestra los resultados, análisis y propuestas derivados del proyecto "Diversidad morfológica y genética del xoconochtli *Stenocereus stellatus* (Pfeiffer) Riccobono, conocimiento, uso y estrategias para su conservación". Se incluye un texto principal que permite exponer de manera sintética los aspectos mas relevantes de los métodos, resultados y análisis generados durante el desarrollo del proyecto. En este texto se encuentran referencias a un conjunto de apéndices, incluidos en este informe, en los cuales se presenta con mayor detalle la información. Estos apéndices son reportes de investigación de las diferentes fases del proyecto. Igualmente, se han incluido como apéndices los primeros dos articulos derivados de este proyecto. Ambos han sido enviados a la revista Economic Botany, que es de circulación internacional. Uno de ellos ("Ethnobotany of the xoconochtli *Stenocereus stellatus* in the Tehuacán Valley and La Mixteca Baja, Mexico") ha sido ya aceptado.

En cada uno de los apartados con resultados, se ha incluido una discusión parcial de la información que particularmente se aborda. Sin embargo, se incluye también una discusión general en la cual se pretende hacer una síntesis de la información sobre historia natural y cultural de *Stenocereus stellatus*, un análisis de las perspectivas de esta planta como recurso potencial, las lineas generales de una propuesta de estrategias para la conservación y utilización de la variabilidad morfológica y genética de esta especie, que pueden resultar de utilidad para sistematizar la evaluación de otros recursos vegetales de importancia potencial que existen en el país.

Se incluye un listado de referencias bibliográficas, la cual contiene las citas empleadas tanto en el texto principal como en los apéndices.

El presente informe constituye un primer análisis de la información generada en el proyecto. Con esta información se están preparando ya algunas publicaciones que permitirán precisar muchos de los aspectos contemplados ahora. Esto será de gran utilidad para apoyar los propósitos generales del proyecto. Por tal razón, en lo subsecuente entregaré a la CONABIO los documentos que se deriven del presente proyecto.

Agradezco el apoyo financiero aportado por la CONABIO, sin éste, la presente investigación no hubiera sido posible. Pero sobre todo, agradezco la amable interacción que mantuvieron con nosotros a lo largo del desarrollo del proyecto

L INTRODUCCION

México, particularmente el área cultural conocida como Mesoamérica, es uno de los centros de domesticación de plantas más importantes del mundo (Harlan, 1975; Hawkes, 1983). La diversidad cultural y biológica que caracterizan esa región son también de las mas sobresalientes en el planeta y son quizás los factores que mas contribuyen a explicar tan dinámica contribución a la generación de cultivares. Estos factores en gran medida determinaron también que Mesoamérica fuera uno de los primeros sitios en los cuales el hombre practicó la agricultura (MacNeish, 1967; Flannery, 1986). Como resultado de su historia cultural, los grupos humanos que han habitado el territorio nacional han desarrollado durante miles de años un extraordinario complejo de formas de interacción hombre-planta. Estas formas de interacción van desde la simple recolección de plantas silvestres hasta el cultivo y selección de variedades de algunas plantas domesticadas para condiciones ambientales y culturales muy específicas. Asimismo, tan larga historia de uso y manejo de las plantas ha generado una amplia gama de recursos vegetales útiles (entre 5,0000 y 7,000 especies, de acuerdo con Caballero, 1985 y Casas *et al.*, 1994), los cuales pueden emplearse potencialmente para satisfacer las distintas necesidades de subsistencia de la población mexicana. Algunas de estas especies (maíz, frijol, cacao, yuca, y otras, quizás no más de 20 especies), son recursos que en la actualidad son fundamentales para el sostenimiento de la población mundial. En ellas la domesticación ha alcanzado niveles muy avanzados, generando una extraordinaria diversidad genética ligada íntimamente a los requerimientos de uso y manejo. Muchas otras especies son relevantes sólo a nivel regional, sin embargo, constituyen recursos de gran importancia potencial a escalas mayores. En estas especies la domesticación presenta niveles intermedios o incipientes, o incluso avanzados, pero en general han sido poco estudiados.

El inventario de todos estos recursos resulta de gran importancia en la búsqueda de opciones de productos de consumo directo o materias primas para la industria. Valiosos esfuerzos han sido y son desarrollados en esta dirección, en las investigaciones etnobotánicas que se realizan por todo el país. Igualmente valioso es el esfuerzo que realizan instituciones tales como el Jardín Botánico y el Centro de Ecología de la UNAM, el Instituto de Ecología A. C., la CONABIO y otras instituciones del país en la sistematización de tan vasta información en bancos computarizados. Sin embargo, junto a esta actividad, también es de mucha importancia dirigir esfuerzos hacia la evaluación de las potencialidades económicas y productivas de los recursos. Con base en tal evaluación sería posible identificar aquellos recursos de alta prioridad. Con tales recursos "prioritarios" sería necesario realizar estudios detallados sobre su diversidad morfológica y genética; sobre los factores biológicos que determinan tal diversidad; asi como sobre el uso y manejo que de tal diversidad han practicado las diferentes etnias mexicanas. Este tipo de estudios serían cruciales para planear la conservación de tal diversidad genética y para emplearla como materia prima en procesos biotecnológicos con el fin de elevar sus potencialidades utilitarias.

El presente documento analiza las potencialidades utilitarias de un recurso específico: el xoconochtli, *Stenocereus stellatus.* Su elección ha sido resultado de estudios etnobotánicos previos efectuados en la región de la Cuenca del río Balsas (Casas *et al.*, 1994; Casas *et al.*, en prensa), y en el Valle de Tehuacán (Casas y Valiente-Banuet, 1995). En ambos estudios se analizaron las potencialidades de los recursos vegetales comestibles silvestres, arvenses y domesticados, en función de la diversidad de usos, importancia en la dieta humana (en cantidad y calidad), su disponibilidad espacial y temporal, su importancia comercial, las posibilidades de manejo intensivo, y la antigüedad de su historia de uso y manejo. De entre una lista de especies de alto valor potencial, destacó por su importancia como especie frutícola ,*S. stellatus.* El presente estudio ha pretendido hacer un seguimiento de la diversidad de usos y manejo en relación con la diversidad genética de esta especie. Asimismo, con este estudio se ha pretendido desarrollar una experiencia metodológica para la conservación de esta especie asi como generar información sobre variación morfológica y genética y biología reproductiva que pueda ser de utilidad a futuros estudios biotecnológicos que permitan elevar las potencialidades de S. *stellatus* como recurso. Con este estudio de caso, se pretende avanzar en la definición de estrategias para el conocimiento detallado de los recursos genéticos de otras plantas mexicanas con alto valor potencial.

Stenocereus stellatus es una cactácea columnar (Figura 1) nativa de las zonas áridas y semi-áridas del centro de México, principalmente Puebla, Oaxaca, Guerrero y Morelos (Figura 2). Es una especie con usos tradicionales múltiples. Estudios etnobotánicos previos entre los Nahuas y Popolocas del Valle de Tehuacán (Casas y Valiente-Banuet 1995) y entre los Nahuas y Mixtecos de la región de la Montaña de Guerrero (Casas *et al.* 1994), permitieron observar que esta cactácea es utilizada como planta comestible, principalmente por sus frutos llamados pitahayas o xoconochtli. Estos frutos son recolectados en poblaciones silvestres y cosechados en plantaciones, tanto para el autoconsumo familiar como para su comercialización en los mercados regionales. Los frutos presentan una pulpa dulce y jugosa y tienen gran demanda como fruta fresca y para la preparación de mermeladas, conservas secas

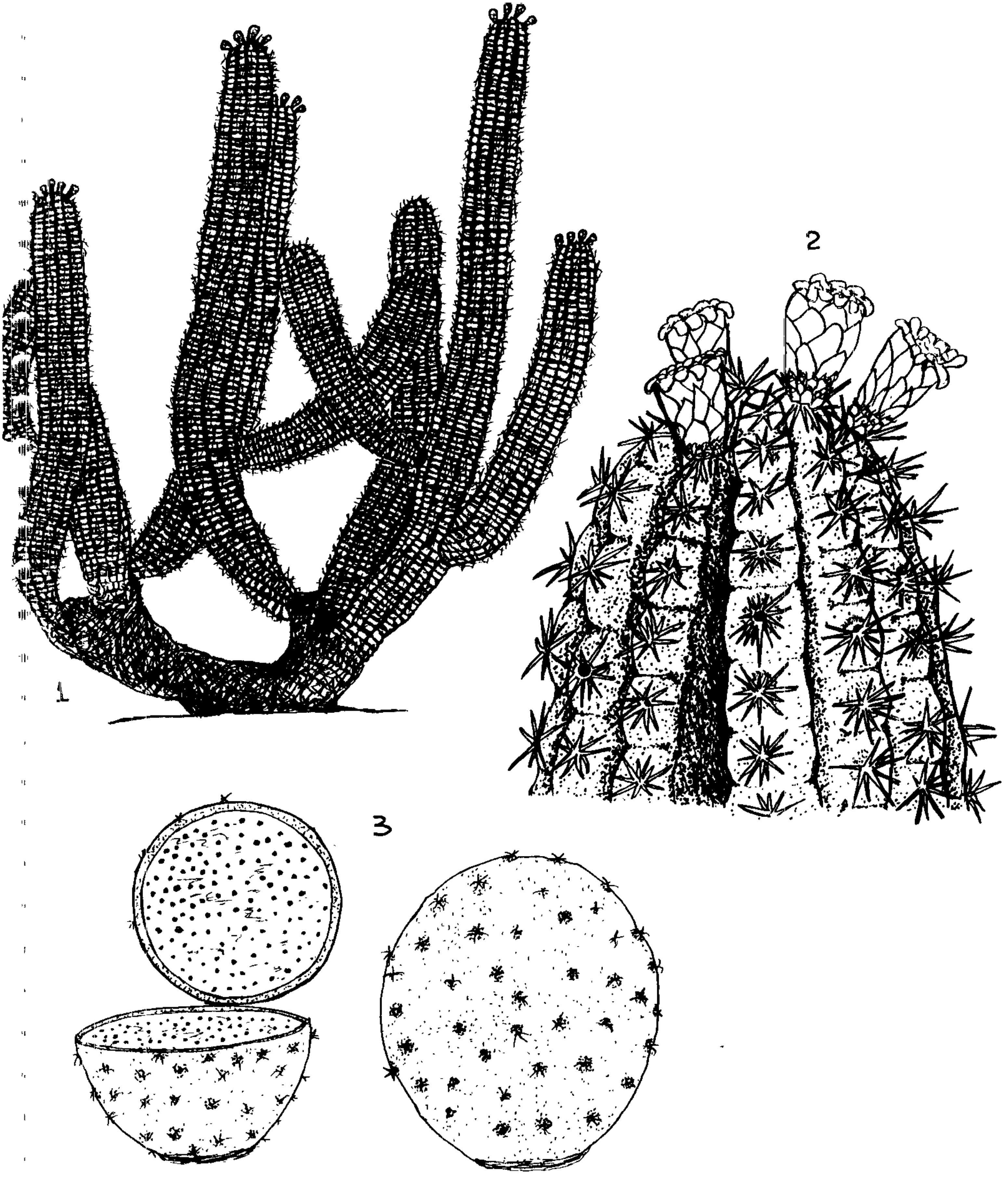

Figura *1*. *Stenocereus stellatus.* I) Un individuo completo, 2) corona de flores, 3) frutos

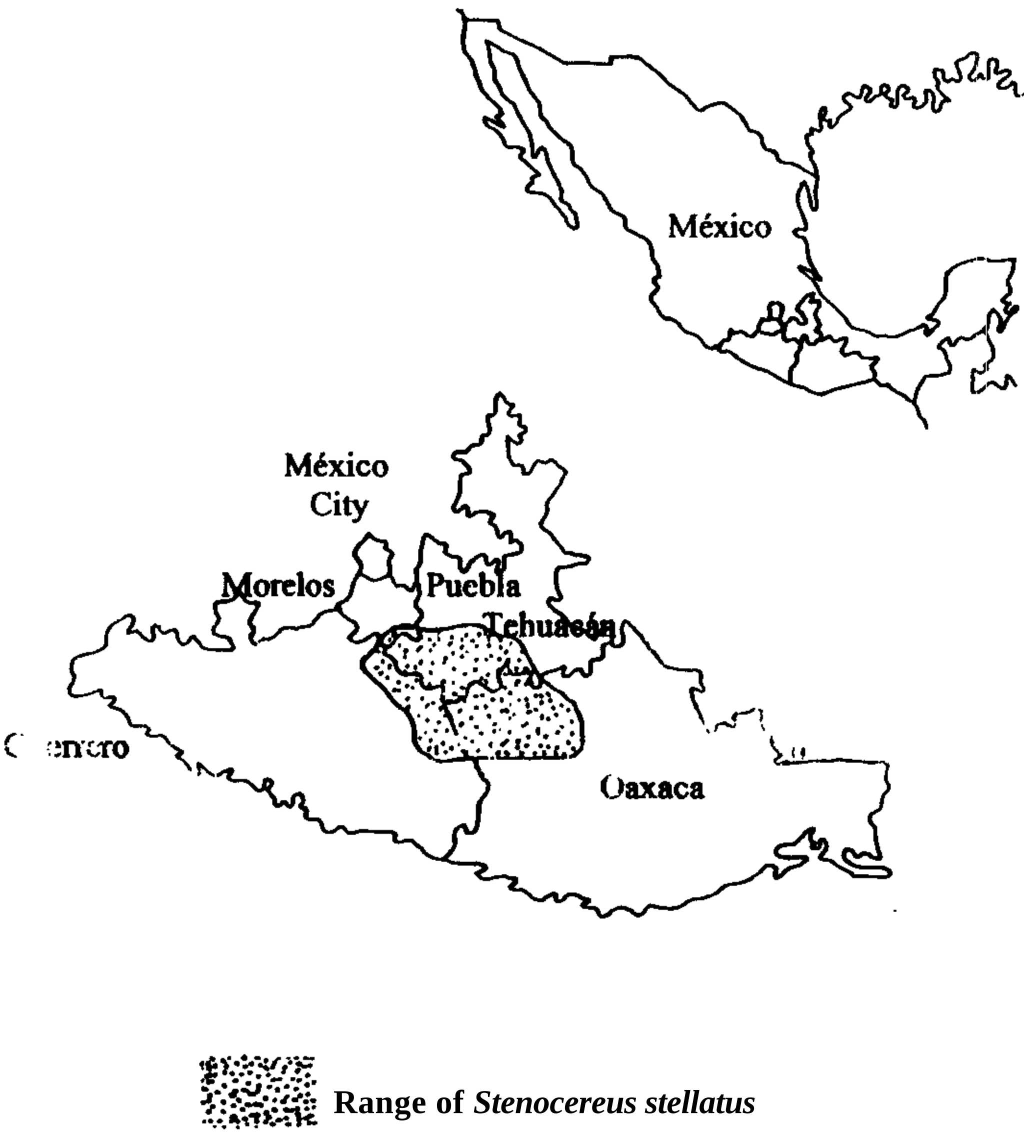

Figura 2. Distribución de *Stenocereus stellatus*

y cristalizadas, asi como para la preparación de bebidas dulces y alcohólicas. Sin embargo, en los estudios mencionados se observó también que los tallos de *Stenocereus stellatus* son utilizados como un buen forraje para cabras y vacas, y secos se usan como leña cuya capacidad calorífica es ideal para la cocción directa de cerámica, sin la utilización de hornos. *S. stellatus* es una de las 29 especies de cactáceas mexicanas llamadas "pitahayas" que son explotadas por sus frutos comestibles (Tabla 1). Además de las especies de *Opuntia, S. stellatus* es una de las especies de cactáceas productoras de frutos con mayor importancia económica (Pimienta-Barrios y Nobel, 1994)

La gente recolecta comúnmente frutos y pedazos de tallos en poblaciones silvestres. Sin embargo, también es posible apreciar otras formas de manejo. Por ejemplo, frecuentemente los campesinos toleran individuos de esta especie (asi como otras especies, principalmente leguminosas, agaváceas y otras cactáceas) cuando abren claros en la vegetación para establecer campos de cultivo de maíz. Después de varios ciclos de uso y de descanso de la tierra, los individuos de las poblaciones de las especies toleradas aumentan su frecuencia, y cuando tal tolerancia es selectiva, es decir, cuando se toleran los individuos con mejores atributos y los demás son eliminados, la frecuencia de fenotipos de mejor calidad utilitaria se ve favorecida. Junto a esta forma de manejo, los campesinos también cultivan esquejes en sus huertas, solares y plantaciones**,** y ocasionalmente también semillas o plántulas tanto de individuos silvestres como de otros previamente cultivados, nativos de la zona o introducidos de otras partes de México.

En los procesos de manejo arriba descritos, son favorecidos diferentes atributos tales como sabor dulce (existen variedades agrias y dulces), mayor tamaño de los frutos, colores de los frutos (existen variedades amarillas, anaranjadas**,** rojas y color púrpura). Todo esto permite suponer que los procesos de domesticación se encuentran avanzados en esta especie. Sin embargo, ni los procesos de selección se encuentran bien definidos, ni la variabilidad intra-específica tanto silvestre como domesticada se encuentra bien caracterizada, ni los mecanismos de flujo de genes entre poblaciones silvestres y cultivadas han sido estudiados.

El uso y manejo del xoconochtli es muy antiguo. En excavaciones arqueológicas del Valle de Tehuacán, MacNeish (1967) y Smith (1967) encontraron restos de frutos de esta planta asociados a restos humanos en estratos con una antigüedad de 4,500 años. Actualmente es posible observar poblaciones silvestres y domesticadas de esta especie coexistiendo en una misma área. Esta situación hace posible analizar comparativamente la estructura fenotípica y

TABLA 1. ESPECIES DE CACTÁCEAS MEXICANAS PRODUCTORAS DE "PITAIHAYAS"

Tribu	Género	Especie	Nombre común	Estatus cultural
Hylocereeae	*Hylocereus*	*H. undatus*	Pitahaya orejona	silvestre-cultivada
		H. purpusii	Pitaya	silvestre
		H. ocamponis	Pitaya	silvestre
Pachycereeae	*Pachycereus*	*P. pringlei*	Cardón gigante	silvestre
		P. pecten-aboriginum	Hecho	silvestre
		P. grandis		silvestre
		P. hollianus	Baboso	silvestre-cultivado
		P. marginatus	Malinche	silvestre-cultivado
		P. weberi	Cardón	silvestre
	Stenocereus	*S. dumortieri*	Pitayo	silvestre
		S. stellatus	Xoconochtli	silvestre-cultivado
		S. treleasi	Tunillo	silvestre-cultivado
		S. griseus	Pitayo de mayo	silvestre-cultivado
		Spruinosus	Pitayo de mayo	silvestre-cultivado
		S. *eichlamii*	Pitahaya	silvestre
		S. fricii	Pitayo de aguas	silvestre-cultivado
		S. martinezii	Pitayo	silvestre
		S. queretaroensis	Pitayo	silvestre-cultivado
		S. quevedonis	Pitire	silvestre-cultivado
		S montanus	Pitaya colorada	silvestre-cultivado
		S. thurberi	Pitayo dulce	silvestre-cultivado
		S . chacalapensis		silvestre
		S. chrysocarpus		silvestre
		S. beneckei		silvestre
		S. standleyi		silvestre
	Carnegiea	*C. gigantea*	Sahuaro	silvestre
	Lophocereus	*L. schotti*	Garambuyo	silvestre
	Machaerocereus	*M. gummosus*	Pitaya agria	silvestre
Echinocereeae	*Echinocereus*	*E. conglomeratus*	Pitaya de agosto	silvestre

genotípica de poblaciones sujetas a diferentes formas de manejo. Asimismo, se pueden realizar estudios de los procesos evolutivos influidos por el hombre que se han llevado a cabo en estas plantas, esto es, estudios de los procesos de domesticación. Estos estudios sugieren ideas novedosas de gran importancia, desde el punto de vista teórico, acerca del origen de la agricultura y de los patrones de uso y manejo de este y otros recursos desde la prehistoria hasta nuestros días. Al mismo tiempo, este estudio permite vislumbrar la diversidad morfológica y genética del recurso que existe en la actualidad, y la diversidad de estrategias tecnológicas desarrolladas por las culturas autóctonas para el uso y manejo de tal diversidad infraespecífica. Ello constituye, sin duda, información fundamental para el desarrollo de las potencialidades de esta planta como un recurso. Al mismo tiempo, el diagnóstico de la variabilidad morfológica y genética resulta de gran importancia para el desarrollo de estrategias de conservación tanto *in situ* como *ex situ* que pueden aplicarse a esta misma especie pero que puede derivar en una base metodológica para la conservación de otras especies. Esto último adquiere relevancia si se considera que las áreas donde se distribuye *Stenocereus stellatus* son importantes reservorios de biodiversidad y riqueza de recursos. Por ejemplo, en el Valle de Tehuacán Dávila *et al.* (1993) reportaron alrededor de 3,000 especies de plantas con flores, de las cuales alrededor de 800 son plantas útiles, de acuerdo con Casas *et al* (1993). Esta diversidad, sin embargo, se encuentra amenazada por la expansión de actividades humanas de considerable poder destructivo. En esta zona, el Instituto de Biología y el Centro de Ecología de la UNAM coordinan actividades dirigidas hacia la conservación de especies en peligro de extinción. Entre estos proyectos destacan: "Mapeo y Análisis de las especies en peligro de extinción en el Valle de Tehuacán-Cuicatlán", auspiciado por la McArthur Foundation, 1990-1992; "Incremento de la colección de cactáceas en el Herbario Nacional y Jardín Botánico", apoyado por la DGAPA, UNAM, 1990; "Banco de germoplasma de especies raras o en peligro de extinción", apoyada por U.S. Fish and Wildlife Service, 1992; "The useful plants of the Tehuacan Valley, Puebla, Oaxaca, Mexico", apoyado en 1992 por el New York Botanical Garden; "Manejo y Conservación de la Biodiversidad Vegetal en el valle de Tehuacán-Cuicatlán, estados de Puebla y Oaxaca, México", apoyado por la DGAPA, UNAM, 1992-1994 y "Flora del Valle de Tehuacán-Cuicatlán" por la CONABIO, entre otros. En este contexto, el presente proyecto ha buscado aportar experiencias metodológicas que pueden resultar de utilidad a tales proyectos de investigación para la conservación.

de la variabilidad morfológica y genética en poblaciones cultivadas y silvestres de esta especie; evaluar sus potencialidades para la producción agrícola y para el mejoramiento genético de este recurso; y definir estrategias para su conservación.

Para el logro de tales metas, se consideró necesario cubrir los siguientes objetivos particulares:

1. Analizar aspectos etnobotinicos tales como uso, manejo y clasificación tradicional infraespecífica de esta planta. El propósito fué entender los aspectos utilitarios mas relevantes, las partes utilizadas y las características de esas partes que son preferidas y seleccionadas por la gente, asi como el reconocimiento de la variación ifraespecífica y su clasificación entre diferentes grupos humanos. Con esta información se pretendió analizar los móviles de la selección artificial y los mecanismos por medio de los cuales se Lleva a cabo por las culturas locales.

2. Analizar características morfológicas de individuos en poblaciones silvestres y cultivadas. El propósito fué analizar patrones de variación morfológica y su relación con diferencias ambientales y formas de manejo por parte del hombre. Con esta información se pretendió discernir aquellos patrones de variación asociados a selección artificial y evaluar el grado de divergencia con respecto a poblaciones silvestres, es decir, evaluar el grado de domesticación de esta especie.

3. Analizar patrones de variación genética dentro y entre poblaciones silvestres y domesticadas en distintas condiciones ambientales y culturales. El propósito fué apreciar tendencias en la diversidad genética en relación con el manejo humano, asi como analizar la disimilitud genética entre poblaciones con el fin de analizar su parentezco y contribuir a reconstruir su historia de manejo.

4. Analizar los sistemas reproductivos de esta especie. El propósito fué iniciar el estudio de fuentes de variación morfológica y genética, asi como entender la naturaleza de las relaciones genéticas dentro y entre poblaciones.

5. Proponer estrategias de conservación y manejo de la variabilidad infraespecífica de *Stenocereus stellatus*

III ESTRATEGIAS GENERALES DE INVESTIGACION

1. Se llevaron a cabo estudios etnobotánicos entre la población Nahua, Mixteca y Popoloca del Valle de Tehuacán, Puebla y la Mixteca Baja, Oaxaca. Estos estudios estuvieron dirigidos a conocer diferentes formas de uso, manejo y clasificación tradicional de esta especie entre los grupos indígenas; los diferentes criterios y mecanismos de selección artificial; el papel de esta especie en la subsistencia de la población que la usa; y a analizar la interacción de todos estos factores para determinar formas de manejo y grados de domesticación Los estudios etnobotánicos incluyeron recorridos de campo, colecta de especímenes, entrevistas con la gente asi como muestreos para evaluar la productividad de frutos en poblaciones silvestres y cultivadas. Los estudios etnobotánicos de campo fueron complementados con estudios etnohistóricos y revisión de estudios arqueológicos con el fin de reconstruir un cuadro de la historia de uso y manejo de esta especie por los hombres Mesoamericanos. Los detalles metodológicos pueden consultarse en los Apéndices 1 y 2.

2. Se analizaron los patrones de variación morfológica en nueve poblaciones de esta especie: 5 poblaciones silvestres en diferentes sitios del Valle de Tehuacán y la Mixteca Baja con condiciones ambientales contrastantes; 2 poblaciones "manejadas *in situ*", una del Valle de Tehuacán y otra de la Mixteca Baja. Estas poblaciones son resultado de la tolerancia y promoción de algunos individuos con fenotipos deseables durante el aclareo de terrenos para la siembra de maíz. Le hemos llamado "manejadas *in situ"* porque se lleva a cabo en areas originalmente con vegetación natural e individuos originalmente silvestres; y finalmente, se analizaron tambien 2 poblaciones cultivadas, una del Valle de Tehuacán y otra de la Mixteca Baja Una muestra de individuos de cada población fueron considerados en el análisis. En total se incluyeron 165 individuos y se analizaron 23 características morfológicas. Se consideraron características de estructuras reproductivas y vegetativas. Se efectuaron análisis estadísticos multivariados para analizar patrones de similitud morfológica en relación con las condiciones ambientales y formas de manejo. Con base en el análisis de frecuencias de rasgos morfológicos, se hizo una estimación de la diversidad fenotipica en cada población. Los detalles de esta investigación se pueden consultar en los Apéndices 3 y 4.

3. Las mismas poblaciones e individuos referidos en el párrafo anterior fueron estudiados en términos de polimorfismo alenzimático en una muestra de enzimas. Este estudio fue usado como referencia para anlaizar patrones de variación genética en las poblaciones. Se estimaron indices de diversidad alélica y genotípica y se les comparó con la diversidad fenotípica estimada en el estudio referido anteriormente. Se analizó la disimilitud genética entre poblaciones como punto de referencia para examinar su historia y su relación con el manejo humano Los detalles de este estudio pueden consultarse en el Apéndice 5

4. Se estudiaron los sistemas de reproducción sexual y asexual con el fin de analizar su papel en la generación de variación y la estructura genotípica y fenotípica de las poblaciones. Se describieron los procesos de propagación vegetativa y se evaluó el número de genotipos idénticos en cada población con el fin de examinar la importancia de la reproducción asexual. Se hicieron experimentos en campo con el fin de evaluar el grado de autocompatibilidad y autoincompatibilidad en los sistemas de reproducción sexual. Se hicieron estudios detallados de la biología floral y fenología asi como experimentos en campo, con el fin de precisar los mecanismos de polinización y los polinizadores de esta especie. Se hicieron colectas de especimenes de visitadores diurnos y nocturnos y se identificaron los polinizadores mas probables. Los detalles de este estudio se encuentran en el Apéndice 6.

IV. AREA DE ESTUDIO

EL VALLE DE TEHUACÁN Y LA MIXTECA BAJA

El presente estudio se llevó a cabo en el Valle de Tehuacán, en el estado de Puebla, y en la región conocida com La Mixteca Baja en el estado de Oaxaca. En estas zonas co-existen poblaciones silvestres y cultivadas de *Stenocereus stellatus* y existen además alrededor de 10 grupos indigenas con una historia cultural en la cual han interactuado con *S. stellatus* por mas de 4,500 años, de acuerdo con los estudios arqueológicos de MacNeish en el Valle de Tehuacán (MacNeish, 1967; Smith, 1967). Estas condiciones representan la posibilidad de analizar procesos de domesticación de una misma especie en diferentes contextos culturales y en diferentes condiciones ambientales.

El Valle de Tehuacán es una región de aproximadamente 10,000 Km2, localizado en la porción sureste del estado de Puebla y el noroeste del de Oaxaca (Figura 3). Es parte de la Cuenca del Papaloapan. Se caracteriza por la presencia de climas áridos y semi-áridos con precipitaciones medias anuales de entre 300 y 500 mm. Se encuentran presentes en esta área una gran variedad de asociaciones de especies formando diferentes tipos de Bosque Tropical Caducifolio y Matorral xerófilo, de acuerdo con la clasificación de tipos de vegetación de Rzedowski (1978). El Valle de Tehuacán es un área con alta diversidad biológica. por ejemplo, Dávila *et al.* (1993) reportan cerca de 3,000 especies de plantas, 30% de las cuales son endémicas. Esta zona es también de una considerable diversidad cultural. Asi, en tan relativamente pequeño territorio se encuentran presentes siete grupos indígenas: Popoloca, Nahua, Mixteco, Mazateco, Chinanteco, Ixcateco y Cuicateco.

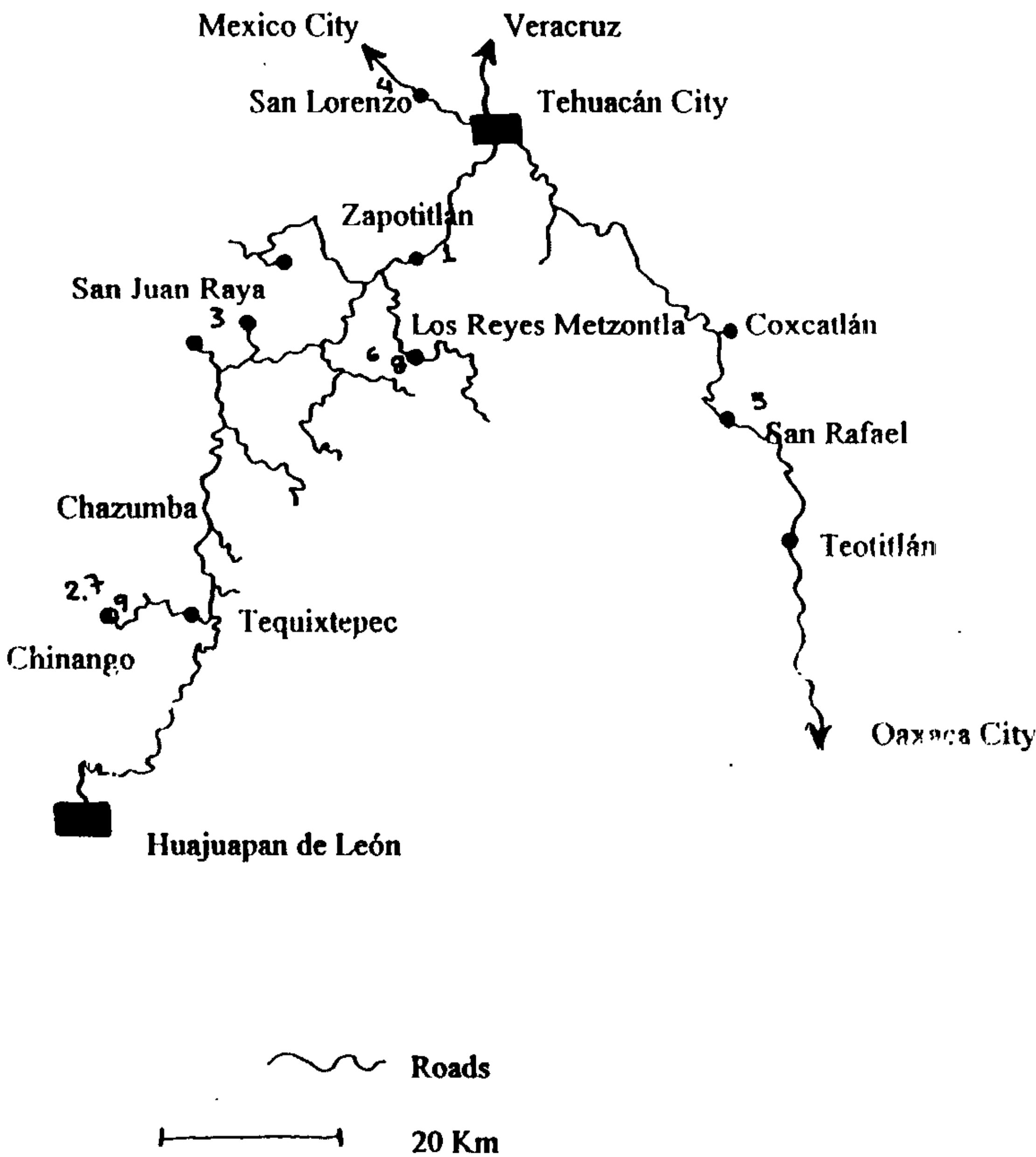

Figura 3. Area de estudio. 1. Población Zapotitlán, 2) población Chinango-silvestre, 3) Población San Juan Raya, 4) Población San Lorenzo, 5) Población Coxcatlán, 6) Población Metzontla-manejada in situ, 7) Población Chinango manejada in situ 8)Población Metzontla cultivada, 9) Población Chinango-cultivada.

La región de La Mixteca Baja se encuentra localizada en el noroeste del estado de Oaxaca, el sureste de Puebla y el noreste de Guerrero. Colinda con la porción sureña del Valle de Tehuacén. Esta región forma parte de la Cuenca del Balsas. Es una región con una topografía conformada por una compleja red de sistemas montañosos, con altitudes de entre 600 y 3,000 m.s.n.m. y tipos de vegetación que van desde Matorrales Xerófilos y Bosques Tropicales Caducifolios en las tierras bajas secas y calientes, hasta Bosques de Encino, Pino y *Abies* en las tierras altas, húmedas y templadas. *Stenocereus stellatus* está ampliamente distribuido en los Matorrales Xeróflos y Bosques Tropicales Caducifolios con entre 600 y 700 mm de precipitación anual. En esta región viven principalmente Mixtecos y en algunas areas conviven con Nahuas, Tlapanecos, Amuzgos y Zapotecos.

POBLACIONES DE *STENOCEREUS STELLATUS* ESTUDIADAS

Para los propósitos de las diferentes fases de este estudio, se eligieron tres grupos de poblaciones de *Stenocereus stellatus* manejadas en forma diferente tanto en el Valle de Tehuacán como en la Mixteca Baja. (Figura 3). Información general sobre aspectos ambientales y culturales de las 9 poblaciones escogidas se encuentran en las Tablas 2 y 3. El primer grupo esta compuesto por cinco poblaciones silvestres:

Población Zapotitlán. Se encuentra localizada dentro del área del Jardín Botánico "Heha Bravo-Hollis" en Zapotitlán de las Salinas, Puebla. Tiene una extensión de aproximadamente 2.6 hectáreas, ocupando un parche de suelos derivados de areniscas. La vegetación es un Matorral Xerófilo en el cual *Stenocereus stellatus* es un elemento dominante, con 273.3 individuos por hectárea. Otros elementos importantes son *Agave karwinskii*, *Opuntia pillifera, Mimosa luisana, Acacia constricta, Bursera* spp., *Lippia graveolens, Neobuxbaumia tetetzo*, *Myrtillocactus geometrizans* y *Stenocereus pruinosus.*

Población Chinango-Silvestre. Se encuentra aproximadamente 40 km fuera de los limites del Valle de Tehuacán, en La Mixteca Baja. Se encuentra asentada en un parche de vegetación primaria de Bosque Tropical Caducifolio en el "Cerro de la Barcina" 5 Km al noroeste de la comunidad de Santa Catalina Chinango, municipio de San Pedro y San Pablo 'Tequixtepec, Oaxaca (30 Km al norte de Huajuapan de León, Oaxaca). Se encuentra también sobre suelos derivados de areniscas ocupando una superficie de aproximafamente 60,000 m^2. *Stenocereus stellatus* es uno de los componentes importantes de la vegetación con 3 5 individuos por hectárea. Otras especies importantes son *Escontria chiotilla, Myrtillocactus geometrizans, Bursera morelensis, B. bipinnata, Acacia farnesiana, A. cochliacantha* y

TABLA 2. CONDICIONES AMBIENTALES DE LAS POBLACIONES DE STENOCEREUS STELLATUS ESTUDIADAS.

Population	Ecological condition	Elevation (m)	Annual mean temperature (°C)	Annual mean precipitation (mm)	Soils	Habitat
Zapotitlán	Wild	1550	21.2*	450*	Derived from sandstones	Thom scrub forest
San Lorenzo	Wild	1700	19.1*	590*	Derived from limestones	Thom scrub forest
San Juan Raya	Wild	1800	20.9*	649.7*	Derived from limestones	Thom scrub forest
Coxcatlán	Wild	1000	23.8*	440.6*	Aluvial	Tropical deciduous forest
Chinango-W	Wild	1700	20.6*	720.5*	Derived from sandstones	Tropical deciduous forest
Metzontla-M	Managed in situ	2000	17.23**	527.87**	Derived from limestones	Thom scrub forest cleared for agriculture

TABLA 2. CONDICIONES AMBIENTALES DE LAS POBLACIONES DE STENOCEREUS STELLATUS ESTUDIADAS

Population	Ecological condition	Elevation (m)	Annual mean temperature (oC)	Annual mean precipitation (mm)	Soils	Habitat
Chinango-M	Managed *in situ*	1700	20.6*	720.5*	Derived from sandstones	Tropical deciduous forest cleared for agriculture
Metzontla-C	Cultivated	1900	17.23**	527.87**	Aluvial	Home gardens
Chinango-C	Cultivated	1600	20.6*	720.5*	Aluvial	Home gardens

*Based on García 1988

**Based on Valiente 1991

TABLE 3. ASPECTOS SOCIALES Y CULTURALES EN LOS SITIOS ESTUDIADOS

Sitio	Grupo étnico	Población	Aspectos económicos
Zapotitlán	Popoloca	6000	Minning, craft manufacturing and commercialization of Onix
San Juan Raya	Popoloca	300	Maize and beans seasonal agriculture; cattle and goat raising
Los Reyes Metzontla	Popoloca	5300	Pottery; maize and beans seasonal agriculture, raising of goats
San Lorenzo	Nahua	200	Maize and beans seasonal and irrigated agriculture; raising of goats
Coxcatlán	Nahua	3000	Sugar cane irrigated agriculture; maize and beans seasonal agriculture; cattle and goat raising
Chinango	Mixtec	300	Maize and beans seasonal agriculture; raising of goats; production and commercialization of fruits of S. stellatus and S. pruinosus

Prosopis laevigata.

Población San Juan Raya. Localizada en "Rancho San Isidro", cerca del poblado de San Juan Raya, municipio de Zapotitlán de las Salinas, Puebla. Es un parche de vegetación de aproximadamente 50,000m^2 de extensión, asentado sobre suelos calizos. Se encuentra cubierto por un Matorral Xerofilo en el cual predomina el "izote" *Yucca periculosa* y por tal razón este tipo de asociación puede ser caracterizado como "izotal". *Stenocereus stellatus* tiene una densidad de población de 29.41 individuos por hectárea. Otros elementos importantes de la vegetación son *Myrtillocactus geometrizans, Neobuxbaumia mezcalaensis, Acacia bilimeckii, A. constricta, Pithecollobium acatlensis, Prosopis laevigata, Ipomoea arborescens* y *Ferocactus robustus.*

Población San Lorenzo. Se encuentra localizada en la Mesa de San Lorenzo, un area con suelos calizos localizada en los limites orientales de la ciudad de Tehuacán. La vegetación es un Matorral Xerófilo del tipo "Izotal", con la predominancia de *Yucca periculosa* y en donde también son importantes *Acacia constricta, A. subangulata, Fouquieria formosa, lpomoea arborescens, Bouvardia longiflora, Pedilanthus aphyllus, Pachycereus marginatus, Coriphanta pallida, Opuntia pillifera, Ferocactus robustus, F. latispinus, Hechtia* spp. y *Bursera* spp. *Stenocereus stellatus* tiene una densidad de población de 34 individuos por hectárea.

Población Coxcatlán. Esta población se encuentra localizada 10 Km al sureste del poblado de Coxcatlán, dentro de los terrenos comunales de la comunidad de San Rafael, muicipio de Coxcatlán, Puebla. Se encuentra asentada sobre un valle aluvial de aproximadamente 150,000m^2. La vegetación está constituida por elementos característicos tanto del Matorral Xerófilo como del Bosque Tropical Caducifolio. La especie mas abundante es *Escontria chiotilla,* la jiotilla, razón por la cual se puede considerar como el tipo de vegetación descrito como "Jiotillal" Rzedowski, 1978). Otras especies comunes son *Bursera morelensis, Ziziphus amolle, Myrtillocactus geometrizans, Pachycereus weberi, Gyrocarpus mocinianum, Acacia cochliacantha, A. constricta, Neobuxbaumia tetetzo, Mimosa luisana, Ceiba parvifolia, Cyrtocarpa procera, Ipomoea arborescens* y *Agave macroacantha. Stenocereus stellatus* también es importante, con una densidad de población de 280 individuos por hectárea.

El segundo grupo de poblaciones está formado por dos poblaciones manejadas *in situ.* Una del Valle de Tehuacán y otra de La mixteca Baja.

Población Metzontla-Manejada *in situ.* Se encuentra localizada en parcelas agrícolas en suelos derivados de areniscas, en un valle intermontano al norte del poblado de Los Reyes Metzontla, muicipio de Zapotitlán de las Salinas, Puebla. El área de este valle es aproximadamente 20,000 m^2 y *Stenocereus stellatus* se encuentra con una densidad poblacional de 120 individuos por hectárea. Otras especies toleradas en la misma forma que *S. stellatus* en este sitio son: *Escontria chiotilla*, *Myrtillocactus geometrizans, Polaskia chichipe* y *P. chende.*

Población Chinango-Manejada *in situ.* Esta población se encuentra a 800 m de la población silvestre de la comunidad de Chinango descrita anteriormente. Tiene una superficie de aproximadamente 80,000 m^2. *Stenocereus stellatus* tiene una densidad de población de aproximadamente 48 individuos por hectárea. *Escontria chiotilla* es tolerada también en el mismo sitio.

El tercer grupo está compuesto por dos poblaciones cultivadas, una del Valle de Tehuacán y otra del La Mixteca Baja:

Poblacion Metzontla-Cultivada. *Stenocereus stellatus* se cultiva en las huertas de las casas indígenas. El 90% de estas huertas carece de riego y por tal razón se cultivan principalmente especies nativas. *S. stellatus* se encuentra con una densidad de población promedio de 780.86 individuos por hectárea. Es el principal componente de las huertas junto con S. *pruinosus* y *Leucaena esculenta.*

Población Chinango-Cultivada. Es parte de las huertas del poblado de Santa Catalina Chinango. *S. stellatus* es el elemento vegetal predominante, con una densidad poblacional de 93.87 individuos por hectárea.

V. INFORMACION ETNOBOTANICA

MATERIALES Y MÉTODOS

1. Se recopiló información bibliográfica sobre investigaciones arqueológicas, códices prehispánicos y postcortesianos, asi como crónicas de la conquista y colonia, con el fin de integrar un panorama de la historia de uso y manejo de esta especie.

2. Se llevaron a cabo, de manera extensiva, exploraciones etnobotánicas a nivel regional en el Valle de Tehuacán, y La Mixteca Baja, entre diferentes grupos étnicos,

principalmente Nahuas, Popolocas y Mixtecos, con el fin de recopilar información sobre el uso y manejo que sobre *S. stellatus* se lleva a cabo actualmente en diferentes condiciones ambientales y culturales. Esta información se consideró relevante para analizar los móviles de la selección artificial, esto es, las formas en que ésta opera, los caracteres seleccionados, y el significado cultural de la domesticación en diferentes condiciones ambientales y culturales.

3. Se efectuaron estudios más detallados en seis comunidades indígenas, dos predominantemente Náhuatl (Coxcatlán y San Lorenzo) donde los productos de S. *stellatus* se obtienen principalmente de la recolección; dos comunidades Popolocas (Zapotitlán de la Salinas y San Juan Raya) en las cuales los productos de *S. stellatus* también proceden predominantemente de la recolección; otra Popoloca (Los Reyes Metzontla) en donde el cultivo de *S. stellatus* se combina con la recolección y manejo de poblaciones silvestres; y una comunidad mixteca (Santa Catalina Chinango) donde también se combinan el cultivo y recolección de partes útiles de esta especie.

En estas comunidades se hicieron entrevistas semi-estructuradas a un total de 26 campesinos que fungieron como informantes clave continuamente, y a 45 campesinos que fungieron como informantes ocasionales. Los informantes clave fueron elegidos por su experiencia en el manejo de S. *stellatus,* de acuerdo con información obtenida con las autoridades de cada comunidad y de acuerdo con el conocimiento de la gente desarrollado a lo largo del estudio. Los 45 informantes ocasionales fueron los propietarios de huertas frutícolas de las comunidades estudiadas, escogidas al azar como muestra para estimar la productividad de esta especie bajo cultivo. Las entrevistas estuvieron dirigidas a elaborar un inventario de formas de usos, formas de preparación y consumo y caracteres morfológicos preferidos para los diferentes propósitos utilitarios. Se efectuó también un estudio de las clasificaciones indígenas (nomenclatura, clasificación y caracterización cultural de las variantes infraespecíficas del xoconochtli). Este último estudio se hizo bajo la consideración de que en los sistemas de clasificación tradicional se permite apreciar el grado de diferenciación que presentan las variantes infraespecíficas y los rasgos sobre los cuales se establece tal diferenciación. Se detallaron aspectos sobre manejo de las poblaciones silvestres sujetas a recolección, tales como épocas de cosecha, estrategias de recolección, estimaciones de productividad de frutos en poblaciones silvestres, asi como prácticas silvícolas mediante las cuales ésta se incrementa. Igualmente, se detallaron las prácticas de manejo de esta especie durante su cultivo y tolerancia durante la apertura del bosque. En particular, se puso énfasis en conocer las técnicas de selección artificial y mejoramiento empírico.

Se hicieron estimaciones de productividad de frutos en poblaciones silvestres, manejadas in situ y cultivadas en las huertas. Para ello se hicieron muestreos de abundancia de individuos en las nueve poblaciones descritas anteriormente. Se contaron los individuos que produjeron frutos durante 1995, el número total de ramas por individuo, el número de ramas que produjeron frutos, el número de frutos por rama y el peso promedio de los frutos. Con base en la evaluación directa del número de frutos producidos y su peso, por individuo en cada muestra, se estimo la productividad de frutos por hectárea en cada población. Los detalles metodológicos de esta parte del estudio pueden apreciarse en los Apéndices 1 y 2.

ASPECTOS HISTORICOS DEL USO Y MANEJO DE *STENOCEREUS STELLITUS*

La única referencia de material arqueológico de *Stenocereus stellatus* es la aportada por Smith (1967), quien identificó restos de esta especie (clasificados como *Lemaireocereus stellatus)* entre los restos vegetales obtenidos en las excavaciones arqueológicas del Valle de Tehuacán coordinadas por MacNeish (MacNeish, 1967). Smith encontró restos de esta especie en estratos prehistóricos de diferentes sitios del Valle de Tehuacán. El mas antiguo corresponde al de la fase "Abejas", con una antigüedad de aproximadamente 4,500 años antes del presente (fechas no calibradas). También identificó a esta especie entre los restos de la fase "Palo Blanco", de aproximadamente 2,000 años antes del presente.

Es importante señalar, sin embargo, que los fechamientos de los materiales publicados por MacNeish (1967) están siendo revisados mas recientemente, encontradándose algunas imprecisiones (Long *et al.* 1989) en los métodos de estimación de la antigüedad de los estratos y errores importantes al extrapolar la fecha de los estratos a restos específicos encontrados dentro de éstos. Igualmente, han sido detectados algunos exores en la identificación del material vegetal (ver por ejemplo Zárate, 1994 y Casas y Caballero, 1996). Esto hace necesario diseñar nuevos estudios en ambas direcciones. Esto es, fechar específicamente los restos de interés con métodos mas modernos de fechamiento y trabajar de nueva cuenta la identificación de los restos arqueológicos. En particular, en el caso estudiado**,** hace falta aún precisar la identidad de restos arqueológicos identificados por Smith (1967) como pertenecientes a otras especies de cactáceas columnares: *Cephalocereus hoppenstedtii*, *Escontria chiotilla*, *Pachycereus hollianus*, *P. weberi*, y *Myrtillocactus geometrizans*, los cuales podrían ser confundidos con restos de otras especies de cactáceas columnares, incluyendo *S. stellatus.*

Los restos arqueológicos de *S. stellatus* son relativamente escasos. Lo mismo ocurre con otras especies de cactáceas columnares que no solamente son abundantes en la zona sino que en la actualidad son además importantes recursos para la economía campesina. Debido a tat escasez, de restos arqueológicos, Smith consideró que todas estas especies fueron poco importantes en la dieta de la gente de la prehistoria. No obstante, basado en evidencias a partir de coprolitos de los mismos sitios y estratos, Callen (1967) encontró que en las fases Ajalpan y Santa María (entre 3,500 y 2150 años antes del presente) los tallos, frutos y semillas de las especies de *Lemaireocereus* (incluyendo varias especies de los géneros *Pachycereus* y *Stenocereus,* entre ellos *S. stellatus)* se encontraban entre los principales constituyentes de la dieta humana en Tehuacán. Aunque la identificación de materiales botánicos en coproloitos es aún mas difícil, es posible distinguir en términos generales las estructuras de cactáceas columnares de las de *Opuntia*, su mas cercana fuente de error. Esta información contradice las conclusiones que pueden obtenerse a partir del muestreo de estratos arqueológicos en las cuevas exploradas. Esto es, las cactáceas columnares podrían haber sido mas relevantes en la dieta humana que lo concluido por Smith (1967). Las cactáceas columnares no sólo son elementos predominantes en el paisaje de la zona sino que además son fuente, todas las especies, de frutos y semillas (y algunas especies también de tallos) comestibles. La abundancia de recursos y su producción a lo largo del año (como se verá en otro apartado del presente estudio) permiten suponer a las catáceas columnares como fuentes importantes de alimentos y otros productos para economías basadas en la recolección y agricultura incipiente.

En coprolitos de las fases "Ajalpan" y "Santa María", Callen (1967) encontró que los tallos y frutos de cactáceas columnares tienen una apariencia tal que sugieren haber sido consumidas directamente. No obstante, las semillas de estas plantas parecen haber sido consumidas después de haber sido asadas. En la fase "Palo Blanco" (2,150-1,300 años antes del presente), los restos de tallos de cactáceas columnares carecen de epidermis, sugiriendo que fueron consumidos después de haber sido asados, el tejido interno fui consumido y la epidermis desechada. No existen evidencias de haber consumido tejidos hervidos de ninguna cactácea.

No existen evidencias arqueológicas que sugieran formas específicas de manejo ni tampoco cambios morfológicos aparentes en los restos encontrados que sugieran procesos de domesticación en ninguna de las especies de cactáceas columnares.

Las referencias etnohistóricas sobre cactáceas columnares son escasas en comparación con las que existen para otras plantas. No existe ninguna información disponible sobre cactáceas columnares en los códices prehispánicos disponibles en la actualidad. no obstante, hay algunas referencias en los documentos post-conquista: 1) el primero de ellos está en la "Historia General y Natural da las Indias" escrita por el capitán Hernández de Oviedo y Valdés, primer cronista del Nuevo Mundo, publicada en 1535 (ver Apéndice 1), en donde se describen por primera vez los frutos de las cactáceas llamadas "**pitahayas**" usadas como alimento por los indígenas. 2) La segunda referencia es encontrada en el Códice Florentino, de 1547, después traducido al español por Fray Bernardino de Sahagún en su "Historia de las Cosas de la Nueva España", publicado en 1582. En este documento se mencionan el "**Netzolli**", el cual de acuerdo con la ilustración parece ser *Escontria chiotilla* (ver Apéndice 1), y el "**Teunochtli**", el cual por la ilustración y el uso como antorcha parece ser *Polaskia chichipe.* 3) La tercer referencia se encuentra en el Códice de la Cruz Badiano, de 1552, en el cual se describe a una cactácea columnar llamada **"Teonochtli"** (identificada por Bravo-Hollis, 1978 como una especie del género *Stenocereus),* el cual era utilizado para tratar los dolores de muelas. 4) Francisco Hernández en su "Historia Natural de la Nueva España", escrita entre 1571 y 1576 describió varias especies de *Opuntia, Ferocactus, Mammillaria, Hylocereus* y *Myrtillocactus geometrizans,* asi como un **"Teonochtli"** usados en la medicina tradicional indígena. El **"Teonochtli",** por la descripción, parece ser el mismo descrito en el Códice Florentino y que a nuestro juicio parece ser *Polaskia chichipe.* 5) En las "Relaciones Geográficas del siglo XVI" solamente se encontró una referencia a cactáceas columnares. En la "Relación de Acatlán", escrita por Juan Vera en 1581 se menciona al **"Teonochtli"** usada por su fruta de sabor **agradable** y sus tallos usados como antorcha, el cual, nuevamente, parece ser *Polaskia chichipe.*

Hasta aqui, es notoria la escasez de referencias sobre el uso de cactáceas columnares en las fuentes historicas del siglo XVI. Y es, además ausente cualquier información sobre el cultivo u otra forma de manejo de cualquiera de las plantas referidas (ver Apéndice 1).

La siguiente etapa de información se encuentra en los siglos XVIII y XIX, en las obras del misionero Miguel Barco, entre 1773 y 1780 (Barco,1988) y Francisco Javier Clavijero en 1852. En sus libros, estos autores hacen excelentes descripciones de la morfología y usos de *Stenocereus turberi, Machaerocereus gumosus, Lophocereus schotii* y *Pachycereus pringlei* en el norte de México. Todas estas especies se describen como recolectadas de poblaciones silvetres.

En relación con las cactáceas, en todos los documentos historicos mencionados aquí, existe un aspecto importante en común: existen varias referencias al cultivo de *Opuntia,* especialmente de las especies destinadas a la producción de grana, pero no existe ninguna en relación con el cultivo de cactáceas columnares. Es difícil asumir que las personas que escribieron estos documentos no se hayan dado cuerna de la presencia de estas plantas en las huertas y solares indígenas. Entonces, la omisión de estas plantas en los documentos historicos tiene dos posibles explicaciones: o los españoles no consideraron importantes estas plantas y por eso no las describieron (como ocurrió con muchas otras plantas), o su cultivo se inició mas recientemente. Se requieren aún mas evidencias para concluir al respecto. No obstante, es importante mencionar que en el Valle de Tehuacán y La Mixteca Baja fué posible observar bajo cultivo las siguientes especies de cactáceas columnares: *Stenocereus stellatus, S. pruinosus, S. treleasi, Pachycereus hollianus* y *P. marginatus,* las cuales son cultivadas intensamente en las huertas y solares. También son cultivadas, aunque en menor escala *Escontria chiotilla, Polaskla chichipe, P. chende* y *Myrtillocactus geometrizans.* Estas últimas mas bien asociadas a una forma de tolerancia y promoción in situ o como producto de su establecimiento espontáneo en áreas antropogénicas. En los casos de *Stenocereus stellatus* y *S. pruinosus* es posible observar una gran variedad de frutos en ambas regiones y, como se discutirá mas adelante, existen dentro de las huertas algunos fenotipos que son exclusivos de las condiciones bajo cultivo, es decir, que no existen en condiciones silvestres. Esta marcada. divergencia sugiere que la selección artificial y probablemete el cultivo de estas especies se remonte a tiempos prehispánicos. Uno de los propósitos de esta investigación es justamente aportar elementos que permitan una reinterpretación de la información que ofrecen los restos arqueológicos. Mayores detalles sobre esta información podrán consultarse en el Apéndice 1.

ASPECTOS ETNOBOTÁNICOS DE *STENOCEREUS STELLATUS* EN EL PRESENTE

Clasificación tradicional

Cuando los españoles llegaron a las Antillas, vieron cactáceas por primera vez. Entoces adoptaron el nombre de **"tuna"** para los frutos de *Opuntia* spp. y **"pitahaya"** para los frutos de varias especies de cactáceas columnares y del género *Hylocereus.* Estos son los nombres mas comunes en México en la actualidad, aunque los pueblos indígenas han conservado sus propios sistemas de clasificación. Los Nahuas clasifican a las cactáceas columnares bajo el término **"nochcuahuitl"** mientras que los Mixtecos lo hacen bajo el término **"tundíchi"** en ambos casos el término significa "árbol de pitahayas" y los Popolocas usan el término **"túchi"** que es nombre que designa los frutos de *Opuntia y* de todas las cactáceas columnares. En todos los casos los frutos son la característica que proporciona el criterio principal de clasificación. Lo mismo puede apreciarse a otros niveles inferiores de clasificación. Así. *Stenocereus stellatus* es nombrado **"xoconochtli"** (pitahaya agria) por los Nahuas**, "ndíchi cáâya**" (pitahaya de arena) por'los mixtecos y **"túchikíshi"** (árbol de pitahayas) por los Popolocas. Las variedades de esta especie, en todos los casos son distinguidas y nombradas primeramente por el color de su pulpa, en un siguiente nivel por su sabor, en uno siguiente por el tamaño del fruto, en uno siguiente por el grosor de la cáscara y finalmente, por la abundancia de espinas (Ver Apéndices 1 y 2 para mayores detalles). Estas características del fruto son, además, las características que la gente toma en cuenta para ejercer selección artificial. En general, la gente considera que las frutas del monte son de color rojo, de sabor mas agrio, de tamaño pequeño, de cáscara gruesa y espinosos. Aunque reconocen que hay variantes mas dulces, o de frutos mas grandes, o de cáscara mas delgada o menos espinosos. Los frutos cultivados pueden diferir en uno o varios de estos caracteres, pero generalmente prefieren los frutos de "color", que quiere decir diferentes al rojo, los frutos grandes, dulces, de cáscara gruesa y menos espinosos. Hay excepciones, pues los Mutes agrios son mejores para hacer aguas frescas o mermeladas y los frutos con cáscara gruesa resisten mas a la pudrición (Ver Apéndices 1 y 2).

Uso y manejo

Aunque esta planta puede ser usada como forraje, leña y para protección de suelos, el principal uso es como alimento humano. Son comestibles los brotes florales, las semillas y ocasionalmente también los tallos jovenes. Pero los frutos enteros son la principal parte comestible. Se consumen generalmente como fruta fresca, aunque también es común secarlos al sol para producir **"xoconochtles pasados",** o preparar mermeladas y jaleas, todo ello como conservas, y hasta el vino **"nochoctli"** producto de la fermentación de la pulpa (Ver Apéndices 1y2).

Se observaron tres formas de interacción entre la gente del área y estas plantas: 1) la recolección de frutos en poblaciones silvestres, en la cual aparentemente no existe un impacto significativo en las poblaciones, pues ésta nunca llega a ser intensa. 2) Manejo *in situ*, el cual se efectúa en las poblaciones silvestres que ocupan las areas que se abren al cultivo de maíz. En este caso, se dejan en pie los árboles con fenotipos favorables y se eliminan otros con menor valor utilitario (con base en las características de los frutos). De entre los individuos dejados en pie, la gente comunmente propaga estructuras vegetativas para ocupar espacios en los cuales los xoconochtles no compiten con el maíz. Esta estrategia de promoción puede también incrementar aún mas la frecuencia de los fenotipos favorables. Y 3) el cultivo, principalmente en las huertas y solares de los hogares indígenas. En este caso, se propagan estructuras vegetativas de poblaciones silvestres o manejadas in situ, especialmente de individuos con fenotipos favorables, o bien de otros individuos previamente cultivados. Comunmente existe intercambio de materiales de propagación entre familias y compadres de la misma comunidad, pero en ocasiones también de comunidades lejanas famosas por la calidad de sus xoconochtles. Es importante mencionar también que dentro de las huertas y solares es común que la gente tolere las plántulas que surgen espontáneamente debido a la propagación de semillas en heces fecales de humanos, murciélagos y aves (como se discute mas adelante) En este caso se tolera la planta por 3 o 4 años, cuando producen frutos. Si los frutos son de buena calidad, la planta se deja en pie, si no lo es, se elimina para darle espacio a otras que si lo son. Esta última estrategia es de importancia pues a través de ella se incorporan a las huertas nuevas variantes producto de la reproducción sexual (ver Apéndices 1 y 2 para mayores detalles).

Productividad de frutos

En los Apéndices 1 y 2 se puede apreciar que los individuos de las poblaciones silvestres y manejadas presentan niveles similares de productividad de frutos, mientras que los individuos son significativamente mas productivos. Esto se explica debido a que presentan, en general, un mayor número de ramas, una mayor proporción de ramas productivas, un mayor número de frutos por rama y un mayor tamaño de frutos. Es importante, sin embargo, señalar que de las poblaciones manejadas, la poblacion de Metzontla presentó una productividad mayor a la de cualquier población silvestre, a diferencia de la población manejada de Chinango. Esto se debe a que los individuos de Chinango tienen menos ramas que los de Metzontla. En Chinango, donde hay poblaciones silvestres y la producción bajo cultivo es elevada, la tolerancia se practica pero no adquiere gran relevancia y los campesinos suelen cortar ramas de estas plantas para evitar competencia por espacio con el maíz. En cambio en Metzontla las poblaciones silvestres son muy escasas y la gente cuida los productos de esta planta en condiciones de manejo *in situ*. Esto sugiere que bajo ciertas condiciones, las poblaciones manejadas in situ permiten incrementar la disponibilidad de recursos, y en algunos casos también la calidad, en comparación con las silvestres.

Papel de *Stenocereus stellatus* en la subsistencia campesina

En Zapotitlán, San Juan Raya, San Lorenzo y Coxcatlán el cultivo de esta planta es de poca importancia. Existen poblaciones silvestres se las cuales se recolectan ocasionalmente los frutos, solamente para consumo de la familia, también ocasionalmente. En Metzontla la producción agrícola enfrenta serios problemas por las frecuentes sequías y debido a u grave deterioro de los suelos. La producción alfarera desde tiempos prehispánicos ha sido el principal soporte de la economía campesina en este poblado**.** Sin embargo, en los últimos años el mercado de estos productos ha declinado sensiblemente. En este caso los solares constituyen un apoyo crucial a la subsistencia campesina. Los xoconochtles son consumidos mayormente que en las comunidades anteriores e incluso comercializados a nivel local y regional. En Chinango la producción agrícola tiene mejores condiciones que en Metzontla y además, los xoconochtles son fuente de ingresos monetarios pues, en general en la Mineca Baja,, su comercialización se encuentra mas desarrollada que en el Valle de Tehuacán. En estas dos últimas comunidades el cultivo de *Stenocereus stellatus* es de gran importancia para la economía campesina. En Metzontla, incluso la producción obtenida en las poblaciones manejadas in situ es importante, a diferencia de Chinango, donde los productos silvestres y manejados in situ son de baja calidad comercial y los frutos cultivados son mas importantes (ver Apéndices 1 y 2 para mayores detalles).

DISCUSIÓN

Este estudio encontró que los frutos son la parte mas significativa de *Stenocereus stellatus* para las culturas locales. Son la parte útil mas importante, lo cual se encuentra reflejado en los sistemas tradicionales de clasificación y son las partes sobre las cuales se ejerce selección artficial. El color y sabor de la pulpa, el tamaño de los frutos, el grosor y espinosidad de la cáscara parecen ser los caracteres con mayor significado en la percepción de la gente y aquellos sobre los que se ejerce directamente la selección. La combinación de estos caracteres de estado determina la existencia de un gran número de variantes que constituyen la materia prima de la selección artificial. Aunque la gente prefier en general los fenotipos con frutos de "color", de sabor dulce, de tamaño grande, cáscara delgada y pocas espinas, diferentes estados en cada uno de estos caracteres pueden conferir ventajas que la gente también puede favorecer. Esto significa que la selección no se ejerce unidireccionalmente hacia un fenotipo específico, sino a varios, lo que permite explicar la gran variabilidad de frutos que se puede observar en los mercados y comunidades rurale del área.

La selección artificial se lleva a cabo aparentemente a través del aislamiento y subsecuente incremento de la frecuancia de fenotipos deseados. La propagación vegetativa es, al parecer la forma mas común y mas sencilla de lograrlo. Esta forma de selección aparentemente ocurre ex situ, en las huertas y solares e in situ en las poblaciones silvestres manejadas en los sitios de ocupación original. No obstante, la tolerancia selectiva de plántulas es un forma de selección artificial que, aunque en menor escala, también existe y tiene gran importancia por su papel en la incorporación de nuevas combinaciones de alelos. Esta fuente de variación es quizás el medio por el cual las variantes exclusivas de los huertos y solares se han podido originar y divergir de los individuos de las poblaciones silvestres.

Las diferencias en productividad fueron muy marcadas entre las poblaciones cultivadas y el resto de las poblaciones. Las características que determinan la productividad de los individuos son todas posiblemente influenciadas por el ambiente, algunas de ellas posiblemente también por la edad de los individuos, pero también en parte pueden tener una base genética. Aún no podemos concluir al respecto. Vale la pena, sin embargo, mencionar que al comparar las poblaciones silvestres, las del Valle de Tehuacán presentaron productividades similares mientras que la población de La Mixteca Baja presento una productividad mayor. La diferencia mas notable entre ambas zonas es la precipitación, y este probablemente sea un factor que contribuya a explicar tal diferencia. Sin embargo, al comparar globalmente todas las poblaciones, todas las poblaciones silvestres y la población manejada de La Mixteca Baja presentaron niveles similares de productividad, la población manejada de Metzontla un nivel significativamente superior a éstas y las poblaciones cultivadas niveles significativamente superiores a todas las demás. Lo que parece indicar que las mejores condiciones de productividad están asociadas al manejo humano y, ya sean ambientales o genéticas, son un resultado evidente.

Las formas de manejo de esta especie parecen estar influenciadas por el papel que juegan sus productos en la subsistencia campesina, por la disponibilidad de recursos silvestres en calidad y cantidad suficientes para la demanda específica y por las condiciones ambientales que determinan la viabilidad de su establecimiento y producción (*i*. e disponibilidad de polinizadores). En los Apéndices 1 y 2 es posible ampliar la información hasta aquí presentada.

VI. VARIABILIDAD MORFOLÓGICA ENTRE POBLACIONES

MATERIALES Y MÉTODOS

En esta parte de la investigación se analizaron los patrones de similitud y diferencias morfológicas entre poblaciones de *Stenocereus stellatus.* Se analizaron poblaciones provenientes de diferentes condiciones ambientales y diferentes formas de manejo con el fin apreciar si los patrones de semejanzas y diferencias pueden explicarse en relación con estos factores o son idependientes de ellos. Con esto se pretendió evaluar el grado de diferenciación morfológica entre las poblaciones silvestres y aquellas sujetas a selección artificial. Se analizaron también las frecuencias en las cuales se presentan los rasgos morfológicos que al parecer son favorecidos por la selección artificial y se compararon entre poblaciones con diferentes formas de manejo. Con esto, se consideró posible evaluar si la selección artificial ha tenido algún efecto en la estructura fenotípica de poblaciones de S. *stellatus.*

Se estudiaron nueve poblaciones en total, las mismas mencionadas anteriormente. Para definir el tamaño de las muestras y las técnicas de muestreo en las poblaciones silvestres y toleradas se tomó en cuenta el tamaño de la población, la magnitud de la variabilidad morfológica presentada por los individuos, asi como la heterogeneidad ambiental en los sitios (diferencias en altitud, suelos y unidades fisiográficas). En el caso de los individuos cultivados, se tomaron muestras al azar de las huertas de dos de las comunidades humanas estudiadas. Se consideraron para este análisis unicamente individuos en edad reproductiva. Se incluyeron en el análisis 23 caracterisicas morfológicas de frutos, semillas y ramas, como se especifica en los

Apéndices 3 y 4. Se utilizaron métodos de análisis estadísticos multivariado (análisis de conglomerados, componentes principales y función discriminante) para comparar las poblaciones y analizar sus similitudes y diferencias de acuerdo con sus condiciones ambientales y las condiciones de manejo a las que se encuentran sujetas. Se efectuaron conversiones de variables cuantitativas a variables multiestado con el fin de contabilizar la frecuencia de los estados de caracteres en cada población. Esta conversión se hizo con base en análisis de varianza univariados que permitieron definir intervalos de valores significativamente diferentes para cada carácter. Con base en el índice de Simpson se obtuvieron estimaciones de grados de diversidad de cada carácter y una estimación promedio de todos los caracteres por población. Para mayores detalles de los métodos empleados se pueden consultar los Apéndices 3 y 4.

RESULTADOS

En los Apéndices 3 y 4 pueden apreciarse los detalles de los resultados obtenidos. El fenograma del análisis de conglomerado claramente distinguió en un extremo un grupo de individuos compuesto casi en su totalidad (86%) por individuos silvestres, casi todos ellos de poblaciones del Valle de Tehuacán (ver la parte superior del fenograma). En otro extremo, en la base del fenograma, separa otro grupo de individuos contituído en su totalidad por individuos cultivados, casi todos ellos provenientes de La Mixteca Baja. En la parte intermedia pueden apreciarse dos grandes grupos constituidos por mezclas de individuos con diferentes formas de manejo. Uno de ellos está formado por individuos silvestres (principalmente de Chinango) y cultivados tanto del Valle de Tehuacán como de La Mixteca Baja. El otro grupo está formado por individuos manejados y cultivados de ambas regiones.

El análisis de componentes principales resultó, en términos generales, consistente con este patrón de clasificación de individuos. En los Apéndices 3 y 4 se presentan las gráficas de los primeros tres componentes principales, los cuales explican el 53% de la variación. En estas gráficas puede apreciarse que el primer componente separa tres grandes grupos de individuos. Uno a la derecha de la gráfica constituido predominantemente por individuos cultivados, otro a la izquierda constituido predominantemente por individuos silvestres y uno en la porción media de las gráficas constituido por individuos manejados *in situ* y algunos cultivados y silvestres. Este análisis mostró que las características mas importantes para definir tal agrupamiento fueron el tamaño del fruto, el peso total de las semillas, el número de Areolas por cm^2 en frutos (carácter relacionado con el grado de espinosidad del fruto, y el grosor y peso de la cáscara.

El análisis de la función discriminante mostró que cuando se analizaron las poblaciones reales como grupos, la mayor identidad como grupos predichos se encontró entre las poblaciones silvestres mientras que las poblaciones cultivadas demostraron tener una mayor proporción de individuos similares a otras poblaciones. Se encontraron similitudes cíe algunos individuos de una población con otros de poblaciones diferentes dentro de la misma área geográfica (Valle de Tehuacán o Mixteca Baja), pero también entre poblaciones con similar forma de manejo (es decir, silvestres con silvestres, manejados con manejados y cultivados con cultivados). Al definir los grupos reales de acuerdo con la forma de manejo, se encontró que alrededor del 75% de individuos de cada grupo real formaba parte de los grupos predichos y el resto se ubicaba en diferentes grupos. Esto indica que los individuos silvestres son en general diferentes a los manejados y los cultivados diferentes a ambos y que las diferencias son estadisticamente significativas (ver Apéndice 3). En el apéndice 3 se puede apreciar la grafica de la primera y segunda función discriminante, las cuales definen los tres grupos de individuos.

En el Apéndice 3 también se muestran los intervalos de valores de cada carácter que fueron transformados en caracteres multiestado, asi como la frecuencia de cada uno de ellos por población y la estimación de indices de diversidad fenotípica también por población. La mayor diversidad fenotípica, de acuerdo con este análisis, se encontró en la población slvestre de La Mixteca Baja, mientras que los más bajos se encontraron en las poblaciones silvestres del Valle de Tehuacán. En La Mixteca Baja la población cultivada tuvo una diversidad fenotípica alta, comparable a la de la población silvestre de esa área, mientras que la población manejada fijé relativamente menos diversa. En el Valle de Tehuacán, en los Reyes Metzontla, tanto la población cultivada como la manejada *in situ* presentaron alta diversidad fenotípica, comparables a la cultivada de La Mixteca Baja y considerablemente mas alta que la encontrada entre las poblaciones silvestres.

DISCUSIÓN

Los análisis de componentes principales y función discriminante mostraron que los caracteres mas relevantes para clasificar a los grupos fueron: 1) tamaño de los frutos (mayor en los frutos cultivados; 2) densidad de espinas en frutos (mayor en los individuos silvestres); 3) peso de la cáscara (mayor en individuos cultivados, pues aunque más delgada, la masa total es mayor debido a que los frutos son de mayor tamaño); 4) grosor de la cáscara (mayor en los individuos silvestres); 5) peso total de las semillas (mayor en individuos cultivados) y 6) tamaño de las semillas (mayor en individuos cultivados). Los cuatro primeros son caracteres directamente seleccionados por la gente, de acuerdo con la información etnobotánica. A estos faltaria agregar los caracteres de sabor y color de la pulpa, los cuales resultaron no relevantes.

En el caso del color de la pulpa, aunque existen seis colores diferentes, la frecuencia de estos es relativamente baja en relación con la frecuencia del color rojo. En el caso del sabor probablemente técnicas mas precisas de evaluación pudieran arrojar otros resultados. El peso total de las semillas y su tamaño individual son características que en la actualidad no son seleccionadas directamente. Aunque estos caracteres podrían haber sido seleccionadas en el pasado, pues como se recordará el uso de semillas ha sido importante (incluso en la actualidad un litro de semillas de xoconochtle se intercambia por 15 litros de maíz), lo más probable es que tengan un relación directa con el tamaño de los frutos y que la selección por un carácter implicara indirectamente a los otros.

Los análisis multivariados clasificaron a los individuos analizados principalmente de acuerdo con su forma de manejo. Incluso, el análisis de función discriminante mostró que existen diferencias significativas entre estos grupos. Este resultado indica que existe un importante nivel de divergencia entre las poblaciones silvestres y aquellas manejadas *in situ o ex situ* (cultivadas) por los campesinos indígenas del área. Estos análisis mostraron también que existen algunos individuos que son comunes en las poblaciones silvestres y que se encuentran entre las poblaciones cultivadas pero en bajas frecuencias; también existen algunos individuos comunes bajo cultivo y que se encuentran en las poblaciones silvestres aunque en bajas frecuencias; y, finalmente, mostraron que existen algunos individuos exclusivos de las poblaciones silvestres y otros exclusivos de las poblaciones cultivadas. Esta información parece confirmar que 1) en parte los individuos cultivados provienen de las poblaciones silvestres y manejadas, 2) que su introducción no ha sido indiscriminada pues hay individuos silvestres que nunca fueron llevados a las huertas; y 3) que algunos fenotipos de los individuos cultivados se originaron y mantuvieron dentro de las huertas y solares y son incapaces de sobrevivir en condiciones silvestres.

Es importante hacer notar también que en los análisis multivariados se presentaron marcadas similitudes morfológicas entre individuos que provienen de diferentes áreas geográficas, con importantes diferencias ambientales. Igualmente, es de hacerse notar que algunos individuos cultivados que provinieron de poblaciones silvestres mantuvieron en las huertas y solares sus características morfológicas silvestres y fueron agrupados junto con los individuos silvestres. Y finalmente, también es de hacerse notar que la variabilidad morfológica de diferentes variantes se expresa incluso aún cuando son cultivadas dentro de una misma huerta, con condiciones ambientales similares. Todos estos elementos permiten sugerir que la variabilidad morfológica analizada, si bien puede tener una relación con el ambiente., parece tener también una importante base genética. Esto significa que en buena medida los cambios en los patrones de variación morfológica son heredables y que la domesticación como un proceso evolutivo está ocurriendo como parte de la maipulación de estas plantas por la gente del área.

Las diferencias significativas entre poblaciones silvestres, manejadas in situ y cultivadas sugieren que los patrones de variación han sido influidos fuertemente por el manejo humano. Esto significa que la evolución de esta especie bajo domesticación ha logrado una sigificativa divergencia morfológica con respecto a las poblaciones silvestres. Esta divergencia es especialmente marcada entre los individuos silvestres y cultivados en las huertas, donde la manipulación de estas plantas y el remplazamiento de variantes es relativamente intenso. La divergencia es también significativa entre poblaciones silvestres y manejadas in situ, pero no tan marcada como en el caso anterior pues el manejo *in situ* está dirigido principalmente a aumentar la frecuencia de fenotipos deseables dentro de las poblaciones silvestres.

Un patrón parecido de divergencia morfológica entre poblaciones silvestres, manejadas *in situ* y cultivadas fué encontrado por Casas y Caballero (1996) en la leguminosa arbórea *Leucaena esculenta.* En ese caso, la mayor divergencia se presentó entre las poblaciones silvestres y manejadas *in situ*, pero el cultivo de *L. esculenta* no era tan importante en el área estudiada como en el caso de *Stenocereus stellatus* en Metzontla y Chinango. Estos dos estudios de caso ilustran como la intensidad de la manipulación de plantas por el hombre pueden influir el grado de divergencia morfológica con respecto a las poblaciones silvestres.

Los casos de *Leucaena esculenta* y *Stenocereus stellatus* también ilustran cómo se han podido llevar a cabo cambios en los patrones de variación morfológica en plantas perennes de vida larga por los pobladores de Mesoamérica, no sólo bajo el cultivo en huertas y solares sino también a través de formas de manejo de poblaciones silvestres *in situ.* Hemos sugerido (Casas y Caballero, 1996) que la domesticación in situ es un modelo atractivo para investigar este proceso en plantas perennes, especialmente en aquellas con sistema de reproducción abierto, tales como *Leucaena* spp. Esto es debido a las dificultades para fijar caracteres deseables por medio de la siembra directa de semillas de fenotipos deseables. No obstante, el caso de *Stenocereus stellatus* sugiere que el espectro de plantas domesticadas in situ podría ser mas amplio. Como se expondrá mas adelante, *Stenocereus stellatus* tiene un sistema de reproducción sexual autoincompatible. No obstante, la fijación de caracteres deseables en esta especie se lleva acabo por la gente a través de propagación vegetativa.

Ejemplos de formas de manejo *in situ* se han descrito también para otras especies de plantas perennes asi como para numerosas anuales (Bye, 1985 y 1993; Caballero, 1994; Casas et al., 1994; Casas y Caballero, 1995 y 1996; Casas *et al.*, en prensa). Desafortunadamente, la operación de mecanismos de selección artificial en formas de manejo *in situ* ha sido poco documentada. No obstante, los casos discutidos aquí que muestran que la selección artificial puede operar in situ, asi como el patrón de manipulación de plantas in situ tan extendido en muchas partes de México, sugieren que la domesticación in situ podría ser, y haber sido en el pasado, una forma común de domesticación de plantas en Mesoamérica.

VII. VARIABILIDAD GENETICA ENTRE POBLACIONES

MATERIAL Y MÉTODOS

Las mismas poblaciones e individuos especificados en los apartado anteriores, fueron incluidas en el análisis de polimorfismo en aloenzimas. El propósito de este estudio fié comparar patrones de diversidad genética dentro y entre las poblaciones en cuestión, considerando sus diferencias en condiciones ambientales, formas de manejo y grados de domesticación. Asimismo, interesó analizar la disimilitud genética entre las distintas poblaciones. Y, finalmente, se hizo una comparación entre los patrones de diversidad geotípica con los patrones de diversidad fenotípica.

Se analizó el polimorfismo en aloenzimas. Con base en pruebas de laboratorio, se pudo determinar que el tejido fotosintético de los tallos es adecuado para este tipo de estudios. Tomando en cuenta que *S. stellatus* se propaga vegetativamente con relativa facilidad y que su crecimiento en invernadero a partir de pequeños propágulos resultó exitoso, se consideró factible colectar pequeñas ramas de los individuos estudiados y utlizarlas como materia prima para este estudio. Con ello, las poblaciones naturales prácticamente no fueron afectadas. Además, puesto que el daño que sufrirían estos materiales durante el estudio sería mínimo (ya que se requerirían no mas de 20 gramos de muestra por individuo), se consideró que los propagulos mantenidos en invernadero podrían constituir un banco de plantas vivas. Las muestras de este banco de germoplasma fueron depositadas en el Jardín Botánico de la UNAM. Los detalles técnicos de la propagación en invernadero pueden apreciarse en el Apéndice 5.

Para el análisis de isoenzimas, se llevaron a cabo electroforésis en geles de almidón. Se efectuaron pruebas de laboratorio para determinar las técnicas que permitieran obtener las bandas con mejor resolución. Se probaron cinco buffers de extracción, obteniéndose mejores resultados con la receta de Goodall y Stoddard (1989). Se probaron doce diferentes sistemas de buffers par gel y electródo, resultando mejor, para todas las enzimas anlaizadas, el sistema de Poulik (Hakim-Elahi, 1976). En total, se probó la resolución de 25 enzimas, los mejores resultados se obtuvieron con ocho de ellas. fosfatasa ácida (ACPH), diaforasa (DIA), esterasa (EST), malato deshidrogenasa (MDH), menadione reductasa (MNR), nicotinamida adenin dinucleótido deshidrogenasa (NADHDH), fofoglucosa isomerasa (PGI) y rubisco (RUB), en cada una de las cuales fue posible analizar unicamente un locus. Se analizaron en total 194 individuos de las nueve poblaciones estudiadas. Se identificaron y analizaron 24 alelos y 45 genotipos para los 8 loci analizados.

Las estimaciones de diversidad genética se efectuaron con base en los índice sesgado y no sesgado de heterozigosidad de Nei (1987), asi como a través del tonteo directo de genotipos heterozigotos. Se calcularon las frecuencias genotípicas esperadas en las condiciones de equilibrio de Hardy-Weinberg y se compararon con las observadas por medio de pruebas de X^2. Se calculó el indice de fijación (F). Los calculos de estosíndices se efectuaron a través del programa BIOSYS-1 release 1.7 (Swoford & Selander, 1989).

Se construyó una matriz de frecuencias alélicas y se calcularon matrices de disimilitud por medio de los coeficientes, sesgado y no sesgado, de distancia genética de Nei (1972 y 1978 respectivamente). Con estas matrices se efectuó un análisis de conglomerados por medio del método UPGMA y análisis de coordenadas principales. Se utilizaron los programas BIOSYS y NTSYS (Rohlf, 1993).

Los índices de diversidad fenotípica y genética se compararon a partir de un análisis de regresión lineal. También se compararon los patrones de similitud y disimilitud entre poblaciones de acuerdo con las frecuencias fenotópicas y alélicas observadas.

RESULTADOS

Los detalles de los resultados de este estudio se muestran en el Apéndice 5. La Tabla 4 que a continuación se presenta permite resumir parte de la información. En esta tabla puede apreciarse que la mayor diversidad genética se encontró entre las poblaciones cultivadas y la manejada *in situ* de Metzontla, mientras que las poblaciones silvestres del Valle de Tehuacán y la manejada *in situ* de Chinango fueron menos diversas. Este es un patrón muy similar al que puede observarse cuando se analizan la diversidad genotipica y fenotípica**.** Cuando se comparan estos patrones entre si, se encuentra que entre la heterozigosidad (H) y la diversidad fenotípica (DF) la correlación es de 0.68, mientras que cuando se comparan la diversidad genotipica y fenotípica la correlación es de 0.85. En el Apéndice 5, finalmente podrán apreciarse los patrones de similitud entre poblaciones cuando se analizan las frecuencias alélicas y fenotípicas. En este caso existen diferencias importantes, pues mientras las frecuencias fenotípicas agrupan a las poblaciones de acuerdo con su forma de manejo (silvestres con silvestres, manejadas con manejadas y cultivadas con cultivadas), las frecuencias alélicas agrupan a las poblaciones silvestres de Tehuacán con la cultivada de La Mixteca Baja, y separan como un grupo diferente a las poblaciones de Metzontla (ver Apéndice 5 para mayores detalles).

TABLA 4. HETEROZIGOSIDAD NO SESEGADA (H), DIVERSIDAD GENOTIPICA (DG) Y DIVERSIDAD FENOTIPICA (DF) ENTRE LAS POBLACIONES ESTUDIADAS

Población	H	DG	DF
Zapotitlán	0.285	0.4071	0.3637
Chinango-Silvestre	0.338	0.4685	0.4797
San Juan Raya	0.222	0.3059	0.3092
San Lorenzo0.270	0.3767	0.3962	
Coxcatlán	0.234	0.3443	0.3670
Metzontla-Manejada *in situ*	0.354	0.4527	0.4452
Chinango-Manejada *in situ*	0.278	0.3893	0.3730
Metzontla-Cultivada	0.353	0.4197	0.3916
Chinango-Cultivada	0.365	0.4164	0.4252

DISCUSIÓN

Las diferentes estimaciones de diversidad genética mostraron que ésta es relativamente baja en las poblaciones silvestres del Valle de Tehuacán y mas alta en la población silvestre de La Mixteca Baja. Las poblaciones cultivadas presentaron niveles altos de diversidad genética en ambas áreas. Entre las poblaciones manejadas *in situ* hubo resultados contrastantes pues mientras la diversidad genética fué alta en la del Valle de Tehuacán, ésta fue baja en la de La Mixteca Baja. En el Valle de Tehuacán, la población cultivada presentó niveles de diversidad marcadamente más altos que los de las poblaciones silvestres, mientras que en La Mixteca Baja tanto la población silvestre como la cultivada presentaron niveles parecidos de diversidad genética. En el Valle de Tehuacán, la población manejada *in situ* tuvo mayor diversidad que las poblaciones silvestres, mientras que en Chinango la situación fué inversa. A nivel de regiones, el promedio de la heterozigosidad no sesgada en La mixteca Baja (0.317), resultó mayor que la encontrada en el Valle de Tehuacán (0.288).

Las comparaciones arriba señaladas indican, en términos generales, que 1) la diversidad genética de *Stenocereus stellatus* en la Mixteca Baja es mayor que en el Valle de Tehuacán; 2) que el manejo humano, particularmente el cultivo en huertas, ha causado un incremento en la diversidad genética y 3) que bajo condiciones particulares, el manejo *in situ* puede incrementar o reducir la diversidad genética de las poblaciones silvestres originales.

Las estimaciones de distancia genética mostraron tres grupos de poblaciones Uno de ellos incluyó a la mayoría de las poblaciones silvestres del Valle de Tehuacán (Zapotitlán, San Lorenzo y Coxcatlán) con la población cultivada de La Mixteca Baja (Chinango-cultivada). En un segundo grupo, las poblacione silvestre y manejada *in situ* de La Mixteca Baja (Chinango-silvestre y Chinango-manejada**)** se agruparon con la restante silvestre del Valle de Tehuacán (San Juan Raya). En un tercer grupo, las poblaciones cultivada y manejada de Metzontla en el Valle de Tehuacán se separaron del resto de las poblaciones.

Estos resultados, en primer lugar indican que entre las poblaciones silvestres y cultivadas de una misma zona existen diferencias genotípicas importantes que sugieren que el flujo genético entre ellas tiene algunas barreras limitantes. En segundo lugar, la similitud genética entre los grupos de poblaciones sugiere relaciones de origen que son de gran utilidad para interpretar la historia del manejo de esta planta por parte del hombre, como se discute a continuación.

La similitud genética entre las poblaciones silvestres del Valle de Tehuacán y la cultivada de La Mixteca Baja por un lado, y la que existe entre las poblaciones silvestre y manejada de La Mixteca con la silvestre de San Juan Raya en el Valle de Tehuacán, podría ser explicada al menos por tres hipótesis: 1) interacción reproductiva entre las poblaciones que componen cada grupo; 2) inmigración de individuos entre las poblaciones que resultaron similares o 3) un origen común. Aunque aún se requiere mas información genética y ecológica para probar estas hipótesis, con la información disponible es posible decir que las dos primeras hipótesis parecen ser mas improbables. En el primer caso, bastaría con mencionar que entre las poblaciones del Valle de Tehuacán y las de La Mixteca Baja las distancias que las separan están entre 60 y 90Km, mientras que las poblaciones silvestres y cultivadas locales en cada región están separadas por entre 2 y 20Km. Lo que significa que en todo caso la interacción local seria mas probable. Lo mismo puede decirse de la migración de plantas. Aunque la gente transporta materiales de propagación vegetativa entre diferentes poblados y en ocasiones también de lugares remotos, los intercambios locales son mucho mas frecuentes

La hipótesis de un origen común parece ser, entonces, una explicación mas consistente. Esta hipótesis podría tener varias implicaciones posibles: 1) las poblaciones de

Chinango derivaron de las de Tehuacán; 2) las poblaciones de Tehuacán derivaron de las de Chinango o 3) todas ellas derivaron de poblaciones ancestrales en común. Considerando la información sobre diversidad genética, parece ser improbable que las poblaciones Chinango derivaran de las de Tehuacán. El proceso contrario podría, en todo caso, ser mas probable. En este caso, las poblaciones de Metzontla sugieren que habría diferentes fuentes de los materiales introducidos al Valle. En la tercer hipótesis, ni el Valle de Tehuacán ni La Mixteca Baja pueden ser descartados de ser centros de origen de las poblaciones estudiadas., y faltaría aún ampliar la muestra de poblaciones para poder concluir adecuadamente.

No obstante, independientemente de cual hipótesis sea mas correcta, una pregunta crucial es cuándo se separaron las poblaciones presuntamente relacionadas. En el caso del grupo conformado por las poblaciones silvestres de Tehuacán y la cultivada de Chinango, la marcada divergencia fenotípica encontrada en este estudio sugiere que tal separación pudo haber ocurrido antes de que la domesticación causara tan dramáticos cambios. Probablemente durante las primeras etapas de la domesticación de esta especie, o probablemente antes de la presencia humana en el Valle de Tehuacán.

Como se ha mencionado anteriormente, los restos arqueológicos mas antiguos de Stenocereus stellatus en el Valle de Tehuacán provienen de estratos de 4,500 años antes del presente. Esto contrasta con el tiempo de presencia humana en el área, la cual, de acuerdo con MacNeish, podría ser de aproximadamente 12,000 años. Aunque la identificación y el fechamiento de los materiales arqueológicos tienen que ser aún corroborados, en principio la información disponible indica que los humanos habitaron el Valle de Tehuacán mas de 6,000 años antes de que empezaran a usar esta planta. Como se ha dicho en alguna parte de este documento, dos de las poblaciones incluidas en este estudio provienen de San Lorenzo y San Rafael, justo en los sitios en donde se encuentran las cuevas de El Riego y Coxcatlán exploradas por MacNeish y en donde se encontraron los restos arqueológicos referidos.. En estos dos sitios la densidad de población y la productividad de frutos es considerable como para pasar desapercibida durante tanto tiempo por los cazadores recolectores de esta región. Estas observaciones podrían implicar que lo que en la actualidad parecen ser poblaciones silvestres en el Valle de Tehuacán, sean más bien relictos de plantas introducucudas en esas areas por el hombre, las cuales llegaron a naturalizarse después de algún tiempo de abandono (probablemente más de 300, como parecen indicar algunos individuos de al menos tal edad de *Neobuxbaumia tetetzo* y *Pachycereus weberi* abundantes en el área de Coxcatlán). La reducida diversidad genética característica de estas poblaciones parece apoyar esta hipótesis, pues en tal caso se habría producido un efecto "cuello de botella".

El análisis de disimilitud genotípica entre individuos (ver Apéndice 5) indica que no todos los individuos de una población son parecidos entre si. Indica que los individuos cultivados poseen algunos alelos exclusivos diferentes a los de los silvestres, y por eso establece una diferencia entre silvestres y cultivados. Pero al mismo tiempo, la introducción de materiales silvestres al cultivo determina que algunos individuos silvestres y cultivados sean parecidos a nivel local.

Se requieren aún mas evidencias para probar las hipótesis aquí planteadas. El número de loci muestreados es aún pequeño. Constituye únicamente lo que fué posible hacer en el tiempo del proyecto, considerando las dificultades técnicas enfrentadas y los retrasos en trámites de compra de equipo. Es aún posible mejorar la resolución de bandas en los geles trabajando con las enzimas incluidas en este estudio y con ello aumentar el número de loci en la muestra. Además, es posible aún mejorar la calidad de resolución en cinco enzimas mis de las probadas. Sin embargo, una herramienta potencial muy útil es el análisis del polimorfismo de ADN. Aunque planteado en el proyecto original, este análisis no fué posible al momento de escribir este informe final. El retraso en la adquisición de material y equipo para la extracción de ADN determinó serios retrasos en todo el proceso de estudio. La extracción de ADN a partir de material seco, con lo cual se pretendió subsanar el problema causado por los retrasos señalados, planteó nuevas dificultades técnicas. No obstante, se ha avanzado en definir técnicas de extracción y éstas serán de utilidad para en los próximos meses retomar esta fase del proyecto.

VIII. BIOLOGIA REPRODUCTIVA

MATERIAL Y MÉTODOS

Stenocereus stellatus se reproduce tanto sexual como asexualmente. El estudio de estos sistemas reproductivos resulta fundamental para entender la información sobre la estructura fenotípica y genotípica de las poblaciones generada en los apartados anteriores; para saber si la selección artificial ha modificado o no los sistemas reproductivos; asi como para analizar las interacciones genéticas entre las poblaciones silvestres y cultivadas
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Con respecto a la reproducción vegetativa, se describieron los mecanismos mediante los cuales ésta ocurre. Junto con la información sobre marcadores genéticos se hizo una evaluación, preliminar aún, sobre la importancia de este mecanismo reproductivo en las diferentes poblaciones.

Con respecto a la reproducción sexual, se exploraron los mecanismos reproductivos. Para ello se hicieron descripciones detalladas de la morfología floral, así como un estudio fenológico durante un año de observaciones en las poblaciones bajo estudio. El conocimiento de la temporalidad del desarrollo de las estructuras florales es una clave importante para entender los mecanismos de polinización, pero al mismo tiempo permite examinar si la selección artificial ha intervenido en la modificación de este proceso, y en qué grado, con el fin de manipular la producción de frutos. Asimismo, esta información permite analizar si el intercambio genético entre poblaciones silvestres y domesticadas es posible. Este estudio se efectuó con base en el registro de las proporciones de flores en antesis por individuo y de individuos en floración por población, en intervalos quincenales a lo largo de un año. Con este registro se pretendió conocer el momento de inicio de la floración, la tasa de floración (número o porcentaje acumulado de flores en antesis o individuos en floración a través del tiempo), el pico de floración (momento del máximo número de flores por individuo e individuos en floración por población), la duración media de la floración, y la terminación de la floración en la o las épocas de floración.

Con respecto a los sistemas de cruzamiento, se efectuaron experimentos con el fin de saber si el sistema es o no autoincompatible y si la polinización se lleva a cabo durante el día o durante la noche. Para ello se escogió una muestra de individuos por población. Con base en la experiencia de Valiente-Banuet *et al.* (en prensa), llevada a cabo con *Neobuxbaumia tetezo*, se montaron los siguientes tratamientos: i) autopolinización; ii) polinización cruzada ii) polinización nocturna iv) polinización diurna; y v) polinización natural. En cada tratamiento se tuvieron al menos 10 repeticiones. Se compararon poblaciones silvestres y cultivadas con el fin de apreciar si la selección artificial ha alterado estos sistemas. En los tratamientos, se marcaron brotes florales, los cuales fueron cubiertos con bolsas de exclusión. Para el tratamiento de autopolinización, simplemente se siguió el desarrollo las flores marcadas hasta la producción de semillas. En el tratamiento de polinización cruzada, las flores fueron polinizadas manualmente con pólen de otra planta, asegurándose que no se trataba del mismo clón. El tratamiento de polinización nocturna fué expuesto, durante la antésis, a visitadores nocturnos, removiendo las bolsas entre las 20:00 y las 05:00 horas. Mientras que en el tratamiento de polinización diurna, las flores fueron expuestas a los visitadores diurnos entre las 06:00, al amanecer, y las 9:00 horas, cuando se cierren las flores. En el tratamiento de polinización natural, las flores no fueron excluidas, simplemente fueron marcadas y seguidas hasta la producción de semillas, y sirvieron como testigo. Al final de la estación se contaron los frutos y semillas producidas en cada tratamiento.

Otro aspecto importante en el estudio de la polinización fué la captura e identificación de las especies animales que visitan las flores de la especie bajo estudio. La base de este estudio fué el catálogo de polen de cactáceas columnares en cuya elaboración, ya avanzada, se encuentra trabajando el grupo del Dr. Alfonso Valiente, en el Centro de Ecología. Este catálogo fié empleado para identificar el polen contenido en el cuerpo de los animales capturados. Los insectos, con excepción de esfingidos, fueron capturados en las flotes manualmente. Los insectos capturados se colocaron en tubos de vial conteniendo un papel secante con acetato de etilo. Los insectos se conservaron como especímenes voucher y fueron identificados. Las aves, murciélagos y esfingidos fueron capturados mediante el uso de redes de niebla. Se identificaron, y de sus cuerpos se obtuvieron muestras de polen aplicando cuadritos de gelatina de fuchsina, los cuales se colocarán en portaobjetos para su identificación. Los ejemplares capturados fueron finalmente liberados. Los detalles de los métodos de investigación se podrán apreciar en el Apéndice 6.

RESULTADOS

Al comparar la morfología floral de individuos de esta especie, se pudo encontrar que, en general, las flores de individuos cultivados de La Mixteca Baja son significativamente de mayor tamaño que las silvestres del Valle de Tehuacán. El estudio detallado de la morfología mostró las siguientes características: tubo floral relativamente grande y robusto (longitud: 4.45-5.63 cm; diámetro del tubo 1.75-2.34 cm; diámetro de la corola: 3.48-3.73); tamaño de los nectarios tal que permite producir y almacenar cantidades relativamente grandes de néctar (1.75-3.73 cm^3); numerosas ameras que permiten una oferta relativamente alta de polen; asi como olor característico de las flores visitadasa por murciélagos, el cual se produce durante la antésis que es nocturna. Todas estas características corresponden con lo que Faegri & Van der Pijl (1979), Grant & Grant (1979) y Rouley (1980) han definido como síndrome de quiropterofilia, en la cual los murciélagos participan en la polinización de las flores.

Se observó que la antésis se inicia a las 19:00 horas, pero las flores están completamente abiertas hasta las 22:00 hrs., aproximadamente una hora despues se Libera el polen, aunque los lóbulos del estigma aún están contraidos. El estigma está completamente turgente y abierto entre la 1:00 y 2:00 hrs. de la madrugada. Las flores comienzan a cerrar a las 6:00 hrs. y están completamente cerradas a las 9:00 hrs, aunque el verticilo interno de tépalos se cierra completamente desde las 7:00 hrs. La producción de néctar (ver apéndice 6) alcanza su pico alrededor de las 2:00 hrs. de la madrugada, coincidiendo con la mayor turgencia del estigma, aunque existe una oferta pequeña de néctar desde las 10:00 hrs.

La Tabla 5 resume en buena medida los resultados de los experimentos sobre sistemas de cruzamiento llevados a cabo en diferentes poblaciones de *Stenocereus stellatus.* Estos indican que muy probablemente el sistema es auto-incompatible y que la polinización efectiva ocurre durante la noche (para mayores detalles ver el Apéndice 6).

TABLA 5. NÚMERO TOTAL DE BOTONES FLORALES, FRUTOS ABORTADOS Y EXITOSOS EN LOS
EXPERIMENTOS DE SISTEMAS DE CRUZAMIENTO

Tratamiento	Botones	Frutos abortados	%	Frutos existosos	%
Autopolinización automática	207	207	100	0	0
Autopolinización manual	98	98	100	0	0
Polinización cruzada	30	13	43.3	17	56 67
Polinización nocturna	40	10	25	30	75
Polinización diurna	35	35	100	0	0
Polinización natural	70	20	28.57	50	71 43

Se identificaron ocho especies de visitadores diurnos (cinco de insectos y tres de aves) y seis especies de visitadores nocturnos (dos especies de esfingidos y cuatro de murciélagos) (ver Apéndice 6). Con base en los resultados de biología floral y experimentos de sistemas de cruzamiento, los polinizadores más probables, aparentemente, los murciélagos. Se identificaron semillas de *Stenocereus stellatus* en las heces fecales de los murciélagos *Leptonycteris curasoae, Choeronycteris mexicana* y *Artibeus jamaicensis,* asi como de las aves *Melanerpes hypopolius, Carpodacus mexicanus, Zenaida asiática, Mimus polyglotos* y *Phainopepla nitens.* Estudios preliminares de germinación de semillas provenientes de heces fecales muestran que las aves son los dispersores más eficaces.

Estudios del desarrollo de las estructuras reproductivas mostraron que las flores de S. stellatus completan su desarrollo entre los primeros brotes florales y la antésis entre 26 y 32 días, mientras que los frutos tardan en madurar entre 56 y 67 días. La duración del período de floración resultó variable en cada población, el menor periodo registrado fue de 91 días y el mayor de 151 días. El inicio y terminación de la floración fui también variable en cada población, pero en todas ellas el máximo pico se encontró entre la primer y tercera semana de julio. No existen barreras temporales para a la polinización de plantas silvestres y cultivadas. Aunque los picos de floración de *Stenocereus pruinosus* no coinciden con los de *S. stellatus,* existen sobrelapes al final del periodo de floración de la primera especie y al inicio del de la segunda especie. En el caso de *Stenocereus treleasi,* el periodo de floración coincide con el de

S. stellatus. Las tres especies presentan antésis nocturna y quiropterofilia, por lo que en teoria la polinización interespecífica podría ser posible, al menos considerando estos factores.

DISCUSIÓN

Aunque la información obtenida sugiere que el sistema de reproducción sexual es un sistema auto-incompatible llevado a cabo con la intervención de murciélagos, nos es posible descartar la posibilidad de que ocurra en alguna medida autopolinización, pues estos sistemas han mostrado ser flexibles en otras especies de plantas (Proctor, Yeo & Lack, 1996). Tampoco es posible descartar la participación de los esfingidos u otros polinizadores diurnos en la polinización de las flores de esta especie. Con todo, la morfología y fisiología floral presentan signos marcados de adaptación a la polinización por murciélagos, lo que sugiere un nivel importante de especialización en esta interacción.

No se observaron diferencias notables ni en el comportamiento temporal ni en la morfología y fisiología de las flores de poblaciones silvestres y cultivadas que permitan afirmar que existen barreras reproductivas entre ellas. La más significativa estaría quizas marcada por los límites espaciales de acción de los murciélagos. Este es un factor limitante importante entre poblaciones distantes, no asi entre poblaciones de una misma localidad.

Aunque la propagación vegetativa de *Stenocereus stellatus* parecería ser una ventaja en el montaje de plantaciones densamente pobladas con relativa facilidad, esto no ocurre en la realidad. Más bien, prevalece una estrategia de cultivo en la que se incluye una considerable diversidad morfológica y genética, tal como se mostró anteriormente. Esta estrategia parece favorecer la productividad de frutos en el cultivo de una especie con sistema reproductivo autoincompatible como lo es *S. stellatus.* Mayores detalles sobre los resultados obtenidos en esta parte del estudio pueden verse en el Apéndice 6.

IX. DISCUSIÓN GENERAL

ASPECTOS GENERALES DE LA HISTORIA NATURAL Y CULTURAL DE *STENOCEREUS STELLATUS*

Stenocereus stellatus es una de las cerca de 45 especies de cactáceas columnares que existen en la zona de estudio (ver Valiente-Banuet *et al.* 1995). Comparte con alrededor de 20 especies de la zona (entre ellas *Stenocereus pruinosus, S. treleasi, S. griseus, Pachycereus hollianus, P. marginatus, Polaskia chende, P. chichipe)* la característica de ser de talla mediana (entre 2 y 7 m de alto), tener propagación vegetativa y reproducción sexual de cruzamiento forzoso asi como relativamente rápido crecimiento vegetativo, alcanzando la edad reproductiva entre 4 y 7 años después de la germinación y aproximadamente 3 años después del establecimiento vegetativo de un nuevo individuo. Todo ello, contrasta con otras cactáceas columnares gigantes de la región (i. e. *Neobuxbaumia tetetzo, N. mezcalaensis, N. macrocephala, Pachicereus weberi, Cephalocereus hoppenstedtii, Mytrocereus fulviceps)* que llegan a medir más de 20 m de altura y presentan un crecimiento vegetativo lento, las cuales empiezan a producir flores después de varias décadas de crecimiento después de la germinación.

En condiciones silvestres, *Stenocereus stellatus* cubre un amplio intervalo de condiciones ambientales. En este estudio se registró su presencia en altitudes de entre 600 y 2,000 metros sobre el nivel del mar, con niveles de precipitación entre los 300 y cerca de 800 mm anuales y temperaturas medias anuales entre 17 y 24 ^{o}C, en suelos derivados de rocas calizas, areniscas y volcánicas, formando parte de una gran variedad de asociaciones vegetales dentro de los matorrales xerófilos y los bosques tropicales caducifolios. No obstante, su distribución está marcadamente restringida a las zonas secas y calientes del Valle de Tehuacán y la porción de la Cuenca del río Balsas comprendida en la parte sur de Morelos, noreste de Guerrero, noroeste de Oaxaca y sureste de Puebla. Desconocemos por el momento los factores que han limitado su presencia en otras zonas vecinas con condiciones ambientales que se encuentran dentro del intervalo señalado.

En la misma región se le encuentra cultivada, principalmente en las huertas y solares, y se le encuentra también bajo formas de manejo *in situ.* Pero aún bajo cultivo su distribución se encuentra restringida a la región señalada. Son alrededor de 15 las especies de cactáceas columnares que en total se cultivan y manejan *in situ* en la región. Todas ellas forman parte del grupo de 20 especies de mediana talla, propagación clonal y crecimiento vegetativo relativamente rápido. Son éstas algunas de las características que han determinado la viabilidad de su cultivo y domesticación.

De entre las 15 especies cultivadas, *Stenocereus stellatus, S. pruinosus* y *Escontria chiotilla* son las de mayor importancia económica en la región, las que con mayor frecuencia se cultivan y manejan *in situ*, las que se encuentran en los mercados regionales, las que mayormente se consumen por los habitantes locales y en las que puede observarse mayor variabilidad en la morfología de los frutos.

De frente a tan considerable variabilidad en los frutos, las preguntas clave que guiaron la presente investigación sobre *Stenocereus stellatus,* pero que desde luego son extensivas a las otras especies son: 1) ¿es esta variabilidad unicamente la expresión de una plasticidad fenotípica resultante de la gran variedad de ambientes de la zona o está también regulada genéticamente y es resultado de una elevada variabilidad genotípica? y 2) ¿es tal variabilidad únicamente resultado de presiones de selección natural o es también resultado de procesos de selección artificial?

La información obtenida en esta investigación muestra que existe una gran similitud en los frutos de individuos de poblaciones asentadas en condiciones ambientales muy diferentes. Este es el caso de las poblaciones silvestres del Valle de Tehuacán, el de la población cultivada del Valle de Tehuacán y las poblaciones manejadas *in situ* en las dos grandes regiones, y el de varios individuos cultivados, manejados y silvestres de La Mixteca Baja. El ejemplo de las poblaciones es muy ilustrativo. Las poblaciones silvestres del Valle de Tehuacán tienen frutos muy similares entre si, no obstante que sus condiciones ambientales varían considerablemente. Estas poblaciones se encuentran en altitudes de entre 1,000 y 1,800 m.s.n.m., precipitaciones de entre 440 y 650 mm anuales, temperaturas medias anuales de entre 19 y 24^{0}C, suelos derivados de rocas calizas y areniscas y en diferentes asociaciones del bosque tropical caducifolio y matorral xerófilo. En contraste, los frutos de los individuos silvestres de La Mixteca Baja resultaron ser de mayor tamaño y en los diferentes análisis multivariados estos individuos se agruparon separadamente de los del Valle de Tehuacán. Las características ambientales de esta población se encuentran, en general, dentro del intervalo de condiciones de las del Valle de Tehuacán, pero los niveles de precipitación pluvial son mayores (720mm). Es posible entonces que estas diferencias en los niveles de precipitación estén determinando en cierta medida las diferencias morfológicas entre ambos grupos de poblaciones. Ello parece reforzarse si se considera que la población de San Juan Raya (en el Valle de Tehuacán) resultó ser genéticamente similar a la población silvestre de La Mixteca Baja y sin embargo sus frutos fueron mas similares a los de las otras poblaciones del Valle de Tehuacán. Estos ejemplos permiten visualizar cómo la variabilidad morfológica es en parte una expresión de plasticidad fenotípica.

Consideremos ahora otro ejemplo de situaciones. Dentro de las huertas de La Mixteca Baja existen individuos de muy diferente origen. En cada huerta existen cultivadas un promedio de siete variedades distintas, todas ellas en condiciones ambientales y de manejo similares. Todas las variedades produjeron frutos diferentes entre si, lo que muestra que sus características morfológicas tienen un componente genético muy importante. Es importante hacer notar además que dentro de estas huertas, una parte de los individuos provienen de ramas de individuos silvestres. Es de destacarse que un buen número de estos individuos se agruparon con los individuos silvestres y manejados *in situ* de esa zona. Lo que indica que no obstante las diferencias ambientales entre las huertas y las poblaciones silvestres, los frutos mantuvieron su similitud morfológica con los de sus parientes silvestres. Estos ejemplos, entonces permiten visualizar que la variabilidad morfológica en los frutos es también en parte resultado de diferencias genéticas. Una evaluación más precisa de la plasticidad fenotípica en estas características será posible cuando, dentro de tres o cuatro años, los materiales de la colección viva en el Jardín Botánico de la UNAM se encuentren en etapa reproductiva.

Para analizar la contribución de la selección artificial en la generación de la variabilidad morfológica y genética de *S. stellatus*, es necesario tomar en cuenta los siguientes elementos: 1) la selección artificial es practicada en la actualidad por la población indígena local. Esto se hace evidente por el hecho de que en los tres grupos étnicos estudiados la gente reconoce la variabilidad infraespecífica, la nombra, la clasifica y establece distinciones con respecto a las formas silvestres. Además, existe un conjunto de valores culturales en tomo a esta variedad que se refiere a las ventajas y desventajas para el uso y manejo de las diferentes características morfológicas. Pero sobre todo, existe una referencia explícita por parte de la gente y una observación directa de cómo se favorecen los rasgos morfológicos preferidos con respecto a los no preferidos. En el manejo *in situ* esto se logra a partir de dejar en pie individuos con rasgos preferidos y en ocasiones también por su propagación intencional, mientras que en el cultivo ex situ en las huertas, la gente selecciona directamente los fenotipos preferidos, obtiene ramas de los y los propaga vegetativamente. 2) Este proceso selectivo tiene resultados evidentes pues en general las poblaciones cultivadas y al menos una de las manejadas *in situ* presentaron diferencias morfológicas significativas con respecto a las poblaciones silvestres. Los diferentes análisis multivariados mostraron que existe un grupo de individuos que son frecuentes entre las poblaciones cultivadas y que existen entre las poblaciones silvestres, pero con bajas frecuencias. Estos individuos cultivados, provienen de poblaciones silvestres, presentan rasgos fenotípicos favorables y la gente los escoge para propagarlos en sus huertas. Entonces, la selección artificial ha estado actuando simplemente elevando las frecuencias de los fenotipos silvestres que le son favorables a las culturas locales y, a lo largo de la historia de manejo, ha logrado reunir tipos favorables de diferentes poblaciones silvestres, de su entorno mas cercano, pero en ocasiones también de sitios mas distantes. Pero esto no es todo. A lo largo de este estudio fue posible identificar un conjunto importante de individuos cultivados que se encuentran exclusivamente bajo condiciones cultivadas**.** Este es el caso de los "xoconochtles aventureros", posiblemente híbridos interespecíficos entre *Stenocereus stellatus* y *S. pruinosus,* y es también el caso de todas las variantes con frutos de mayor tamaño y con pulpa de color diferente al rojo. Hasta el presente no ha sido observado entre las poblaciones silvestres ningún individuo con tales características. Aunque falta estudiar con mayor detalle este hecho, parece ser el caso, muy común en los procesos de domesticación, de variantes con baja adecuación en condiciones naturales las cuales, por ser favorables al hombre, se han mantenido bajo su protección. Vale la pena remarcar que son estos fenotipos, precisamente, los de atributos con mayor valor cultural y por ende comercial. Es posible explicar la presencia de estos individuos pues el manejo de estas plantas dentro de las huertas no se limita a propagar vegetativamente los materiales deseables, sino que además se toleran comunmente las plántulas de semillas que germinaron "espontáneamente" dentro del terreno. Este proceso permite incorporar continuamente nueva variabilidad genética que resulta de la reproducción sexual En este caso la selección se produce mas lentamente pues las plantas son dejadas en pie o eliminadas hasta que alcanzan la edad reproductiva y las características de sus frutos pueden ser apreciadas. Resumiendo, entonces, la selección artificial aprovecha la variabilidad disponible en las poblaciones silvestres como resultado de la selección natural Toma aquella parte de esta variabilidad que le interesa al hombre y la amplifica. Pero además, en los ambientes artificiales permite la sobrevivencia de variantes que en las poblaciones silvestres no pueden lograrlo y, cuando le resultan favorables al hombre, susfrecuencias son también amplificadas.

Es importante agregar que, al menos en la actualidad, los pobladores indígenas locales presentan una gama amplia de valores sobre las características a seleccionar. Generalmente ponen de relieve no mas de cinco características de los frutos: tamaño, color y sabor de la pulpa, grosor de la cáscara y cantidad de espinas en la cáscara. La combinación de tan sólo estas características puede significar un número elevado de variantes posibles. La gente valora como ventajosos y desventajosos cada uno de estos atributos y en función de ello selecciona. De manera que la presión de selección artificial en esta especie y en el contexto cultural estudiado, no se dirige hacia un tipo uniforme, sino a un conjunto amplio de características. Este ejemplo no es la excepción. En realidad, los pueblos indígenas mesoamericanos se han caracterizado por seleccionar y manejar al mismo tiempo una gran diversidad de tipos de plantas de una misma especie. Lo mismo entre las especies que les han aportado sus alimentos básicos (maíz, frijol, calabaza**,** chile, amaranto, etc.), como entre otras especies que complementan su dieta, entre ellas las especies frutícolas como *Stenocereus stellatus.*

Este patrón de selección se expresa en la gran variedad de frutos cultivados que se pueden apreciar en las huertas de una localidad y en los mercados regionales. En el caso especifico, este proceso se expresa en que bajo cultivo no sólo existe una calidad de frutos diferente a la que exsiste en las poblaciones silvestres sino además existe una diversidad morfológica y genética comparable (en el caso de La Mixteca Baja) o incluso superior (en el caso del Valle de Tehuacán) a la que existe en las poblaciones silvestres.

La naturaleza de los sistemas reproductivos de *Stenocereus stellatus* marca pautas importantes en la generación de variabilidad morfológica y genética y en la fijación de características favorables para su establecimiento en condiciones naturales. Asi, su reproducción sexual, que involucra un sistema de cruzamiento forzoso, resulta sumamente dinámico en la combinación de genes, mientras que su propagación vegetativa permite la expansión de las combinaciones mas exitosas. Igualmente, estas características son aprovechadas por las culturas locales, cambiando simplemente el contexto del éxito reproductivo (su conveniencia cultural) e interviniendo directamente para lograrlo (propagando intencionalmente las combinaciones genéticas que le son favorables). En algunas especies domesticadas, el hombre ha favorecido los sistemas reproductivos autocompatibles., pues con ello ha logrado mantener las líneas genéticas que le interesan y ha asegurado la productividad, disminuyendo riesgos inherentes a la participación de agentes externos y asegurando la polinización directa. En el caso estudiado, la domesticación ha mantenido el sistema de reproducción cruzada pues por un lado, la pureza de sus líneas es asegurada mediante la propagación vegetativa y por otro lado, los niveles de productividad que han requerido no se han visto afectados por la dependencia de agentes polinizadores tales como los murciélagos. Por el contrario, conciente o inconcientemente, han obtenido ventajas importantes al mantener este sistema reproductivo.

Como se señaló, el sistema reproductivo sexual es de cruzamiento fozoso y el flujo de polen entre las poblaciones silvestres y cultivadas es. En el caso del Valle de Tehuacán, la población cultivada y manejada *in situ* están separadas de las silvestres por al menos 10 Km de distancia y ello podría constituir una barrera para la interacción entre poblaciones a través de los murciélagos, aunque no está aún probado. Sin embargo, en La Mixteca Baja la separación entre estos tipos de poblaciones es no mayor a los 2 Km, radio dentro del cual la interacción, aunque tampoco probada**,** es posible. En teoría, de existir flujo de polen entre las poblaciones silvestres y cultivadas, esta condición tendería a diluir la divergencia entre estos tipos de poblaciones, al menos a nivel de localidades. Igualmente, la intervención de dispersores de semillas tan dinámicos como las aves, los murciélagos y el propio hombre, permitiría suponer un continuo establecimiento de materiales silvestres en las poblaciones cultivadas y viceversa que tendería a diluir las diferencias entre ellas. No obstante, tanto en La Mixteca Baja como en el Valle de Tehuacán, las poblaciones silvestres y cultivadas a nivel de localidades mantuvieron importantes diferencias tanto morfológicas como genéticas. Ello parece indicar que tanto mecanismos de selección artificial están interviniendo dinámicamente dentro de las áreas antropogénicas para mantener tal divergencia, como mecanismos de selección natural en las poblaciones silvestres. Hemos ilustrado los mecanismos de selección artificial sobre la base de los cuales es posible explicar tal divergencia, pero nada sabemos aún de los posibles mecanismos de selección natural que actúan en las poblaciones silvestres. Ello requerirá nuevas investigaciones.

Una pregunta crucial aún no contestada se refiere a la dimensión temporal de la domesticación de esta planta. Su respuesta requerirá una revisión detallada de los materiales arqueológicos de las cuevas de Tehuacán obtenidos por MacNeish (1967) y una interacción sistemática con investigaciones arqueológicas en sitios prehistóricos de otras áreas en la Cuenca del río Balsas. Por el momento sabemos que la interacción del hombre con esta planta es tan antigua como los estratos en los que MacNeish encontró los primeros restos de ésta asociados al hombre, probablemente 4,500 años antes del presente, en el Valle de Tehuacán, pero probablemente mas antigua aún en otros sitios. El análisis comparativo de los patrones de variabilidad morfológica desarrollados en la presente investigación aporta elementos que podrían ayudar a la interpretación del estatus cultural de los restos arqueológicos. Por ejemplo, sabemos ahora, con mayor detalle, los intervalos de las dimensiones de frutos y semillas asociados a frutos silvestres y cultivados. Pero junto a las investigaciones arqueológicas, es quizás el seguimiento de marcadores genéticos en poblaciones de distintas áreas geográficas una de las fuentes mas poderosas que en el presente tenemos para interpretar el origen de la diversidad morfológica y genética que ha generado esta historia de interacción de los domesticadores mesoamericanos con *Stenocereus stellatus.*

STENOCEREUS STELLATUS COMO RECURSO DE IMPORTANCIA ECONÓMICA POTENCIAL

Con base en la experiencia directa en el trabajo de campo desarrollada en este proyecto, así como con base en información en la literatura, es posible señalar los siguientes aspectos relacionados con la potencialidad económica de *Stenocereus stellatus*, las cuales en buena medida se pueden también hacer extensivas a otras especies de cactáceas columnares tales como *Stenocereus pruinosus, S. treleasi, S. griseus, Escontria chiotilla, Pachycereus marginatus, P. hollianus, Polaskia chichipe, P. chende* y *Myrtillocactus geometrizans,* entre otras:

1. Producción de frutos como alimento humano. En el presente, esta planta tiene importancia sólo a nivel regional, donde se recolecta y cultiva a pequeña escala, en las huertas familiares. Aunque no existen plantaciones comerciales, la producción familiar en sitios como La Mixteca Baja rebasa los niveles actuales de consumo y comercialización. Así, en esa zona, una parte considerable, aún no estimada, de la producción es desaprovechada y se pudre en los mismos sitios donde se produce. Tanto el autoconsumo como la comercialización de los frutos del xoconochtle son immportantes para la economía familiar de la región. Sin embargo, existen problemas para comercializar los frutos ya que por un lado, los mercados locales en las regiones de mayor productividad (La Mixteca Baja) están saturados y aunque los mercados por fuera de la región son propicios, no existen vías adecuadas para canalizar los productos. Entonces, el desarrollo de canales de comercialización contribuiría grandemente a aprovechar la producción que actualmente existe ya en la región y ello ayudaría grandemente a apoyar la economía familiar. En 1994 la CONAZA impulsó un proyecto de fomento a la producción de Stenocereus pruinosus en La Mixteca Baja. Pagaba a los campesinos $6.00 por cada rama plantada en sus propios huertos. Los campesinos lo hicieron, pero muchas de las plantas murieron por falta de interés en mantenerlas por parte de los campesinos. La razón es que para ellos aumentar la producción en sistemas que ya son excedentes, carece de sentido. tendría mayor sentido que la CONAZA apoyara a los campesinos en comercializar sus productos en mercados por fuera de la región.

Los mercados de los estados de Morelos, Puebla, Guerrero y el Distrito Federal son focos potenciales para la comercialización del xoconochtle, e incluso es posible explorar mercados a mayor escala. Sin embargo, un problema inherente a la planta, que limita su comercialización, es la relativamente rápida pudrición de los frutos. De acuerdo con la información obtenida en este estudio, la característica de cáscara gruesa proporciona resistencia a la pudrición. Entonces, es factible ligar a propósitos productivos programas de fitomejoramiento para producir líneas de resistencia a la pudrición que combinen otras características de valor comercial.

Igualmente, el desarrollo de tecnología para la producción de conservas de estos productos es necesario. Es posible rescatar la tecnología tradicional para la producción de frutos deshidratados ("xoconochtles pasados") y es posible también la producción a escala industrial de jaleas, mermeladas y otros productos. Existen avances en esta última dirección en el CIDIR del estado de Oaxaca, aún a nivel de experimentación tecnológica pero que sin duda, podrá hacer importantes aportes para el desarrollo de agroindustrias regionales que permitan apoyar la economía campesina.

Solo en la medida que puedan fortalecerse los mercados y procesos agroindustriales será necesario y factible fomentar la producción y desarrollar tecnología para elevar la productividad y ello planterá, necesariamente, nuevas rutas en los procesos de domesticación de esta planta. La información disponible actualmente permitirá apoyar el diseño de esas rutas potenciales.

2. Producción de flores como alimento humano. En Matehuala, San Luis Potosí, los botones florales de *Ferocactus pilosus*, llamados localmente "cabunches" se colectan y conservan en vinagre y se comercializan como exquisiteces. Se ha ilustrado en este estudio como los botones florales de *Stenocereus stellatus* son preparados de manera similar y consumidos por la población. El trueque indígena regional le da un valor a estos productos del orden de 3 litros de maíz por litro de botones florales. En la perspectiva de comercialización y desarrollo agroindustrial regional, este es sin duda un producto más a explorar y a experimentar tecnología.

3. **Producción de jugo de los frutos.** En algunas regiones de México se extrae el juga de varias especies de *Opuntia* para producir a escala industrial "miel de tuna", "melcocha de tuna" y "queso de tuna". El contenido de azúcar en los frutos de *Stenocereus stellatus* es comparable al de *Opuntia* y, por lo tanto podría ser explorado en esta perspectiva.

4. **Las semillas como alimento.** El contenido de grasas en las semillas de esta especie es considerablemente alto, incluso mayor que el de algunas especies de *Opuntia* que están siendo exploradas como fuentes para la producción de aceite. El uso de las semillas de *S. stellatus* como alimento humano no tiene paralelo con las semillas de *Opuntia*, asi que podrían desviarse diferentes subproductos a partir de las semillas. Una industria basada en el. aprovechamiento de las semillas sería factible ligada a una industria de extracción de jugo.

5. **Productos adhesivos.** La cantidad elevada de mucilagos hace posible la extracción de productos para la elaboración de gomas adhesivas, tal y como se realiza actualmente con *Pachycereus hollianus, Stenocereus thurberi* y *Ariocarpus restusus.* Igualmente es posible explorar el uso de pectinas a partir de esta especie.

6. **Producción de forraje.** La escasez de forraje, sobre todo en la temporada de sequía, en todas las zonas áridas y semi-áridas de México y el pastoreo de áreas forestales son causas de mortandad de ganado y de destrucción de la vegetación que obligan a buscar, urgentemente, estrategias tecnológicas que contribuyan a aliviar este problema. Diferentes especies de *Opuntia* han sido utilizadas en la producción de forraje debido, entre otras razones, a su activo crecimiento vegetativo. Aunque el uso exclusivo de tejidos vegetativos de *Opuntia* es insuficiente para alimentar al ganado, de acuerdo con autores como Colín (1976) y Bravo-Hollis y Sánchez-Mejorada (1991), se pueden lograr mejores contenidos nutricionales de productos forrajeros cuando se mezclan los tallos, las cáscaras de los frutos y una pasta preparada con las semillas. El uso forrajero actual de los tallos y frutos de *S. stellatus* y su relativamente rápido crecimiento vegetativo sugieren que es posible desarrollar aún mas las potencialidades forrajeras de esta especie. Actualmente no existe producción de esta planta con propósitos forrajeros, pero seria factible. En esta dirección, las líneas de más rápido crecimiento vegetativo serían de gran utilidad.

7. **Protección de suelos.** Actualmente *Stenocereus stellatus* es utilizado con estos propósitos en toda la región. Es posible, sin embargo, desarrollar aún mas sus potencialidades. La región estudiada, pero sobre todo La Mixteca Baja, es una de las zonas con mayores problemas de erosión en el país. Son urgentes las medidas de protección y recuperación desuelos. Las 20 especies de cactáceas columnares de mediana talla, propagación clonal y rápido crecimiento vegetativo mencionadas anteriormente, y en especial las 15 de ellas que son cultivadas de alguna manera, son sin lugar a dudas, junto con varias especies de leguminosas arbustivas y arbóreas candidatos importantes para tales programas. Su vocación productiva refuerza aún mas sus ventajas para ser utilizadas en esta dirección.

ESTRATEGIAS PARA LA CONSERVACIÓN Y USO DE LA VARIABILIDAD INFRAESPECÍ FICA DE *STENOCEREUS STELLATUS*

Este documento ha pretendido aportar elementos acerca de las ventajas utilitarias de la variabilidad morfológica y genética de esta especie. Y de ello se desprenden las ventajas productivas potenciales de usar tal diversidad. Mi, por ejemplo, la información que por individuos se cuenta en esta investigación, documenta las líneas de frutos con cáscara gruesa, mayores cantidades de pulpa, sabores dulces y agridulces, mayores cantidades de semillas y partes vegetativas mas robustas, los que provienen de suelos derivados de rocas calizas, areniscas y volcánicas y en otras características ambientales, las cuales son factibles de usarse *para* distintas direcciones en el fitomejoramiento. Los materiales vivos de referencia en el Jardín Botánico de la UNAM, además constituirán materias primas indispensables para el diseño de tales programas de fitomejoramiento.

Igualmente, la información que se cuenta puede resultar de utilidad para programas de conservación y restauración de suelos agrícolas y podría ser de utilidad en programas de restau^r^ación de la vegetación.

La ventaja de contar con información sistematizada de la variabilidad infraespecífica de esta y otras especies de cactáceas columnares puede resultar entonces evidente. Sin embargo, es importante tomar en cuenta la dinámica actividad destructiva que en la actualidad padece nuestro país, de la cual no se escapan las zonas áridas y semiáridas. Y entonces, sistematizar la información parece ser insuficiente y obliga a pensar en estrategias de protección de esta diversidad. Las medidas de protección de esta escala de la biodiversidad, es decir a nivel infraespecífico, parecen tan ineludibles como los de escalas mayores y el diseño de estrategias de conservación para una y otra escala parece ser indivorciable.

En el caso que discutimos en este informe, la declaración del Valle de Tehuacán-Cuicatlán como área protegida, cuyo decreto se encuentra en proceso, abre grandes posibilidades para planear la conservación de una importante diversidad biológica caracterizada por alrededor de 3,000 especies en el caso de la flora, de las cuales cerca del 30% son endémicas. Cuando se analiza la variabilidad infraespecífica, como en el presente estudio, la conservación de áreas como esa adquiere aún mayores dimensiones. Considerando como base el decreto de protección de esa área y el plan de manejo que deberá elaborarse, las líneas generales que se presentan aquí podrían ayudar a formular medidas concretas de conservación para esta y otras especies a mediano plazo.

Con el presente estudio se han dado los primeros pasos para conocer la importante diversidad infraespecífica de *Stenocereus stellatus*, se han dado los primeros pasos también para mantener *ex situ* parte de esta diversidad en el Jardín Botánico de la UNAM y esposible visualizar al menos las grandes líneas de trabajo a seguir en el futuro para la conservación y manejo de tal diversidad infraespecífica:

1) **Muestreo de la diversidad infraespecifica.** Resulta aún necesario documentar, de manera similar a lo efectuado en el presente estudio, la variabilidad morfológica y genética de poblaciones que quedaron por el momento fuera del análisis. Esto es sobre todo importante en la repón de la Cuenca del río Balsas, donde parece existir mayor diversidad fenotípica y genética. Se han observado poblaciones silvestres en las zonas limitrofes de Morelos y Puebla, la Montaña de Guerrero y La Mixteca Baja que serían de gran importancia para una mejor cobertura de información sobre la diversidad de esta especie. En esos mismos sitios S. *stellatus* se encuentra también cultivada y sería importante, por lo tanto, muestrear tanto la vegetación silvestre como las huertas y solares. Los métodos de muestreo practicados en este estudio, asi com la obtención de información sobre variabilidad morfológica parecen ser, en general convenientes para continuar el muestreo. Sin embargo, falta aún refinar más, las técnicas de muestreo de diversidad genética, como se discute previamente. Estas serán de crucial importancia para tomar decisiones en las estrategias de conservación, por tal motivo, su depuración será una de las prioridades en lo subsecuente.

2) **Sistematización de la información.** La colecta y mantenimiento *ex situ* de todos los individuos por muestrear resulta técnicamente complicado y costoso, sobre todo si se piensa en la perspectiva de conservar la diversidad no sólo de esta especie sino además de otras que también son importantes. No obstante, resulta factible diseñar un sistema computarizado que permita manejar la información de campo y laboratorio y que permita

tener acceso a los materiales de interés *in situ.* Ello exije la utilización de métodos precisos de localización geográfica y marcaje. El diseño de estos sistemas deberá ser una actividad de alta prioridad en los próximos años, no sólo para controlar información de *Stenocereus stellatus* sino también de otras especies de importancia potencial en la región. Sistemas similares podrían ser de gran importancia en otras regiones del país para controlar información sobre la diversidad infraespecífica de plantas de importancia potencial en México. Por ello, el desarrollo de una experiencia puntual en el Valle de Tehuacán y zonas vecinas podrían ser doblemente importantes, tanto para las propias tareas de conservación en el área como para diseñar estrategias nacionales.

3). **Conservación *ex situ.*** A partir de la información generada, es posible definir criterios para seleccionar materiales que conviene mantener *ex situ.* Los fenotipos y genotipos raros son sin duda candidatos obligados. También los son aquellos fenotipos que resultan potencialmente de utilidad para el desarrollo de diferentes líneas para el fitomejoramiento. La intervención coordinada de las diferentes instituciones académicas y técnicas relacionadas con aspectos de conservación y producción agropecuaria en la región, es indispensable para generar una red de bancos locales de germoplasma.

4). **Conservación *in situ.*** Esta labor involucra la conservación de comunidades vegetales silvestres, pero también la conservación de la diversidad manejada bajo cultivo. En el primer caso, la labor deberá ser dirigida a identificar las áreas de vegetación natural que deberán mantenerse, y proponerlas para su conservación como parte del plan de manejo que deberá elaborarse, al menos para la reserva de Tehuacán-Cuicatlán. En el segundo caso, los mayores riesgos son que el cultivo de esta especie sea abandonado ya sea por la sustitución de su cultivo por el de otras especies, o por la migración de la gente. En cualquiera de los caso, el apoyo a la producción tal y como se sugiere en el apartado anterior contribuiría de manera importante a reforzar el papel de esta planta en la economía campesina y disminuir los riesgos de su abandono.

El proyecto que presentamos está muy lejos aún de su conclusión. En realidad constituye los primeros pasos de un trabajo que al parecer será sumamente complejo, tan sólo al nivel de la especie abordada**.** Más aún, la enorme riqueza de especies que como *Stenocereus stellatus* existen en México, obliga a pensar en estrategias de evaluación, conservación y uso de la diversidad infraespecífica, como la que se intenta llevar a cabo en este proyecto, para un conjunto mayor de especies. Es, sin embargo, una vía necesaria y de prioridad para incorporar a las perspectivas del desarrollo nacional contemporáneo la diversidad biológica que nos tocó heredar de la historia natural y cultural de México.

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Apéndice 1.

ETHNOBOTANY OF *Stenocereus stellatus*

1. INTRODUCTION.

Ethnobotany can be defined as the study of interactions and interrelationships between humans and plants. Based on this definition, in this research ethnobotanical studies were considered an important source of information about traditional uses, classification and forms of management of *Stenocereus stellatus* by indigenous people who live in the Tehuacán Valley, and La Mixteca Baja region. Such information was considered relevant to analyze the motives of artificial selection, that is, the ways in which it operates, the characters selected, and the human cultural meaning of domestication of this plant species. In this chapter, the results of ethnobotanical studies on traditional classification, use and management of *Stenocereus stellatus* are presented. A comparison of fruit yields among wild and cultivated populations is also presented in order to analyze plant resources availability in relation to their role in human subsistence.

2. METHODS.

Ethnobotanical studies were carried out among the Nahua, the Mixtec and the Popotoca people in the Tehuacán Valley and the Mixteca Baja region, to investigate possible differences in use and management of *S. stellatus* as well as in criteria and mechanisms of artificial selection.

Qualitative data and descriptions of human cultural processes occurring in this or related species were obtained through bibliographic information from archaeological researches, pre-hispanic and post-conquest codices, as well as chronicles of conquistadors. This information was complemented by information from more recent ethnobotanical studies. Substructured interviews were carried out with peasants, to get information on the aspects listed below.

INFORMATION ON USES

This makes it possible to analyze characters of "xoconochtli" preferred by people for different purposes. An inventory of the different variants of xoconochtli and their uses was conducted with a total of 40 informants. Data on the forms of preparation, consumption and storing of useful parts of this plant were also obtained. Information on morphological features preferred for different purposes of use and management was emphasised. Interviews, with indigenous people were directed to obtain: i). An inventory of the different uses of this plant as food, medicine, animal forage, fuelwood, living fences, soil protection, and others. ii). A description of the ways of preparation, consumption and storing of resources obtained from this plant. iii). Information on morphological features that are considered to be the best for different purposes of use and management of this species was emphasised.

Living specimens were obtained during the inventory. They were deposited in the ethnobotanical collection of *Stenocereus stellatus* in the Jardín Botánico, Instituto de Biología, U.N.A M. Mexico.

INFORMATION ON FOLK CLASSIFICATION

This topic was considered important because traditional classifications generally emphasise the features of the plants most important to those who are using the plants. Both living specimens and colour photographs of "xoconochtli" and other species of cacti were shown to twelve informants. They were asked to give the local name for each specimen shown as well as to list the features which characterize them. These studies were directed to know: i). The Indian nomenclature for the cacti and the different variants of "xoconochtli". ii). A recognition of qualities and possible special uses given to different variants of this species. iii). Relationships and classification of the different variants of *Stenocereus stellatus* from the point of view of the indigenous people.

INFORMATION ON MANAGEMENT

Three main forms of management of xoconochtli were recognized: firstly, gathering from the wild (harvesting of fruits directly from natural plant populations); secondly, *in situ* enhancement of wild populations (tolerance, i.e. keeping of individuals of a wild population when the areas occupied by the population are cleared by man; or planting *in situ,* which involves intentional dispersion of vegetative propagules in natural populations after clearings or bumings); and thirdly, cultivation (propagation of seeds and stems of this plant, from wild or cultivated progenitors, in artificial environments). Interviews covered the following aspects:
a) Gathering: i) The members of the family who ordinarily gather edible fruits of "xoconochtli" (and other parts destined for other uses). This information was useful to identify people with wide experience in selecting xoconochtli according to their different qualities as well as to know the ways of transmission of this information among members of the family.
ii) The seasons of the year when the resources are available, as well as the characteristics of the fruits and other parts suitable to be collected, and the variation that populations present in this feature. iii) How people gather fruits and other parts of "xoconochtli". Whether or not they select particular individuals, and the characteristics taken into account for such decision. Tools and procedures used during gathering. Photographic records of tools and techniques were done.
iv) Whether or not there exist practices to promote an increasing of density of'

populations, and if they encourage the abundance of particular individuals in populations. Whether all fruits are removed from favoured individuals, and if such occurs, what happens to seeds of such fruits (are they discarded with household waste, voided in faeces, etc.); whether such seeds germinate and seedlings establish; whether individuals harvested intensively reproduce only asexually or via pollen. v) Whether or not people take special care of particular individuals in the wild populations.

Enhancement of wild populations *in situ*: i) Disturbed areas where individuals of *Stenocereus stellatus* are enhanced. ii) Reasons taken into account by peasants to enhance this and other species. iii) Whether or not particular phenotypes are selectively enhanced, and if so, criteria used for enhancing them. v) Whether or not special care is taken of enhanced individuals.

Cultivation: i) Sources of origin of seeds and vegetative materials for cultivation, and criteria used to select them. ii) Pre-sowing and pre-planting treatments of seeds and vegetative materials. iii) Sowing and planting techniques: preparation of soil, tools used and procedures implemented, density of sowing and planting, etc. iv) Special care such as irrigation, control of pests, pruning, fertilization, etc. v) Techniques of harvesting: who harvests, when they harvest and how they harvest.

FRUIT YIELDS AMONG POPULATIONS.

The amounts of fruits produced in wild, managed and cultivated populations of *Stenocereus stellatus* were evaluated and compared. Five wild populations; two populations managed by enhancement *in situ* and home gardens of two villages were sampled in order to estimate density of population. For wild populations and populations managed *in situ*, transacts were used. In each case, the size of transects was determined depending on the extent of the population. Random samples of home gardens were used to evaluate density and yields under cultivation. The number of sampled individuals producing fruits was counted as well as the total number of branches, the number of branches producing fruits and the number of fruits per branch. Five fruits per sampled individual were collected and weighed to estimate kilograms of fruits produced per individual and per hectare. An analysis of variance was performed to test differences in fruit yield between populations.

3. ***HISTORY OF USE AND MANAGEMENT OF STENOCEREUS STELLATUS.***

PREHISTORY

Smith (1967) reports remains of S. *stellatus* (as *Lemaireocereus stellatus)* from archaeological excavations in the Tehuacán Valley, in the Abejas phase, from approximately 4500 years before present and in the Palo Blanco phase, from approximately 2000 years before present.. In addition, the same author reports remains of arborescent cacti identified as *Cephalocereus hoppenstedti*, *Escontria chiotilla, Pachycereus hollianus, P. weberii* and *Myrtillocactus geometrizans.* Some of these could be confused with *Stenocereus stellatus.*

In the Guilá Naquitz caves, in the Valley of Oaxaca, Smith (1986) reports a ball of gum as the only probable remains of *Stenocereus* in the zone B1 (approximately 7,000 years before present). This is supposed to have been used as an adhesive for hafting projectile points or for medicinal or ceremonial use. However, according to present ethnobotanical information, it is also possible that this gum could have been used as food. Smith also reports remains of many stems and fruits of species of *Opuntia.*

In the Tehuacán Valley, S. *stellatus* and other columnar cacti such as *Escontria chiotilla* (F.A.C. Weber) Rose, *Myrtillocactus geometrizans (C.* Martius) Console and *Echinacactus platyacanthus* Link & Otto are important plant resources at present. However, because archaeological remains of these cacti were not abundant, Smith (1967) considered that they were not significant in the diet of ancient people. He considered that fruits and stems of *Opuntia* (Tournefort) Miller were the only cactus products consumed in significant quantity. Nevertheless, when the number of present resources existing in the Valley is contrasted with the number of resources found in archaeological researches, it is possible to say that the archaeological records in caves, do not represent very well the importance of a number of plant and animal resources. For example, Smith (1967) identified around 64 plant species, which are supposed to have been resources for human subsistence in prehistoric times. This contrasts with present information obtained through ethnobotanical studies by Casas *et al.* (1993), who found approximately 800 plant species used for different purposes by people of the Tehuacán Valley. Human beings occupied the Tehuacán Valley approximately since about 12,000 years ago (MacNeish, 1967 a) and b); Flannery, 1967; Ebeling, 1986). Since ancient times and even at present, people have used a wide spectrum of plant and animal resources. Cacti have been, for sure, very important plant resources since prehistoric times, because of their abundance, quality and easy accessibility. The great diversity of cacti existing in the valley offered an extraordinary variety of options in resources to the ancient gatherers. For example, Davila et al. (1993) registered 74 species of Cactaceae existing in the Tehuacán Valley. And Bravo-

Hollis and Sánchez-Mejorada (1991) and Casas *et al.* (1993), reported almost all of these species as useful plants, mainly used as food. This contrasts with the nine species identified by Smith (1967) by archaeological researches. This also contrasts with information found by Callen (1967) in human coprolites. For example, in the El Riego phase Callen found cactus tissue and seeds forming part of a wild food diet, being the dominant material of coprolites along with *Setaria*, some other grass seeds (including wild maize), pochote roots *(Ceiba parvifolia)*, agave and some meat. In the Coxcatlán phase, stem tissue and fruits of cacti, including *Opuntia* as well as *Stenocereus* and *Pachycereus* (these two genera included within *"Leimairocereus")* were equally dominant material. In the following phases, remains of' *Opuntia* and *Stenocereus* were also identified, changing their relative importance in human diet as the consumption of cultivated plants increased. Although Smith (1967) considers that *()punt('* is the most important element of the cactus food, Callen (1967) found that in Abejas, Ajalpan, Santa Maria, Palo Blanco and Venta Salada phases, consumption of *Stenocereus* stem tissue, fruits and seeds was more important than products of *Opuntia.* This author found evidences that during the Ajalpan and the Santa Maria phases, *Lemaireocereus* species were among the principal plant constituents in human diet in Tehuacán.

In all the phases, remains of raw stem tissue and fruits of *Stenocereus* and *Pachycereus* were found. This indicates a direct consumption of these plant products. However, in the Coxcatlán phase seeds of *Stenocereus* and *Pachycereus* species appeared to have been eaten after being roasted. In the Abejas phase, remains of *Opuntia* appeared without epidermis suggesting that they were roasted. The starchy interior tissue of the stems were eaten and the charred epidermis discarded. The same might have happened with *Stenocereus* and *Pachycereus* in that time, but it is not until the Palo Blanco phase where Callen observed evidence of stems of *Stenocereus* and *Pachycereus* having been eaten after being roasted. There is no evidence of boiling cacti tissue during the prehistory of the Tehuacán Valley.

Based on information from coprolites, Callen (1967) considers that there were two general patterns of the prehistoric human diet in Tehuacán: a wet-season diet, including a variety of fruits and seeds with a little plant tissue and occasionally supplemented by meat; and an early dry-season diet, with an occasional fruit or a few seeds, but mainly plant tissue and meat. It seems that in prehistoric times and until the aldean times, when houses were built, people lived in the caves throughout the year, but according to Smith (1967), there is evidence that people collected the major part of plant material within a radius of twenty miles of a site. Other desirable plants known to grow a day's distance away or more were sought out when needed.

Although there are no clear evidences of cultivation and domestication of cacti in archaeological remains, Smith (1967) suspected that "...the earliest Tehuacán cultigens were probably maguey *(Agave* spp.) and *Opuntia*, owing the ease with which these species are vegetatively propagated and because they are regular dietary items in the area'". The same might be said of such plants as *Stenocereus stellatus* and *Pachycereus hollianus* because these plants are easily propagated from pieces of stem, and according to Callen (1967) these plants (included within the *"Lemaireocereus"* remains) were regular dietary items during the history of human occupation of the Tehuacán Valley. However, as MacNeish (1967) opined, there are no firm evidences to establish this, because it has not been possible to distinguish between wild and cultivated *Opuntia* or any other cactus in archaeological records.

It seems that human interaction with cacti is very old, some thousand of years before their possible cultivation as considered by Smith. Thus, according to data from Guilin Naquitz (Flannery, 1986) and from Tehuacán (MacNeish, 1967), human beings were present in Central Mexico 12,000 years ago or more. These peoples are supposed to have come from the north. Therefore, the earliest human beings of these areas were necessarily familiar with the use and management of cacti and agave. Some historians such as Clavijero (1852), Sahagún (1970 and 1985) and Barco (1988) have made reference to some prehispanic and post-conquest peoples from northern Mexico with a nomadic or semi-nomadic life, who migrated from zone to zone following the seasonal abundance of cacti fruits. A similar pattern could be considered to have been adopted by the ancient gatherers of the deserts of Mexico until they started to manipulate forests for increasing the availability of some particular resources.

HISTORIC RECORDS

Codices drawn by prehispanic **"tlacuilos"** (the Nahua scribes) and the ones drawn and written by the first literate Mexican Indians after the Spanish conquest as well as the chronicles registered by conquistadors and priests make it possible to know about the daily life in Mexico during prehispanic times just before the conquest. A number of these documents contain 'valuable information on uses and forms of management of many plants, some of them identified by botanists thanks to precise descriptions and drawings. The major part of the prehispanic codices were destroyed by the conquistadors and priests, and no reference has been found on columnar cacti in the prehispanic codices available at present. However, there are several references in post-conquest documents. The first document including information on cacti is the ""General and Natural History of the Indies" written by the captain Hernandez de Oviedo y Valdés, the first chronicler of the New World, published in 1535. In chapter :XXVI, he wrote in old Spanish:

"De los Cardones en que nasce la fructa que llaman pitahaya.

No es mala fructa ni dañosa y es de buen parecer a la vista. Los cardones en que nascen estas pitahayas, es cosa fiera e de mucha salvajez la forma de ellos, los cuales son verdes e las espinas, pardas o blanquecinas, y la fructa colorada como he dicho e según aquí la he dibuxado."

This paragraph can be translated as follows: "About the spiny plants on which the fruit called pitahaya is produced. It is not a bad fruit neither harmful and it is good looking The spiny plants on which the pitahayas are produced are very aggresive and very savage in form. The plants are green and the spines brownish or whitish and the fruit is red as I have said and drawn". And in another chapter:

"De unos cardos altos é derechos mayores que lanzas de armas (é aun como picas luengas), quadrados y espinosos, é a los cuales llaman los Chripstianos cirios por que parecen cirios o hachas de cera, excepto en las espinas.

Los cardones que los Cripstianos Llaman cirios en esta isla, hay los assi mismo en otras muchas y en Tierra Firme. Estos son una manera de cardos muy espinosos é salvajes que no hay en ellos parte donde se puedan tocar sin muy fieras espinas, non obstante que la Natura se las pone por órden é á trechos una de otras con mucho concierto é compas repetidas en su composición."

Text which can be translated as: "About some spiny plants tall and more upright than lances of the army, squared and spiny which are called cirios by the Christians because they look like candles with the exception of the spines. The spiny plants called cirios by the Christians in this island, equally are present in many other islands and in the continent. These are a kind of plants very spiny and brutish in which no part can be touched because of the spines, however that the Nature puts the spines in order and in spaces one behind the other in a very ordered and repetitive composition".

The De la Cruz-Badiano codex, from 1552, titled *"Libellus de medicinalibus indorum herbis*" includes descriptions and drawings of plants and instructions for preparation and application of medicines based on these plants. This document includes a plant called "teonochtli" which means "prickly pear of god" in Nahuatl (Aztec) language. This plant has been identified as a species of *Stenocereus* by Bravo-Hollis (1978). The drawing of "teonochtli" is presented in Figure 1. In the foot of the drawing, it is possible to read tae following text in latin:

"DENTIUM DOLOR

Languidi denies et computrescentes cadaverino dente primum pungendi sunt. Deinde longae fruticis nomine ***teonochtli*** *radix teretur et comburetor cum cornu cervino, hi lapides pretiosi* ***yztacquetzalistli, chichiltic tapachtli****, et parum farinae male tritae cum sale debet califieri. Quae omnia panno involuta aliquantisper dentibus comprimantur, nominatim illis qui putredinis damnum uel doloris incommodum persentiunt. Postremo album thus et genus unguenti quad vocamus* ***xochiocotzol*** *prunis comburantur, quorum odore gossipii pensum crassum ,inficiatur et tandem buccis saepe admoveatur, imo quod mellius est alligetur."*

This text can be translated as follows: "TEETH PAIN. The ill and carious teeth have to be picked first with a tooth of a cadaver. Then, the root of a tall shrub called **teonochtli** is milled and roasted, along with deer horn and the following fine stones: **iztac quetzaliztli** and **chichiltic tapachtli,** with a small portion of flour mixed with salt. All these things are heated. All this mixture is covered with a cloth and is applied for a brief time clenching with the teeth, especially the ill or carious ones. Finally, a mixture is made with white incense and a kind of oil called x**ochiocotzol** and and this is burned on live coal and its odour is collected in a piece of cotton which is applied to the mouth with a certain frequency or better, it is tied to the cheek".

The Florentino Codex was written and drawn in 1547 by some of the first Nahuatl writers. This document was translated into Spanish by the priest Fray Bernardino de Sahagún between 1569 and 1582 and published in the monumental book "Historia de las cosas de Nueva España" ("History of the things of the New Spain"). In book II of the Florentino Codex there are many references to the use and the Nahuatl classification of plants of the genus *Opuntia*. Only two drawings and texts (not translated by Sahagún) refer to columnar cacti which cannot be identified with certainty. The first is called **"netzolli"** (Figure 2) with the following inscription in Nahuatl:

"Netzolli: cocomotstic, tlamalintic, mocahauatl, mamae. Netzalla, tequaquaia."

This text can be translated as: "**Netzolli**: tasty fruit, twist, many spines, it has arms, spiny plant, hurting". Based on the drawing and the reference to the character twist this plant is probably *Escontria chiotilla*. The second is called **"teunochtli"** which can be translated as "sacred prickly pear". It seems to be the same species of *Stenocereus* described in the De la Cruz-Badiano Codex. The following inscription is found:

"Teunochtli: axcan mitua uei nochtli, xoxoctic, quiltic, uiac, piaztic, nepaloni, itztic, tlaceuiloni, tlaceuia."

This text can be translated as: **"Teunochtli:** It has big fruits with spines, light ,and dark green, it is cold, it calms thirst"

Francisco Hernández, the official physician of the Spanish King Felipe II went to Mexico to know about the indigenous medicine. He wrote between 1571 and 1576 the "Natural History of New Spain" which contains a valuable inventory of medicinal plants and indigenous medical prescriptions, presumably used since prehispanic times. Hernández describes several species of *Opuntia, Ferocactus, Mammillaria, Hylocereus, Myrtiliocactus geometrizans* and a possible *Stenocereus* species called **"teonochtli".** Hernández (1959) mentions that the different species of *Opuntia* "...have a resin which decreases the 'heat' of the kidneys and urine. Its juice... is admirable against biliary and malign fevers, especially if it is mixed with pitahaya *(Stenocereus* spp.) juice."

The "Geographic Relations of XVI Century" are also an extraordinary source of information on ancient natural resources of Mexico. There are several references on the presence, use and management of *Opuntia* as well as toponimymic names referred to this genus. However, the only reference to columnar cacti is found in the Relation of Acatlán, a village near Tehuacán. This Relation was written by Juan de Vera in 1581 (Acuña, 1935). The reference is again on the **"teonochtli",** maybe the same species mentioned above, which is found in the chapter 22 in which the wild trees are described:

> "Hay otro árbol silvestre llamado TEONOCHTLI, que son unos cardones grandes, que lleva una fruta llamada pitahayas, muy gustosa y agradable, su madera arde como tea, y se sirven della para alumbrarse."

This paragraph can be translated as: "There is another wild tree called TEONOCHTLI, which is a big spiny plant with a fruit called pitahayas very tasty and nice, its wood burns like a candle, and people use it for lighting". Based on this description and the drawing from the Florentino Codex, this plant may be identified as *Polaskia chichipe,* the only columnar cactus used in this manner.

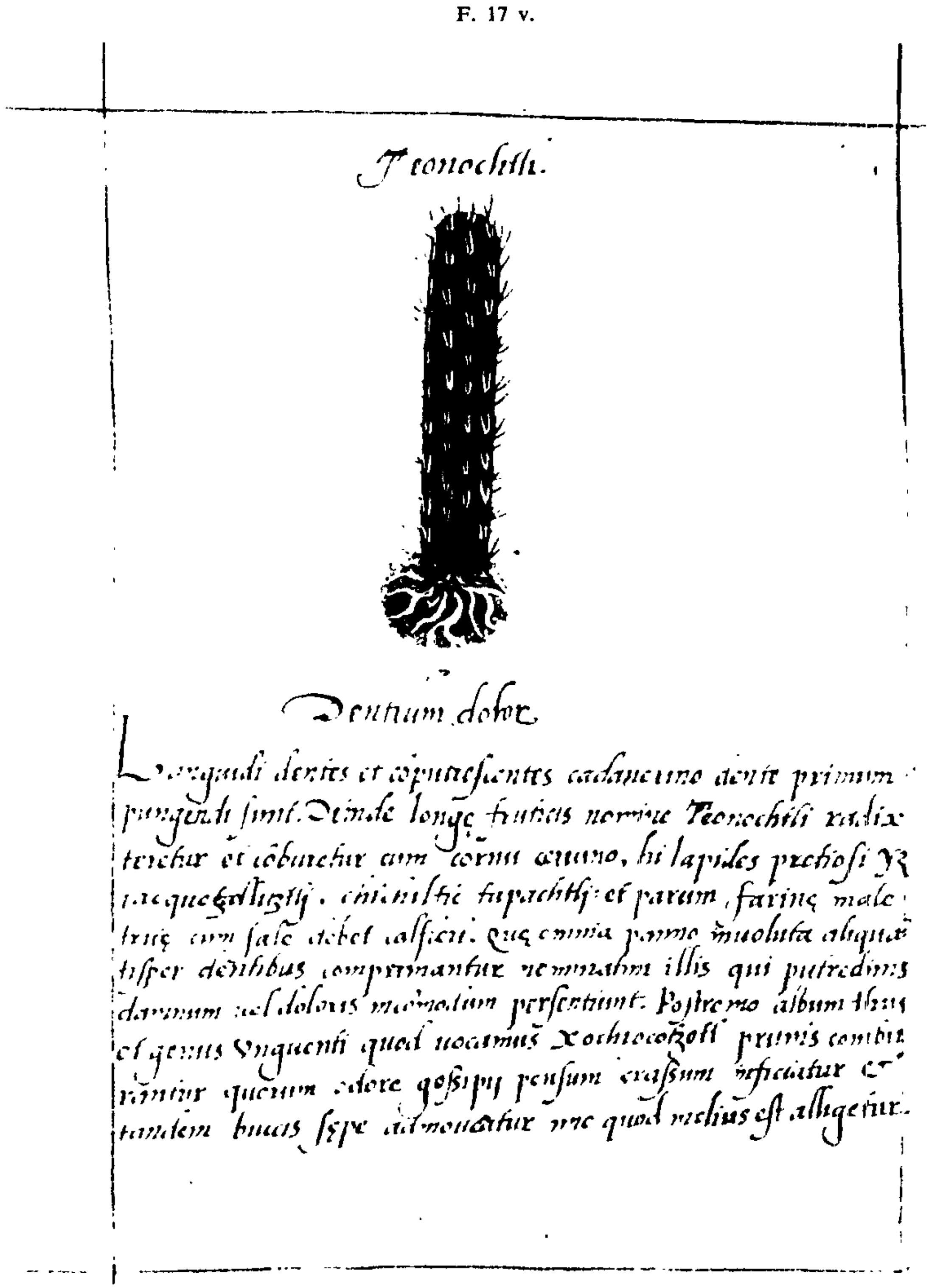
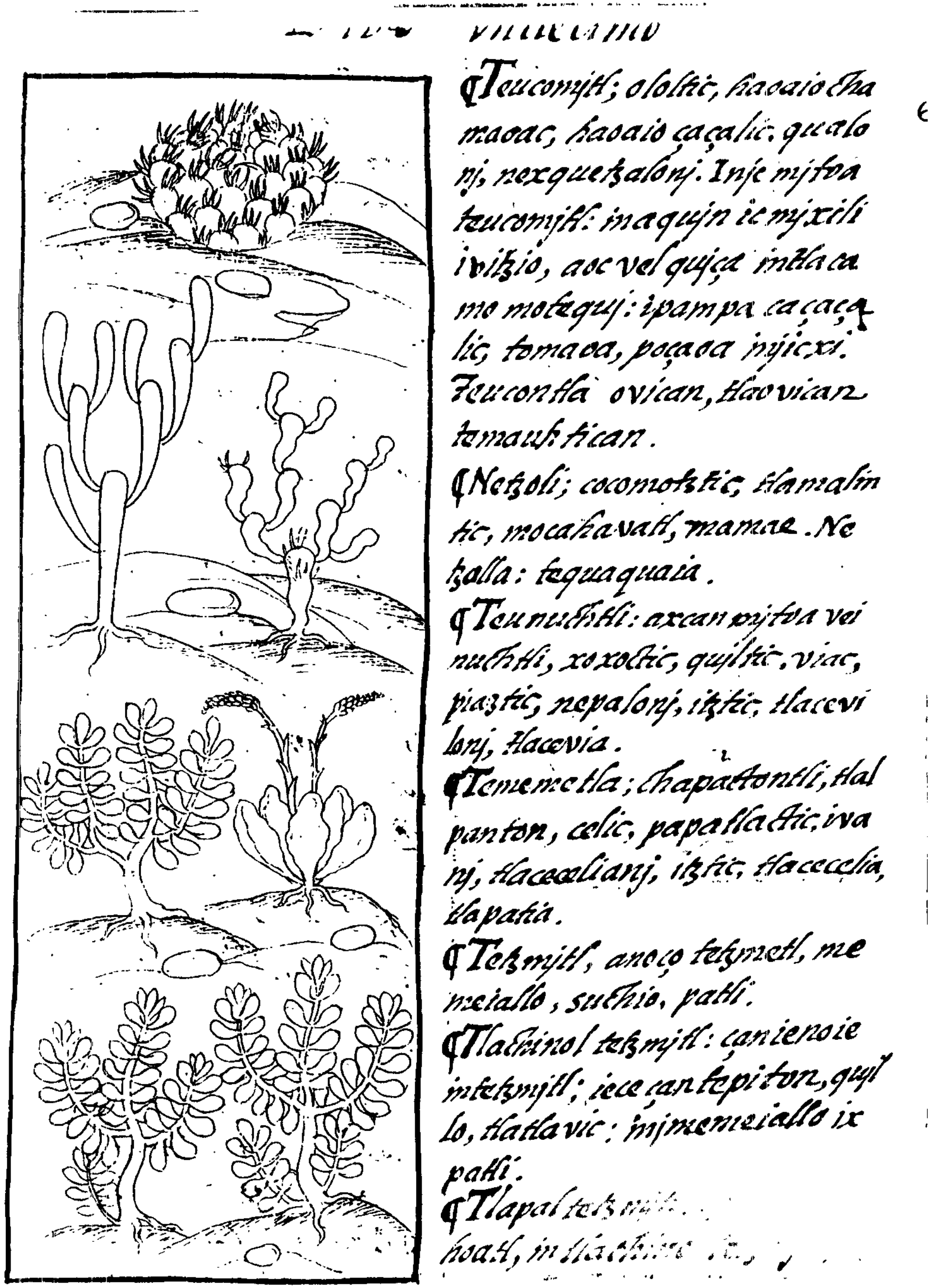


Figure 1. Teonochtli. Taken from the De la Cruz-Badiano Codex.



¶Teucomjtl; ololtic, haoaio chamaoac, haoaio çaçalic. quetzalonj, nexquetzalonj. Inic mjtoa teucomjtl: inaqujn ic mjxili ivitzio, auh vel qujça intlacamo motequj: ipampa çaçaçalic, tomaoa, poçaoa inyicxi. Teucomtla ovican, tlaovican temauhtican.

¶Netzoli; cocomotztic, tlamalintic, mocallaoatl, mamae. Netzolla: tequaquaia.

¶Teunochtli: axcan mjtoa vei nuchtli, xoxoltic, qujltic, viac, piaztic, nepalonj, itztic, tlacevilonj, tlacevia.

¶Tememetla; chapactontli, tlalpanton, celic, papatlactic, ivanj, tlacecelianj, itztic, tlacecelia, tlapatia.

¶Tetzmjtl, anoço tetzmetl, memeiallo, suchio, patli.

¶Tlachinol tetzmjtl: çan ie no ie in tetzmjtl; iece çan tepiton, qujllo, tlatlavic: inimemeiallo ixpatli.

Figure 2 Netzolli and Teunochtli, two columnar cacti. Taken from the Florentino Codex

Other important historical references on columnar cacti are those written in the old California by the missionary Miguel Barco between 1773 and 1780 (Barco, 1988), and Francisco Javier Clavijero in 1852. These authors mentioned that the harvest of pitahayas " ..is the main harvest of the Indians" (in the present Baja California, Mexico). In their books, there are excellent descriptions of morphology and uses of *Stenocereus turberi*, *Machaerocereus gumosus, Lophocereus schotii* and *Pachycereus pringlei.* All these plants are described as having been harvested from wild populations.

In all the historic documents mentioned here, there is an important aspect in common: there are several references on cultivation of *Opuntia,* especially the species dedicated to the production of the "grana" (cochineal), but there is none about the cultivation of any species of columnar cacti. It seems difficult to accept that people who wrote these documents did not realize the presence of columnar cacti in the Indian home gardens as they can be seen at present. Thus, this important omission in the documents has two possible explanations: either the Spanish did not consider the columnar cacti important, and for this reason they did not describe them, (as they did not describe many other plants), or these plants started to be cultivated more recently. More evidence is necessary for clarifying this question. However, it is important to take into account some field observations made in this research. In some areas of the Tehuacán Valley, especially in Zapotitlán, Los Reyes Metzontla and Chilac, wild: populations of *Stenocereus stellatus* are uncommon. They are strongly associated with archaeological zones where remains of prehispanic villages may be observed. This suggests that these "wild" populations might have derived from plants cultivated in prehispanic times. Analysis of morphology and genetic structure of these populations may give more light on this hypothesis.

4. PRESENT ETHNOBOTANICAL INFORMATION.

TRADITIONAL NOMENCLATURE AND CLASSIFICATION

When the Spaniards reached the Antilles, they saw cacti for the first time. They adopted the Antillian name **"tuna"** for fruits of *Opuntia* spp. and **"pitahaya"** for fruiits of several columnar cacti and other cacti such as species of the genus *Hylocereus* (Berger) Britton & Rose. The term "pitahaya" means scaly fruit in the Antillian language (Pimienta-Barrios and Nobel 1994). These are the most common names today in Mexico, although the indigenous people have also preserved their own names and systems of classification.

Nahua classification

The Nahua people, the most numerous Indian group in Mexico and in the Tehuacán

Valley, classify the cacti in six great categories (Figure 3). The first is called **"nopalli"** which includes all the plants of the genus *Opuntia;* the second is called **"nopalxochitl"** ("nopal with flowers") which includes species of epiphytes with plain stems and beautiful flowers, such as species of the genus *Nopalxochia;* the third is called **"huitznahuac"** ("surrounded of spines") or **"comitl"** (which makes reference to the traditional Indian pottery) which includes, all the species of genus of spherical cacti such as *Mammillaria, Ferocactus, Echinocactus,* and others; the fourth is called **"cuaunochtli"** ("tuna or pitahaya of tree") which includes several species of epiphytic cacti such as *Hylocereus;* the fifth includes species of the genus *Lophophora* which are called **"puyotl"** (the root of the transformed word "peyote") because of their hallucinogenic properties; the sixth includes the columnar cacti is designed by the word **"nochcuauitl"** which means "pitahaya tree". It is composed by the term "**nochtli**", a word that designates the fruits of all the species of cacti (tunas and pitahayas) and **"cuauitl"** which means tree. The name of each of these six categories is used by the Nahua as a primary lexeme and an epithet generally referring to some characteristic of a specific part of the plant provides a secondary lexeme. In the case of the category **"nopalxochitl",** the flowers are the pails which are considered for naming the secondary lexeme. For example, the word **"cosnopalxochitl"** includes as a prefix the term costic, meaning yellow, qualifying the kind of nopalxochitl with yellow flowers, indicating the cultural and cognitive significance of the flowers for the Nahua people in relation to these plants. In the case of the **"nopalli"** *(Opuntia)* and columnar cacti, fruits are the most important part used in classification. For example, terms **"iztacnochnopalli", "coznochnopalli" "xoconochnopalli" "tlanecxnochnopalli"** designate nopalli with white, yellow, sour and purple prickly pears respectively. In the case of columnar cacti, the Nahua people use the name **"nochcuauitl"** or more often only **"nochtli"** as a primary lexeme. This reveals the cultural importance of these fruits to the Nahua. For example, *Myrtillocactus geometrizans* is called **"tepepoanochtli",** ("pitahaya from aggressive hills"); *Polaskia chende* (Gosselin) A. Gibson & K. Horak is called **"cotzonochtli"** ("yellow pitahaya"); *P. chichipe* Backeberg is called **"tepequionochtli"** ("pitahaya of escapes -term used for agave escapes- from the hills"); *Stenocereus pruinosus* (Otto) F. Buxbaum is called **"cuapetlanochtli"** ("pitahaya of big tree"); and *S. stellatus is* called **"xoconochtli"** ("sour pitahaya"). Three species of *Opuntia (O. lasciacantha* Pfeiffer, *O. imbricata* (Haworth) De Candolle and *O.joconostle* Weber) are also commonly called **"xoconochtli".** Normally, these species should be called **"xoconochnopalli"** (Figure 3), but the Nahua people often utilize only different qualifications on **"nochtli"** (without the suffix **"nopalli")** as short names for designing different species of *Opuntia.*

The Nahua people recognize four different types of **"xoconochtli"** (S. *stellatus)* based on the color of the flesh: **"chichixoconochtli"** ("red and pink xoconochtli"),

"iztacxoconochtli" ("white xoconochtli"), **"cozxoconoxtli"** ("yellow or orange xoconochtli"), **"tlauecxoconochtli"** ("purple xoconochtli"). They subsequently distinguish between sweet and sour flavors, using the words **"necuti"** and **"xocotl"** respectively, but these epithets never form part of the names of the plant. Similarly, they use "**uitztli**" and **"amo uitztli"** for spiny and non spiny fruits. There are no specific words for variants with thick or thin pericarp. The Nahua prefer variants with sweet flavored, non spiny fruits with thin pericarp.

Popoloca classification

Among the Popoloca people, the classification of xoconochtli follows a hierarchical pattern very similar to that of the Nahua (Figure 4). The term "**túchi**" ("tuna" or "pitahaya") is used as the primary lexeme for grouping species of *Opuntia* and columnar cacti with big edible fruits. The secondary lexeme **"kánda"** distinguishes the genus *Opuntia* while *Stenocereus pruinosus* is designated by the name **"túchichína"** and *S. stellatus* **"túchikíshi",** a name composed by the roots **"túchi"** ("tuna" or "pitahaya") and **"chikíshi"** ("tree") that is, "pitahaya tree". In *Stenocereus* and *Opuntia*, further categories may be designated by colour, for example **"lula"** (white) or "**jatze**" (red) or by flavour: "**íisatu**" (sour) or "**íshetu**" (sweet).

Mixtec classification

The Mixtec people of Chinango classify cacti in three great groups. In one of them the term **"'vindia"** is used as primary lexeme for naming *Opuntia* species (Figure 5). Specific terms may refer to characteristics of cladodes, for example **"vindia ton"** ("black nopal") and **"vindia cúshi**" ("white nopal") are terms referring to the presence of black and white coloured spines respectively. Specific terms may also refer to characteristics of fruits which are called **"chíqui". "Vindia chíqui cuaá"** ("red prickly pear nopal"), **"vindia chíqui cúshi"** ("white prickly pear nopal") are examples of this situation. Spherical cacti are classified using the primary, lexeme "**chimilóô**". People in Chinango only distinguish two species of spherical cacti, "**chimilóô náânu"** ("big spherical cactus") in which *Ferocactus* and *Echinocactus* species are included, and "**chimilóô cuáti**" ("small spherical cacti") in which *Mammillaria* and *Coriphantha* species are included. The third great group is formed by columnar cacti which are classified using the term **"ndíchi"** as primary lexeme which is also used for naming fruits of columnar cacti. Species are distinguished using particular terms. For example, **"ndíchi nóni"** ("maize pitahaya") is used for naming *Myrtillocactus geometrizans;* **"ndíchi quitú"** for *Pachycereus weberi* (J. Coulter) Backeberg; **"ndíchi cáâya"** ("sandy pitahaya") for *S. stellatus;* **"ndíchi cuan"** ("yellow pitahaya") for *S. pruinosus;* **"ndíchi yáâ"** ("white pitahaya") for *Polasikia chichipe* and **"ndíchi laya"** for *P. marginatus.*

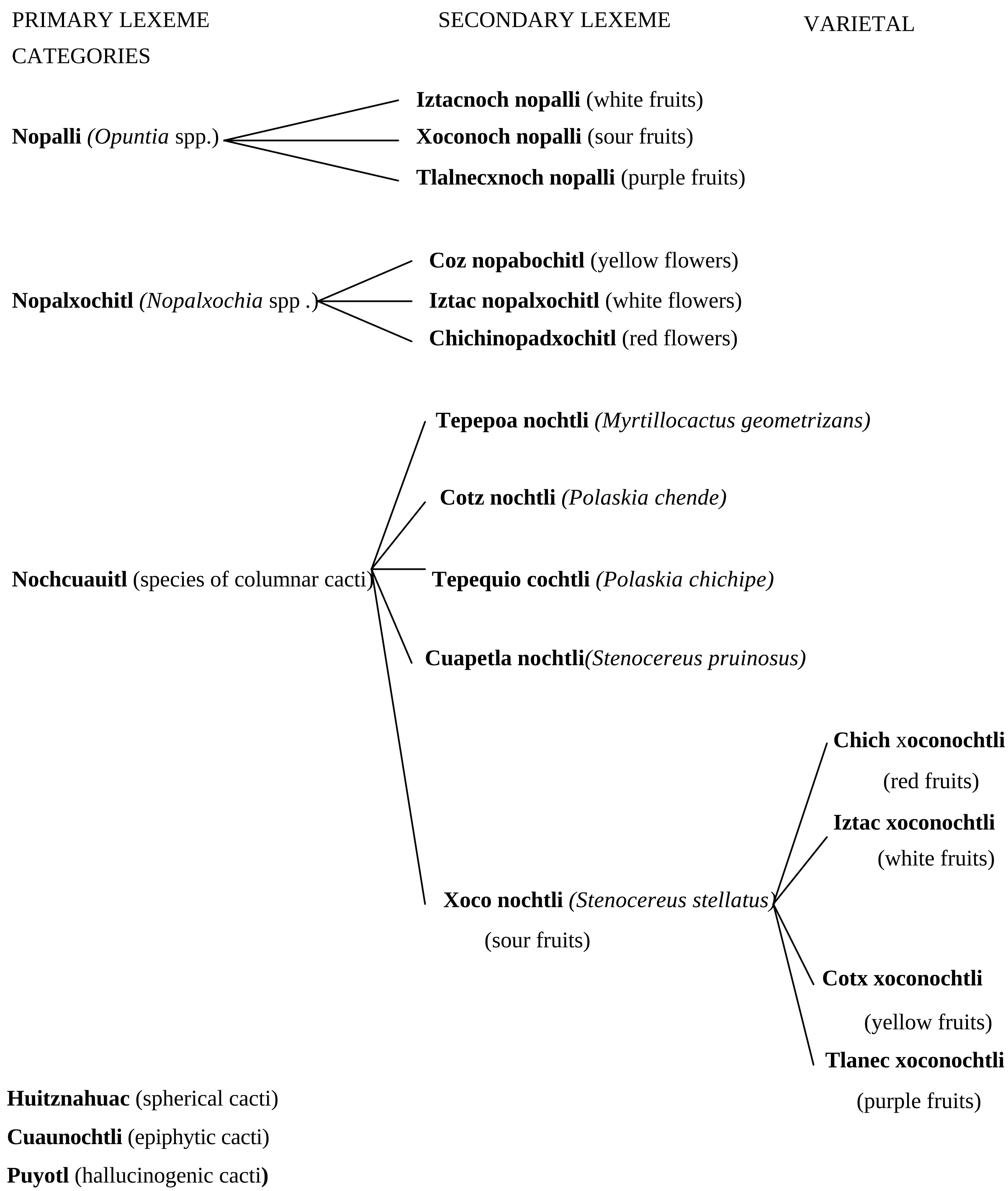


Figure 3. *Stenocereus stellatus* in the context of t he Nahuatl system of classification of cacti.

The Mixtec thus clearly distinguish between fruits *of Opuntia* and fruits of coFamnar cacti naming them as "**chíqui**" and "**ndíchi**", respectively. This resembles the Antillian classification and differs from the Nahua and Popoloca systems of cacti classification. Fruits of spheric cacti are also called "**chíqui**", but these are not considered by the Mixtec for the classification.

Variants of *S. stellatus* are classified on fruit characteristics. The first level of classification is based on colour of the pulp. In Spanish, people distinguish six variants: red, pink, white (or green), purple, orange and yellow. However, in Mixtec people only name four variants (Figure 5). It is important to mention that the Mixtec distinguish two main categories of "xoconochtli" according to their colour: the "red xoconochtli" **("ndíchi cáâya cuaá)** and the "colored xoconochtli" **("ndíchi cáâya color")** in which they group xoconochtli with fruits of the rest of the colours including white fruits. They consider the red colour fruits as a wild characteristic. The Mixtec also recognize variants within each colour according to the thickness of the pericarp and the abundance and persistence of spines. However, for naming these variants, people do not retrieve the complete hierarchical phrase name, but only that part which describes the fruits. For example, they use the names **"ndíchi dóô yáâdi"** and **"ndíchi dóô ndéê**" for xoconochtli with thin and thick pericarp, respectively, and **"ndíchi íño**" and **"ndíchi má íño**" for spiny and not so spiny fruits, respectively.

It is very common to find in home gardens some individuals of "xoconochtli" with morphological characteristics resembling both *Stenocereus stellatus* and *S. pruinosus.* They resemble *S. stellatus* in general appearance, but have deep ribs, light green stems, and vigorous spines, like *S. pruinosus.* They flower during the flowering season of *S. pruinosus* (February-May) and flower again later during the flowering season of *S. stellatus* (June-August). Their Mixtec name is **"ndíchi tucuéê"** meaning "rabid xoconochtli". According to local people, these plants produce *S. stellatus* flavored fruits during the *S. pruinosus* flowering season, and *S. pruinosus* flavored fruits during the *S. stellatus* flowering season. These plants are called "xoconochtli aventureros" in Spanish (meaning "adventurer xoconochtli") and are probably hybrids between the two species.

USES AMONG INDIGENOUS PEOPLE

Stenocereus stellatus is used mainly for it; sweet fruits. Fruits contain a sweet and juicy pulp formed by the seed £uncles which, when mature, are full of sugary liquid (Tables 1 and 2). They are in great demand as fresh fruits, but also as dried fruits ("xoconochtli pasados") and for preparing jams.

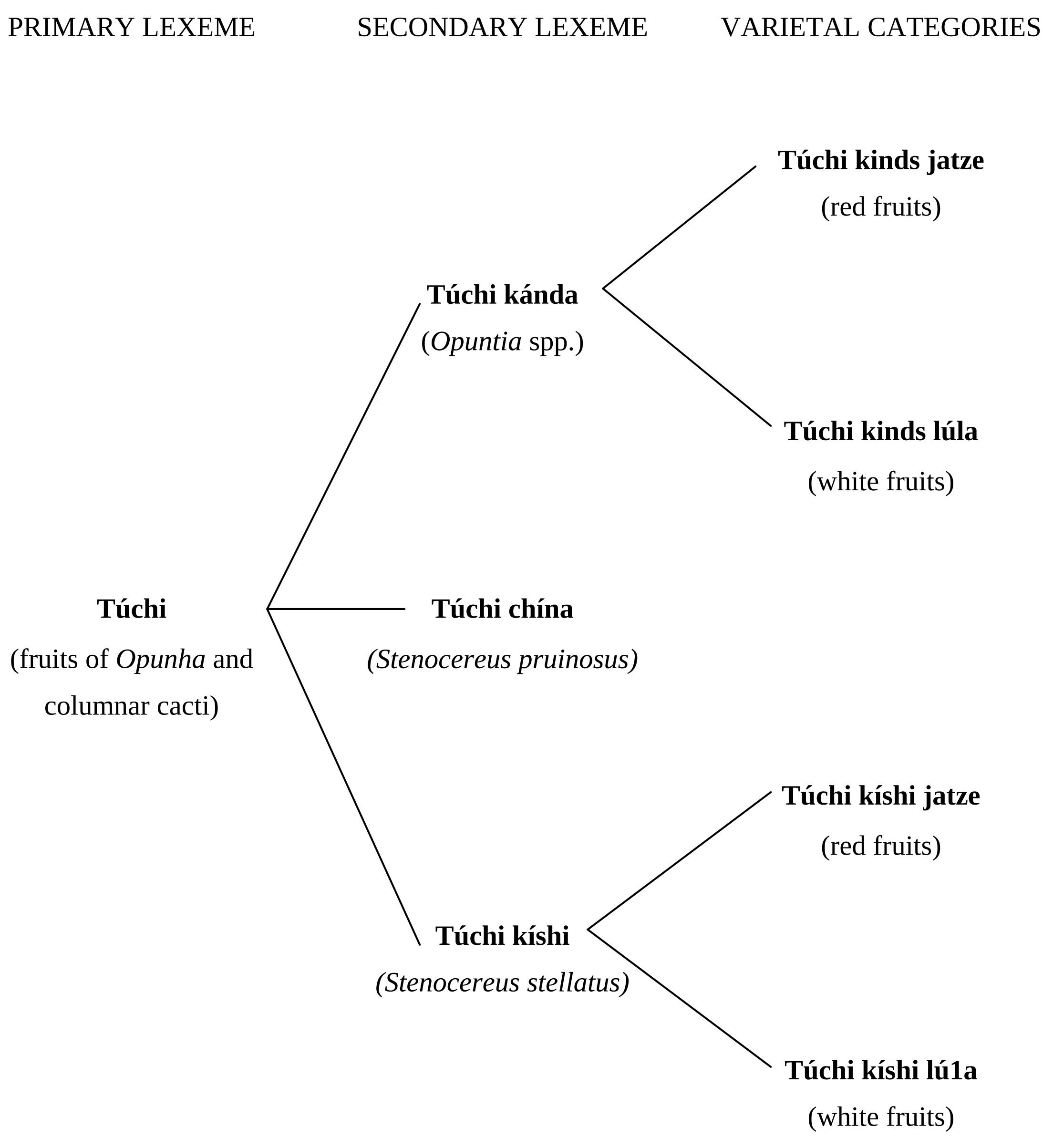


Figure 4. *Stenocereus stellatus* in the context of the Popoloca system of classification of cacti.

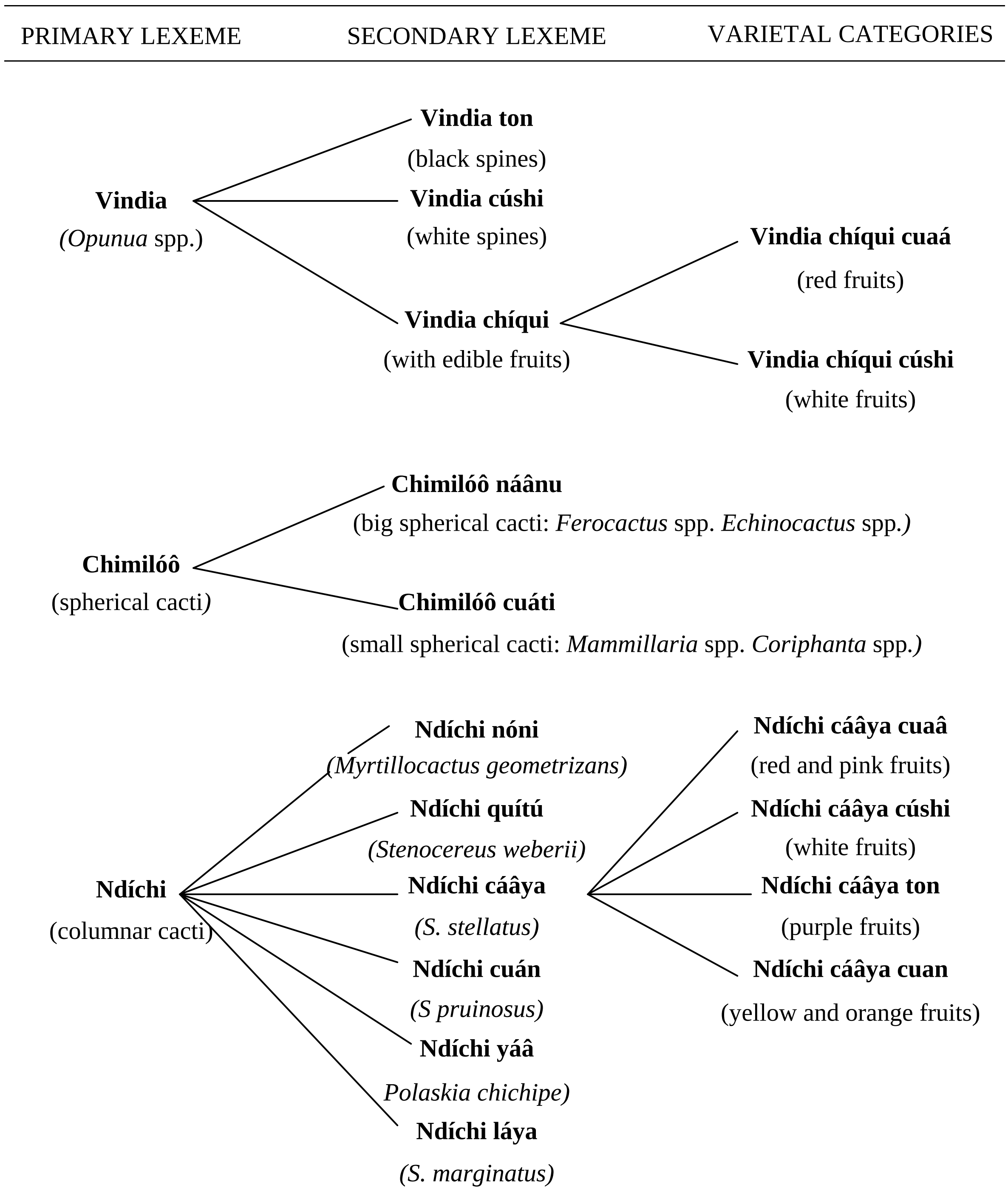


Figure 5. *Stenocereus stellatus* in the context of the Mixtec system of classification of cacti.

An alcoholic drink called "colonche" (from the Nahuatl word "nochoctli", which means "prickly pear pulque") is very common among indigenous people of other states such as San Luis Potosí and Zacatecas, where "colonche" is prepared with juice of fruits of *Opuntia* spp., or Sonora, where the Pápago people prepare "colonche" with fruits of *Stenocereus thurberi* (Engelmann) Buxbaum, *Machaerocereus gummosus*, *Carnegiea gigantea* (Engelmann) Britton & Rose and *Pachycereus pringlei* (S. Watson) Britton & Rose (Felger and Moser, 1974 and 1976,13ravo-Hollis and Sánchez-Mejorada, 1991). Colonche is sometimes prepared from *S. stellatus* in the Tehuacán Valley and Mixteca Baja.

According to Bravo-Hollis and Sánchez -Mejorada (1991), seeds of all cacti are edible, but because of their small size and the hardness of their testa they are not a common food. This use has persisted until the present among indigenous groups of the desert of Sonora in northern Mexico (Felger and Moser, 1974 and 1976; Bruhn, 1973; and Bravo-Hollis and Sánchez-Mejorada, 1991). These peoples extract seeds from fruits of several columnar cacti *(Carnegiea gigantea, Pachycereus pringlei, P. pecten-aboriginum, Stenocereus turberi, Machaerocereus gummosus, Ferocactus covillei, F. wislizenii)* and *Opuntia* species Then, they wash, dry and grind the seeds extracted producing an edible oily paste. Seeds are extracted directly from fresh fruits but may also be retrieved from human feces ("second harvest").

In the Tehuacán Valley, the seeds of *Neobuxbaumia tetetzo* (Coulter) Backeberg, *Pachycereus weberi* and *S. stellatus* are still eaten by the Nahua, the Mixtec and the Popoloca people. Seeds obtained from fresh or dried fruits are washed, dried and roasted. The roasted seeds are ground with chili peppers, onion and green tomato *(Physalis philadelphica* Lamarck) or red tomato *(Lycopersicon esculentum* Miller) for preparing traditional sauces eaten with maize tortillas as the main component of the Indian diet. The basic components of the sauces can be other seasonal wild or cultivated products. For example, seeds of *Leucaena esculenta* (Moc. et Sessé ex A.DC.) Benth. are used between December and March, fruits of *Spondias mombin* L. between April and May, seeds of *N. tetetzo* in June, seeds of *Pachycereus weberi* between February and April, and seeds of *S. stellatus* between July and September. Alternatively, the roasted cactus seeds may be ground into an edible paste which is eaten with "tortillas". Table 9 shows that seeds of *S. stellatus* contain significant quantities of protein and fat. This information permits an understanding of the importance of this resource in the Indian subsistence and its promissory value for human nutrition.

Stems and flowers are occasionally consumed. They are usually eaten during seasons of Food scarcity. Consumption of stems of columnar cacti is not very common at present but they seem to have been a very common food in the past (Callen, 1967) Young stems are prepared by removing the spines, cutting them in longitudinal pieces and removing the medullar portion, then roasting them. After roasting, the cuticle is easily removed. This method of preparation is similar to that for *Opuntia* stems, which are a very common food in Mexico. The flower buds are boiled and then fried with eggs. This is a common form of preparation of flowers of many species of cacti, *Agave, Yucca, Beaucarnea,* and other genera. The boiled flower buds may also be prepared with onion and vinegar. This is particularly common with *Neobuxbaumia tetetzo* but occurs also with flower buds of other columnar cacti, including *S. stellants.*

TABLE 1. PERCENTAGE COMPOSITION OF FRUITS AND SEEDS OF *STENOCEREUS STELLATUS.* (BASED UPON BRAVO-HOLLIS AND SANCHEZ-MEJORADA 1991).

Elements	Pulp		Seeds	
	Fresh	Dried	Fresh	Dried
Proteins	1.00	7.33	21.10	22.21
Raw fiber	0.25	1.83	-	-
Ash	0.48	3.54	-	-
Fats	2.28	2.07	22.20	23.38
Water	86.33	-	5.20	-
Nitrogen free extract	11.66	85.23	-	-

TABLE 2. NUTRITIONAL CHARACTERISTICS OF JUICE FROM FRUITS OF STENOCEREUS STELLATUS

(BASED UPON BRAVO-HOLLIS AND SANCHEZ-MEJORADA 1991)

Characteristics	Amount
Brix degrees at 20°C	10.4°
Citric acid	0.64 g/100ml
pH	3.95
Solids in suspension	0.685 g/100 ml
Solids in solution	9.1015 g/100 ml
Direct reducing sugars	7.9%
Total reducing sugars	8.1%
Vitamin C	11.72 mg/100 ml

Cultural value of all these edible products from "xoconochtli" can be studied in the markets during the exchange for other products. Thus, in some villages (e.g. Los Reyes Metzontla) and markets (e.g. Ajalpan), three to five fresh fruits or six to ten dried fruits of *S. stellatus* are exchanged for one litre of maize; one litre of flower buds for three litres of maize and one litre of seeds for fifteen litres of maize.

Young branches of *S. stellatus* and other species of columnar cacti are also cut and fed to goats, after removal of the spines. The plants are not killed and produce more branches relatively quickly which may grow 20 to 40 cm per year. Whole fruits or pericarp and seeds of fruits whose pulp has been used are also a very good forage. There are no designed plantations of S. *stellatus* for production of forage. However, some variants could be explored in this direction. The experience with *Opuntia* in this respect reveals the promissory value of species such as *S. stellatus* with useful fruits for human or animal consumption, easy propagation by vegetative means, tolerance to poor soils as well as fast growth and production of branches.

Stenocereus stellatus is used in traditional Nahua, Mixtec and Popoloca medicine. Boiled stems are eaten as a remedy for gastritis. Broken bones are treated by applying gum extracted from the stems to the affected part and then binding it.

For manufacturing pottery, a "bed" of hard wood with high specific heat is made by people from Los Reyes Metzontla from species such as *Acacia* spp., *Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C. Johnston, and *Lippia graveolens* Kunth. Objects to be fired are put on this bed and covered with "soft" wood with a lower specific heat. *Ipomoea arborescens* G. Don, *Agave* spp., *Polaskia chichipe* and *S. stellatus* are among the most important sources of "soft" wood.

Individuals of *S*. *stellatus* along with *Myrtillocactus geometrizans, S. pruinosus, Pachycereus marginatus* and *P. hollianus* (F.A.C. Weber) F. Buxbaum are commonly grown as living fences and as barriers for soil protection in terraces around the borders of cultivated slopes.

TRADITIONAL MANAGEMENT

In the study area, people commonly gather fruits or cut stems of *Stenocereus stellatus* from wild populations. They also commonly tolerate individuals that are naturally established when they clear new land for corn fields or enhance abundance of this plant in the natural populations *in situ* by planting branches and taking care of them. In addition, people take branches from wild individuals to plant them in home gardens or as living fences around agricultural fields. Pieces of stems and sometimes seeds and seedlings of previously cultivated individuals are also used for these purposes.

Gathering of wild xoconochtli is especially important in Coxcatlán and Zapotitlán, where there are dense wild populations, as well as in Chinango, where plants are more scattered but yield more fruits per plant (Table 3). People collect fruits selectively, preferring variants with relatively sweeter flavour, thinner pericarp, fewer spines and bigger size for consumption of fresh fruits. When the fruits are gathered for preparing jams or dried fruits ("xoconochtli pasado"), the harvest is less selective. Adults and children of both sexes collect the fruits during the season. They may eat the fruits on the same place where they collected or may collect fruits for consumption at home or for sale in the local traditional markets such as in Coxcatlán In this village, all the xoconochtli is harvested from wild populations. In Chinango, the main portion of xoconochtli products is obtained from the home gardens, but this is complemented with resources from the wild. People carry fruits to the main market of the municipality, and to the most important regional markets in San Pedro Chazumba and Huajuapan de León, Oaxaca. Also, local exchange of xoconochtli for maize occurs with some communities of Puebla and Oaxaca, and for ceramic with Los Reyes Metzontla. In Coxcatlán the whole harvest of xoconochtli is from wild populations because it is not cultivated there. In the remaining localities where wild populations of *S. stellatus* were found, gathering is less important. Fruits are consumed where they are collected and sometimes carried home.

People in all the studied areas enhance the availability of xoconochtli in managed areas, generally where they cultivate corn. During the clearing of forest for establishing corn fields, people spare some useful perennial plants such as *Beaucarnea gracilis, Stenocereus pruinosus, S. stellatus, Myrtillocactus geometrizans, Pachycereus hollianus, P. weberi, P. marginatus Prosopis laevigata, Leucaena* spp., *Pithecellobium dulce* (Roxb.) Bentham, *Polaskia* spp. and *Escontria chiotilla.* It is a common practice that people also sow in these areas seeds of the species of legumes mentioned and plant vegetative propagules of the columnar cacti (with the exception of *P. weberi,* which cannot be propagated vegetatively and grows very slowly).

The individuals of these tolerated species, of course, compete with the cultivated plants. Therefore, people carefully select which species are the best for sparing. Their decision takes into account the usefulness of the species to spare. People prefer to tolerate the species mentioned above in the following order: *Leucaena* spp. *Prosopis laevigata, S. stellatus, S. pruinosus, Pachycereus hollianus, P. marginatus, M. geometrizans, Pithecellobium dulce*, *E. chiotilla, Polaskia* spp., *P. weberi* and *Beaucarnea gracilis.* They also take into account the characteristics of the useful products of the individuals of each species. In the case of *S.*

stellatus people prefer to spare individuals with big fruits, sweet flavor, thin pericarp and few spines. However, the tolerance of other phenotypes is also common, especially when there are no other competing species or phenotypes.

Individuals of *S. stellatus* cultivated in home gardens may represent tolerated seedlings which established from seeds dispersed through bird, bat or human faeces. Generally, people do not recognize variants of xoconochtli based on vegetative characteristics. Therefore, decisions on eliminating or sparing S. *stellatus* individuals are generally taken after four or five years when the individuals produce fruits.

However, the most important form of cultivation is by planting branches. In all the places studied where cultivation is carried out, people generally cut vigorous branches at the articulation level from mature desired individuals. Branches used for this purpose measure between 20 and 100 cm. They are left exposed to the sun, for ten or fifteen days in order that the cut surface may dry. This reduces fungal and bacterial infections. After this period, the branches are planted either horizontally or vertically in holes 10 to 40 cm deep with cattle or goat dung added as fertilizer before planting. They are usually planted just before the rainy season. A few fruits may be obtained after one year, but during the second year the plants commonly do not produce. Thus, the production does not really start until the third year and in some cases until the fourth year after planting. *S. stellatus* is neither irrigated nor pruned, but ash is commonly deposited, as fertilizer, on the soil covering the main stems.

ROLE OF *S. STELLATUS* IN SUBSISTENCE OF INDIGENOUS PEOPLE

Popoloca people of Zapotitlán subsist from the exploitation of mines of onyx and the manufacturing of handicrafts of this material. They harvest occasionally fruits of xoconochtli from small but dense populations (Table 3) spread as patches around the town. Also, there are home gardens with few individuals of *S. stellatus.* Fruits of xoconochtli are consumed only by members of the family and they are never marketed. Popoloca people of San Juan Raya base their subsistence on traditional agriculture of maize, raising of goats, extraction and marketing of fuelwood and the manufacturing of products of *Yucca periculosa* F. Baker. There are some few individuals of xoconochtli in home gardens, but the main harvest of fruits is from wild populations, although density of population and yield is very low (Table 3). Fruits of both wild and cultivated xoconochtli are destined only for home consumption.

The Popoloca people of Los Reyes Metzontla base their subsistence on the manufacturing of pottery and the raising of goats on a small scale. They also practice seasonal agriculture of maize but the poor soils and the low and irregular precipitation determine extremely low yields. People exchange ceramics for money or for maize and other agricultural products. In this village, home gardens are relatively more important in the subsistence of the people than in the former places, which is evident since these are better procured and constituted by more plant elements. Only approximately 10% of the home gardens are irrigated and the great majority depends on the rainy season. For this reason, the main components of home gardens are native plant species. Among the most common species are *Stenocereus stellatus, S. pruinosus , Pachycereus marginatus, P. hollianus, Opuntia* spp., *Agave* spp., *Leucaena esculenta, Psidium guajava* L. *and Spondias mombin. Stenocereus stellatus* is one of the most important elements of home gardens. However, people of Los Reyes only occasionally market the products of xoconochtli. These are mainly products for consumption of the local families. There are also managed wild populations which are formed by individuals tolerated during the clearing of the area and individuals planted there. Wild populations of S. *stellatus* were not observed in the area of Los Reyes Metzontla. A widely accepted opinion among local people is that "wild" xoconochtli are restricted to zones where archaeological remains exist. Fruits of xoconochtli from this population and from other similar patches, complement the production of the home gardens and also, they are only consumed by the local families.

In Coxcatlán, the alluvial valley of the Salado river is very wide in the area around Coxcatlán. This favours irrigated agriculture. Sugar cane is the main crop in the area which is processed in the factory of the neighbouring village of Calipan. Although maize and other basic grains are cultivated in the irrigated area, these are mainly produced in agricultural fields on the hills. This is possible because in this zone the pluvial precipitation is higher and the soils are deeper than in the zone described above. Thus, Nahua people of Coxcatlán base their subsistence on agriculture which is complemented by cattle and raising of goats. The major part of home gardens of this village are irrigated and people prefer to cultivate there species with high requirements for water such as *Persea americana* Miller, *Diospyros digyna* Jacq., *Citrus* spp. and others. Introduced variants of cultivated *Opuntia* species are the only cultivated cacti. Other products of useful cacti (mainly *Escontria chiotilla, Myrtillocaactus geometrizans* and *Stenocereus stellatus)* are harvested in wild populations. These products are destined mainly for the consumption of local families and they are also marketed but only at local level.

In San Lorenzo there are wild populations of *S. stellatus* occuring with a low density of population but good yield per hectare (Table 3). Within this plant population of approximately 20 km^2, there are some patches of maize fields. Considering the antiquity of human occupation of the area (around 10000 years before present according to MacNeish 1967), it is possible that this plant population has been used and managed for long time. At present, useful wild products of this forest are harvested by the Nahua and Mestizo people of San Lorenzo and Tehuacán. However, this harvest is only occasional and for home consumption.

In Chinango, the Mixtec people depend on traditional agriculture of maize and beans, raising of goats as well as production and marketing of fruits of *S. stellatus* and *S. pruinosus.* Home gardens of the village represent a cultivated stand, and wild and managed populations occur in natural and disturbed areas. People harvest xoconochtli fruits for both self consumption and marketing. In the home gardens, *S. stellatus* and *S. pruinosus* are by far the most abundant species cultivated.

FRUIT YIELDS AMONG POPULATIONS

Table 3 presents the results of sampling and estimations of fruit yields among populations. It shows that density of population ranges from 22 to 780 plants per hectare. It reveals that there is no clear pattern of abundance of trees in relation to forms of management. Thus, .although the least density is found in a wild population (San Juan Raya) and the most dense population is cultivated (Metzontla-C), there are also highly dense wild populations (such as Coxcatlán and Zapotitlán) and one non dense cultivated population such as Chinango.

However, when other parameters related to fruit yield are analyzed, differences arise. Thus, Table 4 shows that the rest of the evaluated parameters (number of reproductive branches, number of fruits per branch, number of fruits per individual, weight of fruits and kilograms of fruits per individual) were significantly higher in cultivated populations, lower in wild populations (with the exception of the wild individuals from Chinango-W) and with a wide range of variation in populations enhanced *in situ.*

The lowest yields were observed in San Juan Raya and San Lorenzo wild populations (Table 3). In these populations, the population density, the number of producing branches and the number of fruits per branch were also the lowest. Fruit yields in Zapotitlán and Coxcatlán wild populations were higher because, although fruit size was low, populations were dense. The wild population of Chinango (Chinango-W) was less dense than Zapotitlán and Coxcathm populations however, this population presented a fruit yield similar to these two populations in terms of kilograms per hectare. This is because fruits from this population are bigger than in Zapotitlán and Coxcatlán.

TABLE 3.FRUIT YIELDS AMONG STUDIED POPULATIONS (*MEAN VALUES; ** STANDARD ERRORS)

Population	Zapotitlán	Sn. Lorenzo	Sn. Juan R.	Coxcatlán	Chinango-W	Metzontla-M	Chinango-M	Metzontla-C	Chinango-C
Cultural status	Wild	Wild	Wild	Wild	Wild	Managed in situ	Managed in situ	Cultivated	Cultivated
Sampled area (m^2)	1500	10000	8500	6000	6000	1000	7500	2572.5	65000
Density of population (individuals per ha)*	273.3	34	29.4	280	35	120	48	780.9	93.9
S E.**	±107.29	±10.87	±8.60	±43.51	±17.26	±20	±14.45	±226.74	±20.16
Num. of individuals sampled	41	34	25	168	21	12	36	275	452
Num. of individuals sampled with fruits	24 (58.54%)	18 (52.94%)	5 (20.00%)	22 (13.10%)	9 (42.86%)	12 (100.00%)	8 (22.2%)	275 (100.00%)	423 (93.6%)
Individuals per ha. producing fruits	160	18	5.9	36.7	15	120	10.7	780.9	87.9
Num. of branches per individual*	6.96	19.1	11.20	6.39	14.22	19 00	675	22.13	21.52
S.E**	±0.88	±4.76	±3.81	±1.27	±4.30	±3.03	±1.35	±2.29	±3.01

...TABLE 3 FRUIT YIELDS AMONG POPULATIONS

Population	Zapotitlán	Sn. Lorenzo	Sn. Juan r	Coxcatlán	Chinango-W	Metzontla-M	Chinango-M	Metzontla-C	Chinango-C
Num of branches with fruits per individual*	3.04 (43.7%)	5.5 (28.9%)	2.6 (23.2%)	2.54 (39.8%)	7.11 (50%)	7.42 (39%)	3.13 (46.3%)	8.58 (38.6%)	15.54 (72.2%)
S.E**	±0.51	±1.38	±0.98	±0.58	±3.43	±1.69	±0.92	±1.06	±2.34
Num. of fruits per branch*	7.22	4.88	4.48	4.65	11.08	4.78	8.84	10.98	12.20
S.E**	±0.90	±1.01	±1.27	±0.84	±2.05	±0.69	±0.90	±1.05	±0.75
Number of fruits per individual*	19.63	37.67	12.00	12.77	81.67	39.17	25.13	98.92	187.11
S.E**	±3.44	±12.97	±7.52	±3.39	±37.72	±10.68	±6.17	±14.49	±29.76
Weight of fruits (g)*	22.33	23.16	19.40	18.65	41.70	32.11	37.92	38.81	72.23
S.E**	±1.87	±2.30	±2.44	±2.58	±6.12	±2.84	±4.88	±2.89	±4.04
Kg. of fruits per individual*	0.45	1.19	0.17	0.281	4.61	1.46	1.01	3.73	13.62
S.E.**	3-0.09	±0.47	±0.07	±0.09	±2 43	±0.47	±0 30	±0.55	±2.36
Number of fruits per ha.	3140.08	678.06	70.80	468.66	1225.05	4700.40	268.89	77246.63	16446.97
Kg. of fruits per ha.	72	21.42	1.00	10.31	69.15	174 00	10.81	2912.76	1197.20

TABLE 4. ANALYSIS OF VARIANCE FOR PARAMETERS RELATED TO FRUIT YIELD AMONG POPULATIONS. POPULATIONS NOT FOLLOWED BY THE SAME LETTERS ARE SIGNIFICANTLY DIFFERENT FOR THE CORRESPONDENT CHARACTERISTIC ACCORDING TO TUKEY HIGHEST SIGNIFICANT DIFFERENCE (95%).

D.F=151 WITHIN GROUPS AND 8 BETWEEN GROUPS

	Homogeneous groups				
Population	Number of producing branches	Number of fruits per branch	Weight of fruits	Number of fruits per tree	Kg. of fruits per tree
Zapotitlán	A	AB	A	A	A
Sn. Lorenzo	A	A	AB	A	A
Sn Juan R.	AB	AB	ABC	AB	A
Coxcatlán	A	A	A	A	A
Chinango-W	AB	BCD	AB	ABC	AB
Metzontla-M	AB	AB	AB	A	A
Chinango-M	A	ABCD	AB	ABC	A
Metzontla-C	AB	CD	B	ABC	A
Chinango-C	BC	D	C	CD	B

The population enhanced *in situ* of Metzontla (Metzontla-M) presented a much higher production than any of the wild populations. This is explained by the bigger fruit size as well as the higher proportion of individuals and branches per individual producing fruits. In contrast, the *in situ* managed population of Chinango (Chinango-M) presented a lower fruit yield, even lower than that of the wild population of the same area. This can be explained because in Metzontla people take especial care of *in situ* enhanced individuals while in Chinango these are only tolerated. Differences between the wild and *in situ* managed populations of Chinango are mainly due to differences in the number of branches. This could be due only to a difference in age.

The highest production of fruits was found in the home gardens of Metzontla This is explained by the high density of population, number of branches producing fruits and number of fruits per branch. However, the most productive individuals are those from Chinango. These individuals presented the highest number of producing branches and the biggest fruits. And, although they yield fewer fruits per branch than individuals from Metzontla, they produce the most of kilograms of fruits per individual.

DISCUSSION

Ethnobotanical research revealed that fruits are the most significant part of *Stenocereus stellatus* utilized in the area. Fruits are also the most important useful part of xoconochtli, and its classification is based on characteristics of this part. Seeds and stems are utilized only occasionally, and not used in any folk classification of this species. All this suggests that studies on domestication should centre on variation in fruits.

A great diversity of fruit characteristics were observed in wild and cultivated populations. Five fruit characters are used in classification of infra specific variation among the three Indian groups studied. These characters are 1) Colour. This is used to make a first division of categories within xoconochtli, other columnar cacti and also *Opuntia* species. Red fruits are considered characteristic of the wild plants, while white fruits are considered as the "best" cultivated variants of xoconochtli. 2) Size. People distinguish between "small" and "big" fruits. Small sized fruits are considered to have been harvested from the wild, while big fruits generally are associated with cultivation. 3) Flavour. People recognize three different flavours of xoconochtli fruits: sweet, sour and insipid. The first two are preferred for different purposes, but sweet flavour is identified with cultivated plants, while sour flavour is considered characteristic of wild plants. 4) Thickness of the pericarp. People distinguish between fruits with thin and thick pericarps, associating thin pericarps with cultivated plants. 5) Spiny fruits. Spiny fruit is considered a wild character. Fruits from cultivated plants have fewer spines

Combinations of character states for these 5 characteristics determine the existence of a significant number of variants. All these variants constitute the raw matter for artificial selection. The crucial aspect in this respect is to identify the variants preferred by people, according to their cultural values, and how they are promoted in the wild and in home gardens.

People consider the best xoconochtli to be large in size, white, sweet flavored with thin pericarp and few spines. However, they generally maintain variants of different characteristics for different purposes. For example, sour fruits are good for preparation of drinks and jams; spiny fruits are more resistant to predators; fruits with thick pericarp resist rotting and are better for long distance transportation. Artificial selection thus seems to be directed to favour a number of different combinations of fruit characteristics, each playing a particular cultural role. This pattern of selection may determine complex patterns of variation of xoconochtli associated with human manipulation. An important aspect, which will be analysed in other chapters is the distribution of frequencies of these different phenotypes in wild, wild managed *in situ* and cultivated populations, in order to elucidate effects of human selection enhancing particular phenotypes and in which proportions.

According to present information, isolation and subsequent increasing of individuals with desired phenotypes from wild populations through vegetative propagation seems to be the main firm in which artificial selection is carried out. This process may be achieved *ex situ* by carrying branches of the desired plants to home gardens, or *in situ*, by sparing desired plants and eliminating the non-desired ones. However, tolerance and care of seedlings which are then enhanced or eliminated depending on the quality of their fruits was also observed. In addition, it was observed that some variants known in cultivation are not present in wild populations, for example white fruits.

Strong differences were observed between wild and cultivated fruit yields. These differences are mainly due to the size of fruits and the number of branches per individual producing fruits, as illustrated in the case of cultivated individuals from Chinango compared with the rest of the studied populations. The number of branches could be a factor determined by the age of the individuals and care of individuals by people. However, increase in size and number of fruits, seems to be an effective way to increase yield per individual. Therefore. it is possible to expect the increasing of fruit size as an important route of artificial selection.

The management of xoconochtli seems to be influenced by the role of xoconochtli products in the subsistence of people, the availability of xoconochtli in the wild, and environmental factors determining success in the establishment of this plant species In

Coxcatlán, for instance, xoconochtli is almost absent in home gardens. The Nahua people in this area are farmers but home gardens only complement the agricultural economy. People cultivate in home gardens several species of fruit trees, but not xoconochtli because, as people say, "there are a lot in the wild". In contrast, in Los Reyes Metzontla, although home gardens also complement subsistence, this complementation seems to be more important than in Coxcatlán because of the lower yields in maize agriculture. Along with this, the scarcity of wild xoconochtli strongly encourages people to cultivate this plant.

In other villages such as Zapotitlán and San Juan Raya, wild populations of xoconochtli are not as dense as in Coxcatlán, but xoconochtli plays a very secondary role in people subsistence, and cultivation is not relevant. On the other hand, in Chinango, production, consumption and marketing of xoconochtli fruits play a more important role in people subsistence. In this area, although wild populations of xoconochtli are present, yields are significantly higher in home gardens. In this village, cultivation is therefore a way for increasing quantity and quality of these plant resources. There, interactions between people and xoconochtli are more intense and artificial selection is more active than in the rest of the villages studied.

The *in situ* enhanced population from Metzontla presented significantly higher fruit yield than other wild populations around this village (Zapotitlán and San Juan Raya). The range of fruit size was similar to that found in wild populations and also to that found in cultivated individuals in home gardens of the village (which were significantly bigger than the local wild fruits). This may be a result of the selective sparing of trees practised during clearings of terrains for agriculture and/or the introduction of good phenotypes to the population. This was not observed in Chinango, where *in situ* enhanced and wild populations did not present significant differences in fruit size but cultivated individuals had much larger fruit. In Chinango, cultivated xoconochtli are of better quality than the wild xoconochtli and enough to cover requirements of people (this, illustrated by the fact that cultivated fruits are not completely harvested). In Chinango, wild and *in situ* managed populations are complementary sources of this resource, for this reason they are gathered and spared, but they do not seem to be an important complement. Thus, people concentrate efforts of management and artificial selection in home gardens. Nevertheless, the situation in Metzontla suggests that, as with cultivation in home gardens, *in situ* enhancement may involve mechanisms of artificial selection which could modify the abundance of particular phenotypes according to human convenience.

ECONOMIC POTENTIAL

The following are some potential uses of *Stenocereus stellatus* which are proposed based on the experience of field work in Tehuacán as well as information in literature:

1. **Fruits as human food.** Demand of xoconochtli fruits might be increased in a wider area in Mexico. However, this depends strongly on developing better forms of fruit preservation. At present, there are problems in the commercialization of fresh fruits due to difficulties in transportation from rural villages to the principal urban marketing centres. This causes considerable loss of products. Only well organized communities such as those in the La Mixteca Baja have been able to solve partially this problem. Traditionally, people consider that variants with thicker pericarp are more resistant to rotting. This character could be explored by breeders for increasing resistance. Also, technology for fruit preservation is important In this respect, new technologies for preservation of fruits are being developed on an industrial scale in the CIDIR, in the state of Oaxaca, Mexico. This institution is working with *S. stellatus* and other columnar cacti. They have tested successfully the industrial production of dried fruits and jellies. Probably this will open new possibilities in commercialization at national and international level and therefore, it will enhance the production of *S. stellatus.*

2. **Flowers as human food.** In Matehuala, San Luis Potosí, Mexico, the flowering buds *of Ferocactus pilosus,* locally called "cabunches", are preserved in vinegar and sold in cans as delicacies. The edible flowering buds of *S. stellatus* (and some other cultivated cacti) are viable products to be industrialized in this form.

3. **Fruit juice.** The juice of fruits of *Opuntia* species fruits have been industrialized in Mexico for the production of "prickly pear honey", "prickly pear melcocha" and "prickly pear cheese". The first is obtained by boiling the juice to the density and texture of honey. The second is a more dense honey, obtained by boiling for more time. The "prickly pear cheese" is elaborated by grinding "melcocha" to the consistency of fresh cheese. The content of sugar in *S. stellatus* is comparable to that of *Opuntia* species utilized for this purpose. Therefore, xoconochtli is a potential resource for obtaining these products. Furthermore, it is possible to produce vinegar and alcohol by fermentation of the juice.

4. **Seeds as food.** Content of fat in the seeds of *S. stellatus* is considerably high, even higher than that of some *Opuntia* species which have been explored for production of edible oil. Oil might be possible products from seeds. This is especially interesting when it is considered that seeds might be a sub-product of the industrialization of fruit juice.

5. Production of forage. According to Colín (1976) and Bravo-Hollis and Sánchez-Mejorada (1991), the highest nutritional value of *Opuntia* species as forage is achieved when stems, fruit pericarps and a paste prepared by grinding seeds (only pigs, are able to break the seed testa) are mixed. Based on observations of the consumption of *S. stellatus* by goats and cattle in Tehuacán, it is possible to propose this species to be explored in such direction.

6. Soil protection. Based on observations on the use of *S. stellatus* in barriers for soil protection in Tehuacán and taking into account characteristics such as its wide root system, its quick growth, the ease of vegetative propagation and its resistance to poor soils and dry climates, this species might be used more extensively in programmes of soil protection and restoration.

7. Adhesive products. The high amount of mucilaginous tissue makes possible the extraction of products for the elaboration of adhesive gums, as it has been made from *Pachycereus hollianus, Stenocereus thurberi* and *Ariocarpus retusus* (Bravo-Hollis and Sánchez-Mejorada, 1991). At present, pectines are obtained from several species of *Opuntia* and columnar cacti, which are used in the preparation of marmalade and jams. This is another potential use of *S. stellatus.*

Apéndice 2

ETHNOBOTANY OF THE XOCONOCHTLI STENOCEREUS STELLATUS (CACTACEAE) IN THE TEHUACAN VALLEY AND LA MIXTECA BAJA, MEXICO

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Casas, Alejandro (The University of Reading. Department of Agricultural Botany. School of Plant Sciences. Whiteknights PO Box 221, Reading RG6 6AS, UK. Jardín Botánico, Instituto de Biología, Universidad Nacional Autónoma de México. Apartado Postal 70-614, México, D.F. 04510, México), **Javier Caballero** (Jardín Botánico, Instituto de Biología, Umiversidad Nacional Autónoma de México. Apartado Postal 70-614, México, D.F. 04510, México), **Barbara Pickersgill** (The University of Reading. Department of Agricultural Botany. School of Plant Sciences. Whiteknights PO Box 221, Reading RG6 6AS, UK) and **Alfonso Valiente-Banuet** Centro de Ecología, Universidad Nacional Autónoma de México. Apartado Postal 70-275 , México, D.F. 04510, México). ETIHNOBOTANY OF THE XOCONOCHTLI STENOCEREUS STELLATUS (CACTACEAE) IN THE TEHUACAN VALLEY AND LA MIXTECA BAJA, MEXICO). Ethnobotanical information is presented on use, management, folk nomenclature and classification of the "xoconochtli" (Stenocereus stellatus) as well as on the role of this plant in subsistence of the Nahua, Mixtec and Popoloca peoples from the Tehuacán Valley and La Mixteca Baja in Central Mexico. Among all three groups of peoples, S. stellatus was used for various purposes but mainly for its edible fruits. Different variants of this species were distinguished, named and classified by people according to characteristics of the fruit, particularly size, color and flavor of the pulp, spininess and thickness of the peel. Wild plants characteristically had small red sour fruits with many spines and thick peel, while individuals selected for cultivation usually differed in one or more of these characters. Three general forms of interaction between people and this species were found: 1) gathering of useful products from the wild; 2) management of wild populations in situ which involves the sparing and enhancing of individuals with more desirable characteristics and the removal of others during clearance of the land for agriculture; and 3) cultivation, mainly in home gardens, by propagation of vegetative parts from desirable individuals. Fruit yields in wild, managed in situ and cultivated populations were measured and compared. These were similar in wild and managed in situ populations but significantly higher in cultivated populations. Forms of management of this plant species are discussed in terms of availability of useful products and demand on them according to their role in the culture of local people.

Se presenta información etnobotánica del "xoconochtli" (Stenocereus stellatus) sobre usos, manejo, nomenclatura y clasificación folk asi como su papel en la subsistencia de la población Nahua, Mixteca y Popoloca del Valle de Tehuacán y la Mixteca Baja, regiones localizadas en la parte central de México. Estos grupos indígenas utilizan al "xoconochtli" de diferentes maneras pero principalmente lo usan por sus frutos comestibles. Distinguen, nombran y clasifican diferentes variantes de esta especie de acuerdo con las características de sus frutos, especialmente por su tamaño, el color y sabor de la pulpa, así como por la cantidad de espinas y grosor de su cáscara. Los individuos silvestres generalmente presentan frutos pequeños, rojos y de sabor agrio, con cáscara gruesa y espinosa, mientras que los individuos cultivados pueden diferir en una o varias de estas características. Se encontraron tres formas generales de interacción entre la gene y estas plantas: 1) recolección de productos utiles en poblaciones silvestres; 2) manejo de poblaciones silvestres in situ el cual se lleva a cabo durante el aclareo de terrenos para agricultura, y en el cual se dejan en pie y se promueven los individuos con las caracteristicas mas deseables y otros son eliminados; y 3) cultivo, principalmente en huertas, a través de la propagación de partes vegetativas de individuos con características deseables. Se evaluó y comparó la productividad de frutos en poblaciones silvestres, manejadas in situ y cultivadas. La productividad resultó ser similar en poblaciones silvestres y manejadas in situ, aunque significativamente superior en las poblaciones cultivadas. Se discuten las diferentes formas de manejo mencionadas en relación con la disponibilidad de recursos de esta planta y su demanda por parte de la población de acuerdo con su papel en la cultura local.

Key words: Ethnobotany, Tehuacán Valley, plant domestication, pitaya, Stenocereus stellatus

Stenocereus stellatus (Pfeiffer) Riccobono is a multipurpose cactus from central Mexico. It has been reported used as human food (fruits, seeds and stems) as well as forage (stems and fruits), firewood (stems), for living fences and for prevention of soil erosion (Bravo-Hollis and Sánchez-Mejorada 1991; Casas, Viveros and Caballero 1994). Apart from Opuntia species, S. stellatus is one of the most economically important species of fruit-producing cacti (Pimienta-Barrios and Nobel 1994). In some areas this species is mainly harvested from the wild, but it is also cultivated. There is a considerable demand for its products in the markets of the regions where the species occurs.

Use of this species by humans appears to be very old. Smith (1967) reports remains of S. stellatus (as Lemaireocereus stellatus) from archaeological excavations in the Tehuacán Valley. This author reports remains of this species in the Abejas phase, from approximately 4500 years before present and in the Palo Blanco phase, from approximately 2000 years before present. However, because archaeological remains of this cactus were not abundant, Smith (1967) considered that it was not significant in the diet of ancient people. Nevertheless, based on evidences from coprolites Callen (1967) found that in the Ajalpan and Santa María phases, stem tissue, fruits and seeds of "Lemaireocereus" species (including within this genus several species of Pachycereus and Stenocereus, among them possibly S. stellatus) were among the principal plant constituents in human diet in Tehuacán.

In coprolites from the Ajalpan and Santa María phases, Callen (1967) found remains of raw stem tissue and fruits of "Lemaireocereus", suggesting a direct consumption of these plant products. However, in the Coxcatlán phase "Lemaireocereus" seeds appeared to have been eaten. after being roasted. In the Palo Blanco phase, remains of "Lemaireocereus" stems lacked any epidermis, suggesting that they had been roasted. The starchy interior tissue of the stems was eaten and the charred epidermis discarded. There is no evidence of boiling cacti tissue during the prehistory of the Tehuacán Valley.

There is no evidence either of cultivation and domestication of any of the columnar cacti species from archaeological remains. However, at present wild and domesticated populations of S. stellatus coexist in arid and semi-arid regions of Central Mexico, mainly in the Tehuacán Valley and part of the Balsas river basin (Figure 1). During August and

September in the field and traditional markets of these regions, a great variety of forms, sizes, colors and flavors of "xoconochtli" can be appreciated. This raises the question of whether this variability is only an expression of the great diversity of environments characterizing these areas, or whether it is also a result of human cultural processes intervening through artificial selection. Coexistence of wild and cultivated individuals of S. stellatus makes especially interesting the study of domestication process of this species in the area. Under such circumstances, it is possible to analyze comparatively the phenotypic and genotypic structure of populations in different environments and forms of management. This information can then be used to make inferences on the process of evolutionary change as caused by human selection.

Here, we present ethnobotanical information on traditional classification, use and management of Stenocereus stellatus in order to visualize usefulness of this species, useful parts, characteristics preferred and selected by people as well as mechanisms of artificial selection. We also present a comparison of fruit yields among wild managed and cultivated populations in order to analyze the occurrence of different forms of management in relation to availability of the main useful products of this plant and in relation to their role in human subsistence.

STUDY AREA

The Tehuacán Valley is a region of 10000 square kilometers, located in the southeast of the state of Puebla and the northwest of the state of Oaxaca (Figure 2). It forms part of the Papaloapan river basin, and it has an arid to semi-arid climate, with a mean annual precipitation of 300 mm. Natural vegetation consists of tropical deciduous forest and several types of thorn-scrub forest (as defined by Rzedowski 1978). Dávila et al. (1993) report nearly 3000 species of flowering plants in the area, thirty percent of them being endemic. Popoloca, Nahua, Mixtec, Mazatec, Chinantec, Ixcatec and Cuicatec ethnic groups inhabit different parts of the Valley.

The Mixteca Baja region is located south of the Tehuacán Valley, in the northwest of' the state of Oaxaca, the southeast of Puebla and the northeast of Guerrero states. It is part of the Balsas river basin, which is an extremely complex mountainous region with altitudes ranging from 600 to 3000 meters above sea level and types of vegetation from thorn-scrub and tropical deciduous forests in the lower dry and warm lands to pine forests in the higher wet and temperate areas. Stenocereus stellatus occurs in the thorn-scrub and tropical deciduous forests where precipitation is between 600 and 800 mm per year.

In both areas, most people are indigenous peasants or "campesinos" who base their subsistence on cultivation of maize, beans, squashes and chili peppers and gathering a wide spectrum of wild plants. Many of these wild plants are managed to different degrees (Casas, Viveros and Caballero 1994; Casas and Caballero 1995; Casas et al. n.d.).

Two groups of villages were studied in the Tehuacán Valley (Figure 2). The first group includes the Popoloca villages of Zapotitlán de las Salinas, San Juan Raya, and Los Reyes Metzontla. The second group includes the Nahua villages of Coxcatlán, near the famous cave explored by MacNeish (1967), and San Lorenzo located on the Mesa de San Lorenzo, a travertine area which constitutes the roof of caves of the also famous site El Riego, in the eastern limits of the City of Tehuacán. A third group includes the Mixtec village Santa Catalina Chinango, Oaxaca in La Mixteca Baja. General information on environmental and cultural aspects of these sites are presented in Tables 1 and 2.

METHODS

ETHNOBOTANICAL STUDIES

A survey was conducted among the Nahua, Mixtec and Popoloca peoples in order to investigate patterns of use, management and mechanisms of artificial selection on S. stellatus in different human cultural contexts. Semi-structured interviews were conducted with a total of 26 constant key informants and nearly 45 occassional informants from the villages around the area studied. Constant key informants were local people with experience in management of S. stellatus, according to information given by local authorities and others identified through the survey. Occassional informants were the owners of home gardens sampled at random for estimations of fruit yields. The following information was searched:

1) An inventory of the different variants of xoconochtli and their uses, forms of preparation, consumption and storing of useful parts. Information on morphological features preferred for different purposes was emphasized. Living specimens were obtained during the

inventory. They are deposited in the ethnobotanical collection of Stenocereus stellatus in the Jardín Botánico, Instituto de Biología, U.N.A.M., Mexico.

2) Folk classification. Both living specimens and color photographs of "xoconochtli" and other species of cacti were shown to twelve of the permanent informants in order to elicit the Nahua, Popoloca and Mixtec folk nomenclature and classification of the different variants of Stenocereus stellatus in relation to other cacti They were asked to give the local name for each specimen shown as well as to list the features which characterize them.

3) Management. Cultural and ecological aspects determining different forms of management of the "xoconochtli" were assessed in order to visualize mechanisms of artificial selection. Information was elicited on how people select particular individuals during gathering and for cultivation, characteristics that influence such decisions and the origin of propagation materials for cultivation as well as the treatment of these materials before, during and after planting.

FRUIT YIELDS AMONG POPULATIONS.

The amounts of fruits produced in wild, managed and cultivated populations of Stenocereus stellatus were estimated and compared. For this, five wild populations, two populations managed in situ and two cultivated populations in home gardens of two villages were sampled. Mean density of population was estimated in each case as the average of densities in units of sampling. For wild populations and populations managed in situ, transects 50x10 or 100x10 m were used as units of sampling. In each case, the number of transects was determined depending on the extension of the population. Random samples of home gardens were units of sampling to evaluate density and yields under cultivation. Fruit yields of individuals from 27 home gardens were evaluated. Home gardens sampled constituted l0% of the total number of home gardens in the villages studied. The number of individuals sampled producing fruits was counted as well as the total number of branches, the number of branches producing fruits and the number of fruits per branch produced by individuals sampled. Five fruits per cactus individual sampled were collected and weighed to estimate kilograms of fruits produced per individual and per hectare. Analyses of variance were performed to test differences in different parameters related to fruit yield between populations.

RESULTS

TRADITIONAL NOMENCLATURE AND CLASSIFICATION

When the Spaniards reached the Antilles, they saw cacti for the first time. They adopted the Antillian name **"tuna"** for fruits of Opuntia spp. and **"pitahaya"** for fruits of several columnar cacti and other cacti such as species of the genus Hylocereus (Berger) Britton & Rose. The term "pitahaya" means scaly fruit in the Antillian language (Pimienta-Barrios and Nobel 1994). These are the most common names today in Mexico, although the indigenous people have also preserved their own names and systems of classification.

The Nahua people, the most numerous Indian group in Mexico and in the Tehuacán Valley, distinguish columnar cacti from other cacti by grouping them in the category **"nochcuauitl"** (Table 3). This name is composed by the term "**nochtli**", a word that designates the fruits of all the species of cacti (tunas and pitahayas) and "**cuauitl**" which means tree. This term is used by the Nahua as a primary lexeme and an epithet generally referring to some characteristic of a specific part of the plant provides a secondary lexeme (Table 4). However, more often the Nahua use only the term "**nochtli**" as a primary lexeme. This reveals the cultural importance of these fruits to the Nahua. Three species of Opuntia (O. lasciacantha Pfeiffer, O. imbricata (Haworth) De Candolle and O. joconostle Weber) are also commonly called "**xoconochtli**". Normally, these species should be called "**xoconochnopalli**" (Figure 3), but the Nahua people often utilize only different qualified "**nochtli**" (without the suffix "**nopalli**") as short names for designating different species of Opuntia.

The Nahua people recognize four different types of "**xoconochtli**" (S. stellatus) based on the color of the flesh (Table 5). They subsequently distinguish between sweet and sour flavors, using the words **"necuti"** and **"aocoti"** respectively, but these epithets never form part of the names of the plant. Similarly, they use **"uitztli"** and **"amo uitztli"** for spiny and non spiny fruits. There are no specific words for variants with thick or thin pericarp. The Nahua prefer variants with sweet flavored, non spiny fruits with thin pericarp.

Among the Popoloca people, the classification of xoconochtli follows a hierarchical pattern very similar to that of the Nahua. The term **"túchi"** ("tuna" or "pitahaya") is used as the primary lexeme for grouping species of Opuntia and columnar cacti with big edible fruits. This term is distinguished from **"lúchi"** that includes spherical cacti (Table 3). The secondary lexeme **"kánda"** distinguishes the genus Opuntia while Stenocereus pruinosus is designated by the name **"túchichína"** and S. stellatus **"túchikíshi",** a name composed by the roots **"túchi"** ("tuna" or "pitahaya") and **"chikishi"** ("tree") that is, "pitahaya tree" (Table 4). In Stenocereus and Opuntia, further categories may be designated also by color (Table 5) or by flavor: **"íisátu"** (sour) or **"íshetu"** (sweet).

The Mixtec people of Chinango classify cacti in three great groups: **"vindia"**' (Opuntia species), **"chimilóô"** (spherical cacti) and **"ndíchi"** (columnar cacti) (Table 3). Species are then distinguished by secondary lexemes (Table 4). The Mixtec distinguish between fruits of Opuntia, called **"chíqui"** and fruits of columnar cacti, called **"ndíchi"**. This resembles the Antillian classification and differs from the Nahua and Popoloca systems of cacti classification. Fruits of spherical cacti are also called **"chíqui",** but these are not considered by the Mixtec for the classification.

Variants of S. stellatus are classified on fruit characteristics. The first level of classification is based on color of the pulp. In Spanish, people distinguish six variants: red, pink, white (or green), purple, orange and yellow. However, in Mixtec people only name four variants (Table 5). It is important to mention that the Mixtec distinguish two main categories of "xoconochtli" according to their color: the "red xoconochtli" **("ndíchi cáâya cuaá")** and the "colored xoconochtli" **("ndíchi cáâya color")** in which they group xoconochtli with fruits of the rest of the colors including white fruits. They consider the red color fruits as a wild characteristic. The Mixtec also recognize variants within each color according to the thickness of the pericarp and the abundance and persistence of spines. However, for naming these variants, people do not retrieve the complete hierarchical phrase name, but only that. part which describes the fruits. For instance, they use the names **"ndíchi dóô yáâdi"** and **"ndíchi dóô ndéê** for xoconochtli with thin and thick pericarp, respectively, **and "ndíchi íño"** and **"ndíchi má íño"** for spiny and not so spiny fruits, respectively.

It is common to find in home gardens some individuals of "xoconochtli" with morphological characteristics resembling both Stenocereus stellatus and S. pruinosus. They resemble S. stellatus in general appearance, but have deep ribs, and vigorous spines. like in S.

pruinosus. They flower during the flowering season of S. pruinosus (February-May) and later during the flowering season of S. stellatus (June-August). Their Mixtec name is **"ndichi tucuéê"** meaning "rabid xoconochtli". According to local people, these plants produce S. stellatus flavored fruits during the S. pruinosus flowering season, and S. pruinosus flavored fruits during the S. stellatus flowering season. These plants are called "xoconochtli aventureros" in Spanish (meaning "adventurer xoconochtli") and are probably hybrids between the two species.

USES AMONG INDIGENOUS PEOPLE

Stenocereus stellatus is used mainly for its sweet fruits. Fruits contain a sweet and juicy pulp formed by the seed funicles which, when mature, are full of sugary liquid (Tables 6 and 7), They are in great demand as fresh fruits, but also as dried fruits ("xoconochtli pasados") and for preparing jams.

An alcoholic drink called "colonche" (from the Nahuatl word "nochoctli", which means "prickly pear pulque") is very common among indigenous people of other states such as San Luis Potosi and Zacatecas, where "colonche" is prepared with juice of fruits of Opuntia spp., or Sonora, where the Pápago people prepare "colonche" with fruits of Stenocereus thurberi (Engelmann) Buxbaum, Machaerocereus gummosus (Engelmann) Britton & Rose Carnegiea gigantea (Engelmann) Britton & Rose and Pachycereus pringlei (S. Watson) Britton & Rose (Bravo-Hollis and Sánchez-Mejorada 1991; Felger and Moser 1974 and 1976). Colonche is sometimes prepared from S. stellatus in the Tehuacán Valley and La Mixteca Baja.

According to Bravo-Hollis and Sánchez -Mejorada (1991), seeds of all cacti are edible, but because of their small size and the hardness of their testa they are not a common food. However, some species were widely used as food by some Indian groups since prehistory (Callen 1967). This use has persisted until the present among indigenous groups of the desert of Sonora in northern Mexico (Bravo-Hollis and Sánchez-Mejorada 1991; Felger and Moser 1974). These peoples extract seeds from fruits of several columnar cacti and Opuntia species. Then, they wash, dry and grind the seeds extracted producing an edible oily paste. Seeds are extracted directly from fresh fruits but may also be retrieved from human feces.

In the Tehuacán Valley, the seeds of Neobuxbaumia tetetzo (Coulter) Backeberg, Pachycereus weberi and S. stellatus are still eaten by the Nahua, the Mixtec and the Popoloca people Seeds obtained from fresh or dried fruits are washed, dried and roasted. The roasted seeds are ground with chili peppers, onion and green tomato (Physalis philadelphica Lamarck) or red tomato (Lycopersicon esculentum Miller) for preparing traditional sauces eaten with maize tortillas as the main component of the Indian diet. The basic components of the sauces can be other seasonal wild or cultivated products. For example, seeds of Leucaena esculenta (Moe. et Sessé ex A.DC.) Benth. are used between December and March, fruits of Spondias mombin L. between April and May, seeds of N. tetetzo in June, seeds of Pachycereus weberi, between February and April, and seeds of S. stellatus between July and September. Alternatively, the cactus seeds may be ground into an edible paste which is eaten with "tortillas". Table 6 shows that seeds of S. stellatus contain significant quantities of protein and fat. This information permits an understanding of the importance of this resource in the Indian subsistence and its promissory value for human nutrition.

Stems and flowers are occasionally consumed. They are usually eaten during seasons of food scarcity. Consumption of stems of columnar cacti is not very common at present but they seem to have been a very common food in the past (Callen 1967). Young stems are prepared by removing the spines, cutting them in longitudinal pieces and removing the medullar portion, then roasting them. After roasting, the cuticle is easily removed. The flower buds are boiled and then fried with eggs. This is a common form of preparation of flowers of many species of cacti., Agave, Yucca, Beaucarnea, and other genera. The boiled flower buds may also be prepared with onion and vinegar. This is particularly common with Neobuxbaumia tetetzo but occurs also with flower buds of other columnar cacti, including S. stellatus.

Cultural value of all these edible products from "xoconochtli" can be studied in the markets during the exchange for other products. Thus, in some villages (e.g. Los Reyes :Metzontla) and markets (e.g. Ajalpan), three to five fresh fruits or six to ten dried fruits of S. stellatus are exchanged for one liter of maize; one liter of flower buds for three liters of maize and one liter of seeds for fifteen liters of maize.

Young branches of S. stellatus and other species of columnar cacti are also cut and fed to goats, after removal of the spines. The plants are not killed and produce more branches relatively quickly which may grow 20 to 40 cm per year. Whole fruits or pericarp and seeds of fruits whose pulp has been used are also a very good forage.

For manufacturing pottery, a "bed" of hard wood with high specific heat is made by people from Los Reyes Metzontla from species such as Acacia spp., Prosopis laeyigata, (Humb. & Bonpl. ex Willd.) M.C. Johnston, and Lippia graveolens Kunth. Objects to be fired are put on this bed and covered with "soft" wood with a lower specific heat. Ipomoea arborescens G. Don, Agave spp., Polaskia chichipe and S. stellatus are among the most important sources of "soft" wood.

Individuals of S. stellatus along with Myrtillocactus geometrizans, S. pruinous, Pachysereus marginatus and P. hollianus (F.A.C. Weber) F. Buxbaum are commonly grown as living fences and as barriers for soil protection in terraces around the borders of cultivated slopes.

TRADITIONAL MANAGEMENT

In the study area, people commonly gather fruits and useful stems of Stenocereus stellatus from wild populations. People collect fruits selectively, preferring variants with relatively sweeter flavor, thinner pericarp, fewer spines and bigger size for consumption of fresh fruits. When the fruits are gathered for preparing jams or dried fruits ("xoconochtli pasado"), the harvest is less selective. Adults and children of both sexes collect the fruits during the season.

A second form of interaction between people and this plant is management in situ. People in all the studied areas commonly tolerate individuals that are naturally established when they clear new land for corn fields. Also they may enhance abundance of this plant in by planting branches from the tolerated individuals and taking care of them. During the clearance of forest for agriculture, people spare some useful perennial plants such as Beaucarnea gracilis, Stenocereus pruinosus, S. stellatus, Myrtillocactus geometrizans, Pachycereus hollianus, P. weberi., P. marginatus Prosopis laevigata, Leucaena spp., Pithecellobium dulce (Roth.) Bentham, Polaskia spp. and Escontria chiotilla. It is a common practice that people also sow in these areas seeds of the species of legumes mentioned and plant vegetative propagules of the columnar cacti (with the exception of *P. weberi,* which cannot be propagated vegetatively and grows very slowly).

The individuals of these tolerated species compete with the cultivated plants. Therefore, people carefully select which species are the best for sparing. Their decision takes into account the usefulness of the species. People prefer to tolerate the species mentioned above in the following order: *Leucaena* spp. *Prosopis laevigata, S. stellatus, S. pruinosus, Pachycereus hollianus, P. marginatus, M. geometrizans, Pithecellobium dulce E. chiotilla, Polaskia* spp., *P. weberi* and *Beaucarnea gracilis.* They also take into account the characteristics of the useful products of the individuals of each species. In the case of *S. stellatus* people prefer to spare individuals with big fruits, sweet flavor, thin pericarp and few spines. However, the tolerance of other phenotypes is also common, especially when there are no competing species or phenotypes.

The third form of interaction is cultivation, mainly in home gardens or as living fences around. agricultural fields. The most important form of cultivation is by planting branches from wild or previously cultivated individuals. People generally cut vigorous branches at the articulation level from mature desired individuals. Branches used for this purpose measure between 20 and 100 cm. They are left exposed to the sun, for ten or fifteen days in order that the cut surface may dry. This reduces fungal and bacterial infections. After this period, the branches are planted either horizontally or vertically in holes 10 to 40 cm deep with cattle or goat dung added as fertilizer before planting. They are usually planted just before the rainy season. A few fruits may be obtained after one year, but during the second year the plants commonly do not produce. Thus, the production does not really start until the third year and in some cases until the fourth year after planting. *S. stellatus* is neither irrigated nor pruned, but ash is commonly deposited, as fertilizer, on the soil covering the main stems.

Individuals of *S. stellatus* cultivated in home gardens may also represent tolerated seedlings which established from seeds dispersed through bird, bat or human feces. Generally, people do not recognize variants of xoconochtli based on vegetative characteristics. Therefore, decisions on eliminating or sparing S. stellatus individuals are generally taken after four or five years when the individuals produce fruits.

FRUIT YIELDS AMONG POPULATIONS

Table 8 shows information related to fruit yields among populations. It indicates that density of population ranges from 22 to 780 individuals of S. stellatus per hectare, with no clear pattern of abundance of individuals in relation to forms of management. Thus, although the lowest density is found in a wild population (San Juan Raya) and the highest density in a cultivated population (Metzontla-C), there are also highly dense wild populations (such as Coxcatlán and Zapotitlán) and one non dense cultivated population such as Chinango-C.

However, Table 9 shows that yields in terms of number and kilograms of fruits per individual were significantly higher in cultivated populations than in wild and managed in situ populations. The lowest yields were observed in San Juan Raya and San Lorenzo populations (Table 8). In these wild populations, the density of population, the number of producing branches and the number of fruits per branch were also the lowest. Fruit yields in populations from Zapotitlán and Coxcatlán were higher because, although fruit were small, populations were dense. The wild population of Chinango (Chinango-W) was less dense than Zapotitlán and Coxcatlán populations however, fruit yield in this population was similar to these two populations in terms of kilograms per hectare. This is because fruits from this population are bigger than in Zapotitlán and Coxcatlán.

The population managed in situ from Metzontla (Metzontla-M) presented a much higher production than any of the wild populations. This is explained by the bigger fruit size as well as the higher proportion of individuals and producing fruits. In contrast, the in situ managed population of Chinango (Chinango-M) presented a lower fruit yield, even lower than that of the wild population of the same area. Differences between the wild and in situ managed populations of Chinango are mainly due to differences in the number of branches which are removed by people in order to enhance better conditions for maize. This practice was not found in Metzontla where, for the contrary, people take special care of the managed in situ populations.

The highest production of fruits was found in the home gardens of Metzontla. This is explained by the high density of population as well as the absolute number of branches producing fruits and the relatively high number of fruits per branch. However, the most productive individuals are those from Chinango. These individuals presented the highest number of producing branches, the biggest fruits and the highest number of fruits per branch They thus produce the most of kilograms of fruits per individual.

ROLE OF S. STELLATUS IN SUBSISTENCE OF INDIGENOUS PEOPLE

Popoloca people of Zapotitlán occasionally harvest fruits of xoconochtli from small but dense populations (Table 8) spread as patches around the town. Also, there are home gardens with a few individuals of S. stellatus. Fruits of xoconochtli are consumed only by members of the family and they are never marketed. In San Juan Raya, there are some few individuals of xoconochtli in home gardens, but the main harvest of fruits is from wild populations, although density of population and fruit yield are very low. Fruits of both wild and cultivated xoconochtli are destined only for home-consumption. In Los Reyes Metzontla, wild populations of S. stellatus were not observed. However, this species is one of the most important plant elements in home gardens. In this village, only approximately 10% of the home gardens are irrigated and the great majority depends on the rainy season. For this reason, the main components of home gardens are native plant species such as Stenocereus stellatus, S. pruinosus , Pachycereus marginatus, P. hollianus, Opuntia spp., Agave spp. and Leucaena esculenta. Fruit yields of S. stellatus are high in home gardens, and although people from Los Reyes occasionally market the products of xoconochtli, these are mainly products for consumption of the local families. Fruits from managed in situ populations complement the production of the home gardens.

In Coxcatlán, most of home gardens are irrigated but people prefer to cultivate there species with high requirements for water such as Persea americana Miller, Diospyros digyna Jacq., Citrus spp. and others. Introduced variants of cultivated Opuntia species are the only cultivated cacti. Other products of useful cacti (mainly Escontria chiotilla, Myrtillocactus geometrizans and Stenocereus stellatus) are harvested in wild populations. These products are destined mainly for the consumption of local families and they are also marketed, but only at the local level.

In San Lorenzo there are wild populations of S. stellatus occuring at low densities but with good fruit yield per hectare (Table 8). At present, useful wild products of this forest are harvested by the Nahua and Mestizo people of San Lorenzo and Tehuacán. However, this harvest is only occasional and for home consumption

In Chinango, the Mixtec people in part depend on production and marketing of fruits of S. stellatus and S. pruinosus (Table 2). Home gardens of the village represent a cultivated stand, and wild and managed populations occur in natural and disturbed areas. In the home gardens, S. stellatus and S. pruinosus are by far the most abundant species cultivated. The main portion of xoconochtli products is obtained from the home gardens and it is complemented with resources from other populations. People harvest xoconochtli fruits for both home-consumption and marketing. People carry fruits to the main market of the municipality, and to the most important regional markets in San Pedro Chazumba and Huajuapan de León, Oaxaca.

DISCUSSION

This study found that fruits are the most significant part of Stenocereus stellatus utilized in the area. Fruits are the most important useful part of xoconochtli, and traditional classification of this species is based on characteristics of these parts. Other parts such as seeds or stems are utilized only occasionally, and they are not used to define categories in folk classifications of this species. All this reveals the importance of fruits in domestication of this species.

A great variability of fruit characteristics was found in wild and cultivated populations, but five fruit characters are used in classification of infra specific variation among the three Indian groups studied. These characters are: 1) Pulp color, character which is used to make a first division of categories within xoconochtli as well as in other cactus species. Red fruits are considered characteristic of the wild plants, while other colors occur only in cultivated individuals. White fruits are considered as the "best" cultivated variants of xoconochtli. 2) Fruit size. People distinguish between "small" and "big" fruits Small sized fruits are considered to be a wild characteristic, while cultivated individuals generally have bigger fruits. 3) Flavor. People recognize three different flavors of xoconochtli fruits: sweet, sour and insipid. The first two are preferred for different purposes, but sweet flavor is identified with cultivated plants, while sour flavor is considered characteristic of wild plants. 4) Peel thickness. People distinguish between fruits with thin and thick pericarps, associating thin pericarps with cultivated plants. 5) Fruit spininess. Spiny fruits are considered to occur commonly in wild individuals while fiuits from cultivated plants have fewer spines.

Combinations of states for these 5 characters determine the existence of a wide number of variants which constitute a raw matter for artificial selection. Among these variants, there are some preferred by people according to their cultural values. As mentioned, people generally consider as the "best" xoconochtli those with the largest size, white and sweet pulp, with thin peel and few spines. However, they maintain variants of different characteristics because they are used for different purposes. For instance, sour fruits are good for preparation of drinks and jams; spiny fruits are more resistant to predators; fruits with thick pericarp resist rotting and are better for long distance transportation. Artificial selection thus seems to favour a number of different combinations of fruit characteristics, each playing a particular cultural role. This pattern of selection may determine complex patterns of variation of xoconochtli associated with human manipulation.

Artificial selection is apparently carried out by isolation and subsequent increasing of individuals with desired phenotypes from wild, managed in situ or cultivated populations. Vegetative propagation seems to be the main form through which artificial selection is carried out. This process is carried out ex situ by carrying branches of the desired plants to home gardens, or in situ by sparing and enhancing desired plants and eliminating the non-desired ones. However, tolerance and care of seedlings as well as their selective enhancing or elimination is also an important process. This process allows to explain the occurrence of some variants known in cultivation that are not present in wild populations, for instance, fruits with pulp color others than red.

Although wild and managed in situ populations studied occur in very different environmental conditions, these populations were not significantly different in parameters related to fruit yields. However, cultivated populations presented significantly higher fruit yields than all these populations. Such differences were mainly due to the bigger size of fruits as well as the higher number of branches producing fruits and number of fruits per branch in cultivated individuals. These characteristics may be affected in part by environmental conditions and in part they may also have a genetic basis. We do not know yet the extent of influence of these two factors. However, the influence of human management increasing productivity of this plant is evident among individuals cultivated in home gardens.

Forms of management of xoconochtli seem to be influenced by the role of its products in the subsistence of people, the availability of xoconochtli in the wild, and environmental factors determining success in the establishment of this plant species. In Coxcatlán, for instance, xoconochtli is almost absent in home gardens. The Nahua people in this area are farmers but home gardens only complement the agricultural economy. People cultivate in home gardens several species of fruit trees, but not xoconochtli because, as people say, "there are a lot in the wild". In contrast, in Los Reyes Metzontla, although home gardens also complement subsistence, this complementation seems to be more important than in Coxcatlán because yields of maize are very low. Along with this, the scarcity of wild xoconochtli strongly encourages people to cultivate it.

In other villages such as Zapotitlán and San Juan Raya, wild populations of xoconochtli are not as dense as in Coxcatlán, but xoconochtli plays a very secondary role in human subsistence, and cultivation is not relevant. In Chinango, production, consumption and marketing of xoconochtli fruits play a more important role in subsistence. In this area, although wild populations of xoconochtli are present, fruit yields are significantly higher in home gardens. In this village, cultivation is therefore a way for increasing quantity and quality of fruits. There, interactions between people and xoconochtli are more intense and artificial selection is presumably more active than in the rest of the villages studied.

The in situ managed population from Metzontla presented a significantly higher fruit yield than any wild population. The range of fruit size was in part similar to the small fruits from wild populations and also in part similar to the bigger fruits from individuals cultivated in home gardens of the village. This may be a result of the selective sparing of trees practiced during clearings of terrain for agriculture and/or the introduction of good phenotypes to the population. This was not observed in Chinango, where wild and in situ managed populations did not show significant differences in fruit size but cultivated individuals had much larger fruits. In Chinango, cultivated xoconochtli are of better quality than the wild xoconochtli and sufficient enough to cover requirements of people (this, illustrated by the fact that cultivated fruits are not completely harvested). In Chinango, wild and in situ managed populations are complementary sources of this resource, for this reason they are gathered and spared, but they do not seem to be an important complement. Thus, people concentrate efforts on management and artificial selection in home gardens. Nevertheless, the situation in Metzontla suggests that, as in cultivation in home gardens, in situ management may involve mechanisms of artificial selection which could increase frequencies of particular phenotypes according to human convenience.

So far, we have examined the apparent signs of artificial selection on Stenocereus stellatus by people. However, it is still necessary to evaluate the effect of this artificial selection in populations. At present, comparisions of morphological and genetic variation as well as of reproductive mechanisms between the three groups of populations analyzed here are being carried out by the authors. The evaluation of the degree of divergence in these aspects among populations is a way to evaluate the effect of natural and artificial selection and the degree of domestication in this plant species.

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Figure 1. Distribution of Stenocereus stellatus

Figure 2. Localities of populations studied.

TABLE 1. ENVIRONMENTAL CONDITIONS OF THE POPULATIONS OF STENOCEREUS STELLATUS STUDIED.

Population	Ecological condition	Elevation (m)	Annual mean °	Annual mean precipitation	Soils	Habitat
Zapotitlán	Wild	1550	21.2*	450*	Derived from sandstones	Thorn scrub forest
San Lorenzo	Wild	1700	19.1*	590*	Derived from limestones	Thom scrub forest
San Juan Raya	Wild	1800	20.9*	649.7*	Derived from limestones	Thorn scrub forest
Coxcatlán	Wild	1000	23.8*	440.6*	Aluvial	Tropical deciduous forest
Chinango-W	Wild	1700	20.6*	720.5*	Derived from sandstones	Tropical deciduous forest
Metzontla-M	Managed in situ	2000	17.23	527.87	Derived from limestones	T'horn scrub forest cleared for agriculture

TABLE 1. ENVIRONMENTAL CONDITIONS OF THE POPULATIONS OF STENOCEREUS STELLATUS STUDIED.

Population	Ecological condition	Elevation (m)	Annual mean temperature (oC)	Annual mean precipitation	Soils	Habitat
Chinango-M	Managed in situ	1700	20.6*	720.5*	Derived from sandstones	Tropical deciduous forest cleared for agriculture
Metzontla-C	Cultivated	1900	17.23**	527.87**	Aluvial	Home gardens
Chinango-C	Cultivated	1600	20.6*	720.5*	Aluvial	Home gardens

*Based on García 1988

**Based on Valiente 1991

TABLE 2. SOCIAL AND CULTURAL ASPECTS IN THE SITES STUDIED

Site	Ethnic group	Population	Economy
Zapotitlán	Popoloca	6000	Mining, craft manufacturing and commercialization of O n i x
San Juan Raya	Popoloca	300	Maize and beans seasonal agriculture; cattle and goat raising
Los Reyes Metzontla	Popoloca	5300	Pottery; maize and beans seasonal agriculture; raising of goats
San Lorenzo	Nahua	200	Maize and beans seasonal and irrigated agriculture; raising of goats
Coxcatlán	Nahua	3000	Sugar cane irrigated agriculture; maize and beans seasonal agriculture; cattle and goat raising
Chinango	Mixtec	300	Maize and beans seasonal agriculture; raising of goats; production and commercialization of fruits of S. stellatus and S. pruinosus

TABLE 3, PRIMARY LEXEMES FOR CLASSIFICATION OF CACTI BY THE NAHUA, MIXTEC AND POPOLOCA PEOPLES

Group	Nahua	Mixtec	Popoloca
Opuntia species	**Nopalli**	**Vindia**	**Túchi**
Columnar cacti	**Nochcuauitl**	**Ndíchi**	**Túchi**
Spherical cacti	**Huitznahuac**	**Chimilóô**	**Lúchi**

TABLE 4. SECONDARY LEXEMES FOR CLASSIFICATION OF COLUMNAR CACTY BY THE NAHUA, MIXTEC AND POPOLOCA PEOPLES

Species	Nahua	Mix-tee	Popoloca
Myrtillocactus geometrizans	**Tepepoa nochtli** "agressive hills pitahaya"	**Ndíchi nóni** "maize pitahaya"	**Túchi lásha** "small pitahaya"
Pachycereus weberi	**Noch cuauitl** "pitahaya tree"	**Ndíchi quítu**	absent in the area
Polaskia chichipe	**Tepequio nochtli** "hill escapes pitahaya"	**Ndíchi yáá** "silvery pitahaya"	**Túchi cásha** "scaled pitahaya"
Stenocereus pruinosus	**Cuapeda nochtli** "big tree pitahaya"	**Ndíchi cuán** "yellow pitahaya"	**Túchi chína** "big pitahaya tree"
Stenocereus stellatus	**Xoco nochtli** "sour pitahaya"	**Ndíchi cááya** "sandy pitahaya"	**Túchi kíshi** "pitahaya tree "

TABLE 5. CATEGORIES FOR CLASSIFICATION OF VARIANTS OF STENOCEREUS STELLATUS BY THE NAHUA, MIXTEC AND POPOLOCA PEOPLES

Variant	Nahua	Mixtec	Popoloca
Red	Chichi xoconochtli	Ndíchi cáâya cuaá	Túchi kíshi jatze
Pink	Chichi xoconochtli	Ndíchi cáâya cuaá	Túchi kíshi jatze
Purple	Tlanec xoconochtli	Ndíchi cáâya ton	Túchi kíshi katza
Yellow	Cotz xoconochtli	Ndíchi cáâya cuan	non named
Orange	Cotz xoconochtli	Ndíchi cáâya cuan	non named
White	Iztac xoconochtli	Ndíchi cáâya cúshi	Túchi kíshi lúla

TABLE 6. PERCENTAGE COMPOSITION OF FRUITS AND SEEDS OF

STENQCEREUS STELLATUS. (BASED UPON BRAVO-HOLLIS AND SANCIJFZ-MEJORADA 1991).

Elements	Pulp		Seeds	
	Fresh	Dried	Fresh	Dried
Proteins	1.00	7.33	21.10	22.21
Raw fiber	0.25	1.83	-	-
Ash	0.48	3.54	-	-
Fats	2.28	2.07	22.20	23.38
Water	86.33	-	5.20	
Nitrogen free extract	11.66	85.23	-	-

TABLE 7. NUTRITIONAL CHARACTERISTICS OF JUICE FROM FRUITS OF STENOCEREUS STELLATUS

(BASED UPON BRAVO-HOLLIS AND SANCHEZ-MEJORADA 1991)

Characteristics	Amount
Brix degrees at 20°C	10.4°
Citric acid	0.64 g/100ml
pH	3.95
Solids in suspension	0.685 g/100 ml
Solids in solution	9.1015 g/100 ml
Direct reducing sugars	7.9%
Total reducing sugars	8.1%
Vitamin C	11.72 mg/100 ml

TABLE 8.FRUIT YIELDS AMONG STUDIED POPULATIONS (*MEAN VALUES; **STANDARD ERRORS)

Population	Zapotitlán	Sn. Lorenzo	Sn. Juan R	Coxcatlán	Chinango-W	Metzontla-M	Chinango-M	Metzontla-C	Chinango-C
Cultural status	Wild	Wild	Wild	Wild	Wild	Managed in situ	Managed in situ	Cultivated	Cultivated
Sampled area (m^2)	1500	10000	8500	6000	6000	1000	7500	2572.5	65000
Density of population (individuals per ha)*	273.3	34	29.4	280	35	120	48	780.9	93.9
S.E.**	±107.29	±10.87	±8.60	±43.51	±17.26	±20	±14.45	±226.74	±0.16
Num. of individuals sampled	41	34	25	168	21	12	36	275	452
Num. of individuals sampled with fruits	24 (58.54%)	18 (52.94%)	5 (20.00%)	22 (13.10%)	9 (42.86%)	12 (100.00%)	8 (22.2%)	275 (100.00%)	423 (93.6%)
Individuals per ha. producing fruits	160	18	5.9	36.7	15	120	10.7	780.9	87.9
Num. of branches per individual*	6.96	19.1	11.20	6.39	14.22	19.00	6.75	22.23	21.52
S.E**	±0.88	±4.76	±3.81	±1.27	±4.30	±3.03	±1.35	±2.29	±3.01

TABLE 8. FRUIT YIELDS AMONG POPULATION

Population	Zapotitlán	Sn. Lorenzo	Sn. Juan R	Coxcatlán	Chinango-W	Metzontla-M	Chinango-M	Melzontla-C	Chinango-C
Num. of branches with fruits per individual*	3.04 (43.7%)	5.5 (28.9%)	2.6 (23.2%)	2.54 (39.8%)	7.11 (50%)	7.42 (39%)	3.13 (46.3%)	8.58 (38.6%)	15.54 (72 2%)
S.E**	±0.51	±1.38	±0.98	±0.58	±3.43	±1.69	±0.92	±1.06	±2.34
Num. of fruits per branch*	7.22	4.88	4.48	4.65	11.08	4.78	8.84	10.98	12.20
S.E**	±0.90	±1.01	±1.27	±0.84	±2. 0 5	±0.69	±0.90	±1.05	±0.75
Number of fruits per individual*	19.63	37.67	12.00	12.77	81.67	39.17	25.13	98.92	187.11
S.E**	±3.44	±12.97	±7.52	±3. 3 9	±37.72	±10.68	±6.17	±14.49	±29.76
Weight of fruits (g)*	22.33	23.16	19.40	18.65	41.70	32.11	37.92	38.81	72.23
S.E**	±1.87	1-2.30	±2.44	±2.58	±6.12	±2. 8 4	±4.88	±2.89	±4.04
Kg. of fruits per individual*	0.45	1.19	0.17	0.281	4.61	1.46	1.01	3.73	13.62
S.E.**	±0.09	±0.47	±0.07	±0.09	±2.43	±0.47	±0.30	±0.55	±2.36
Number of fruits per ha.	3140.08	678.06	70.80	468.66	1225.05	4700.40	268.89	77246.63	16446.97
Kg. of fruits per ha.	72	21.42	1.00	10.31	69.15	174.00	10.81	2912.76	1197.20

TABLE 9. ANALYSIS OF VARIANCE AND MULTIPLE RANGE TEST FOR PARAMETERS RELATED TO FRUTT YIELDS BETWEEN WILD, MANAGED IN SITU AND CULTIVATED POPULATIONS. POPULATIONS NOT FOLLOWED BY THE SAME LEVERS ARE SIGNIFICANTLY DIFFERENT ACCORDING TO TUKEY HIGHEST SIGNIFICANT DIFFERENCE (95%).

(FOR ALL CASES, 2 AND 158 D.F. BETWEEN AND WITHIN GROUPS RESPECTIVELY)

Population	Num. of fruits per branch	Weight of fruits	Num. of fruits per individual	Kg. of fruits per individual
Wild	A	A	A	A
Managed in situ	A	A	A	A
Cultivated	B	B	B	B
Mean suares between groups	567.069	23402.032	306142.77	1.5694E0009
Mean squares within groups	22.858	450.272	14638.12	8.8794E0007
F-ratio	24.809	51.973	20.914	17.674
Significance level	0.0000	0.0000	0.0000	0.0000

TABLE 10. ANALYSIS OF VARIANCE FOR PARAMETERS RELATED TO FRUIT YIELDS BETWEEN WILD POPULATIONS. POPULATIONS NOT FOLLOWED BY THE SAME LETTERS ARE SIGNIFICANTLY DIFFERENT ACCORDING TO TUKEY HIGHEST SIGNIFICANT DIFFERENCE

Population	Num. of fruits per branch	Weight of fruits	Num of fruits per individual	Kg. of fruits per individual
Zapotitlán	AB	A	A	A
Sn. Lorenzo	A	A	AB	A
S. J. Raya	AB	A	AB	A
Coxcatlán	A	A	A	A
Chinango-W	B	B	B	B
Mean square Between groups	78.127352	843.71223	8280.7197	33449429
Mean square Within groups	18.901569	115.76657	2551.7802	7774634
F-ratio	4.133	7.288	3.245	4.302
Sig. level	0.0048	0.0001	0.0174	0.0038

Apéndice 3

MORPHOLOGICAL VARIATION IN POPULATIONS OF *Stenocereus stellatus*

1. INTRODUCTION.

According to Britton and Rose (1920) and Bravo-Hollis (1978), *Stenocereus stellatus* is a columnar, arborescent, succulent plant 2 to 3 meters high, branching at base, of pale bluish green colour, with 8 to 12 ribs approximately 2cm deep. It is characterized by the presence of 9 to 13 radial spines at each areole. Its flowers are solitary at the areoles, appearing at or near the top of the plant, being red or pink, narrowly campanulate or tubular, about 5 to 6 cm long. Fruits are red, spiny, globular, fleshy, with pulp red, pink, purple, yellow, orange or white about 3 to 5 cm in diameter. Ovules are numerous, with branched funiculus. Seeds are small bearing a black testa.

Some of these characters, particularly fruits, present a considerable variation among wild and cultivated populations. Differences in environmental conditions or in age may influence the variation in the expression of these characters, but their expression may also have a genetic basis. Such morphological variation is in part the result of a long time of natural evolution. But in part, it may also be the result of manipulation of these plants by humans. It is commonly difficult to distinguish between natural and artificial evolutionary processes. However, this is a crucial problem for analyzing how domestication has operated and the degree of advance of this process. In part of the research, an attempt to analyze this problem is presented based on the analysis of variation of morphological features that are meaningful for humans who use this plant species.

As examined previously, through ethnobotanical studies it was possible to identify morphological features of *Stenocereus stellatus* preferred by people because of their advantages for use. Colour, flavour, amount of edible matter, peel thickness and spininess of fruits appeared to be significant characteristics distinguished by people, used for classification and in assessing quality of products in the particular cultural context studied. These morphological features are the basis on which individuals are selected for use and for preferential propagation.

In this part of the research, the purpose was to analyse how individuals from different geographic areas and environments differ in morphology, and also to analyse differences between individuals from wild populations and from populations submitted to different ways of management and different degrees of domestication. Frequencies of these significant morphological features among populations were also compared. With this study, it was considered possible to evaluate whether or not artificial selection has had any effect on the phenotypic structure of populations of *Stenocereus stellatus* and to relate the level of any such effect to the degree of intensity of manipulation of plant populations.

2. METHODS

SAMPLING OF POPULATIONS.

Individuals sampled. Clonal propagation in *Stenocereus stellatus* may cause serious problems to define in the fieldwork what is an "individual". An individual was considered as a unit of branches emerging together from the soil. Because morphological comparisons would be made mainly on fruits, only individuals of reproductive age were sampled. To define this age, different populations were observed during the reproductive season. Size of the smallest plants producing buds, flowers or fruits was measured. From this pilot study, it was considered that individuals may produce flowers when they are 90 cm or more in height. However, for purposes of estimation of density of population both seedlings and young ramets were counted along the transects.

Sample size. Sample size was decided taking into account firstly the real size of each population. The limits of each natural population sometimes were defined by eco-geographical factors such as streams, changes in soils or changes in composition of the vegetation. But also, limits were marked by the presence of areas of human disturbances such as roads, human settlements or agricultural fields. In all cases, it was possible to estimate the area occupied by the population and the density of population. An *a priori* limit for sample size was defined as at most 50 individuals. At least nine populations would be analyzed, time constraints made impractical to study more. The diversity of environmental conditions in which the population was located such as differences in altitude, changes in components of the vegetation, soils, physiographic units such as valleys, slopes, hilltops, orientation of slopes, density of population, among others, were also considered in defining the sampling strategy.

Transects were considered adequate for sampling wild and managed *in situ* populations in order to represent as much as possible, individuals from different environmental conditions within the population. The width of transects was decided considering a minimum distance in which the spatial representation of individuals in all directions was possible. Considering sizes and distances between plants, it was determined that the transects should be at least 5 m wide. But in some low density populations it was necessary to consider wider transects (20 m in the population with the lowest density). The length of transects was defined according to the size of the population, the environmental heterogeneity and the density of the population. In all cases studied, the length was decided in order to include the maximum longitudinal distance covered by the populations. Transects so defined included fewer than 50 individuals in all cases except in Coxcatlán, where the *a priori* criterion for limiting samples to 50 individuals was involved.

In cultivated populations the sampling strategy was different. In these cases, the basic units were home gardens. In these units, people propagate vegetatively plant materials of different origin and different characteristics. They know which plant materials are the same clone and which are different. Considering this, it was possible to sample a higher number of individuals than in wild populations by identifying and sampling the different clones and counting the number of each. It was considered that by sampling in this form the sample would include more morphological and genetic variation than a sample of 50 individuals without any distinction. Thus, the maximum size of the sample of cultivated xoconochtli was determined by the number of home gardens containing at most 50 clones.

In preliminary samplings it was found that the 50 different variants could be found in around 10 home gardens. For this reason, in each of the villages sampled 10 was considered as a basic number of home gardens. This number could be increased when the information contained in the home gardens sampled was not enough for representing the variation existing in the village. But also, this number could be decreased when information was repetitive. In each village sampled, 10 home gardens were chosen at random. In Los Reyes Metzontla, the sample of home gardens was randomised by drawing a general scheme of the village. Then, in two opposite sides of the scheme two lines with numbers from 1 to 50 were drawn. Lines crossing the scheme were drawn connecting points of the lateral numbered lines. These points were determined by generating pairs of random number in a calculator. The points of intersection of these lines defined random points in the space. Home gardens nearest. to these points were sampled. In Chinango, where a map of home gardens was available, the sample of home gardens was randomized by giving a number to each home garden, and then selecting by random numbers the home gardens for sampling.

Not all individuals sampled were included in the analysis of morphological variation because not all of them produced flowers and fruits during the time of the study. 165 individuals of *Stenocereus stellatus* were finally included in this study, 69 of them from five wild populations, 20 from two populations managed *in situ* and 76 from home gardens of two indigenous villages. General information on samples is presented in Table 1.

TABLE 1. GENERAL INFORMATION ON SAMPLES OF *STENOCEREUS STELLATUS*

Population	Cultural status	Sampled area (m2)	Density of population (ind. Per. ha.)	No. of individuals sampled	No. of individuals analysed	Labels in BDM*
Zapotitlán	Wild	1700	142	40	24	S 1-S24
Chinango-W	Wild	3060	49	19	9	S25-S33
Sn. Juan Raya	Wild	6000	22	18	5	S34-S38
Sn. Lorenzo	Wild	5000	34	30	18	S39-S56
Coxcatlán	Wild	3000	567	50	13	S57-S69
Metzontla-M	Enhanced	1000	120	12	12	Ml-M12
Chinango-M	Enhanced	4000	72.5	22	8	M13-M20
Metzontla C	Cultivated	3125	780	26	26	C1-C26
Chinango-C	Cultivated	6500	94	69	50	C27-C76

*Basic Data Matrix

Labelling of individuals. Individuals sampled were marked through metallic labels and numbers drawn with waterproof ink were used. This was done because the same individuals would be visited several times for studies of morphologic and genetic variation and for studies on reproductive biology.

MORPHOLOGICAL CHARACTERS ANALYZED.

Morphological characters which are supposed to be affected directly or indirectly by artificial selection were considered. The following list includes binary and multistate qualitative characters as well as discrete and continuous quantitative characters. In the case of quantitative characters at least 3 units (branches, ribs, areoles, spines or fruits) were measured to obtain mean values.

Vegetative characters

1. Length of the highest branch.
2. Diameter of the highest branch.

These characters may be strongly influenced by age and environmental conditions. However, they were included in the analysis because they are related to the size and vigour of the plant.

3. Number of ribs. When possible, five branches per plant individual were considered. The number of ribs was counted always at the middle part of the branch.

4. Width of ribs. This feature was measured through a calliper. Three ribs per tree were chosen at random and they were measured always at the middle part of the branch.

5. Deepness of ribs. A calliper was used as well. Ribs measured were the same as those measured for width.

These characters are commonly used for classification of species of the genus *Stenocereus.* These characters are especially important because hybridization between *S. stellatus* and *S. pruinosus* and *S. treleasi* seems to be possible. *S. pruinosus* has narrower, deeper and fewer ribs than *S. stellatus* while *S. treleasi* has more narrow and numerous ribs than *S. stellatus.* A possible meaning of variation in these characters for domestication was explored.

6. Number of spines per areole. Five areoles per individual were chosen at random and the total number of spines in each was recorded.

7. Size of the principal spines. Estimated as the product of the length X the diameter at the middle part of the spine. Principal spines of ten areoles chosen at random, were measured per individual.

8. Distance between areoles. Distances between five pairs of areoles selected at random were measured through a calliper.

These characters were evaluated in order to analyze whether domestication has affected natural mechanisms of defence of this plant.

Erect and prostrate patterns of branch growth were also explored as interesting vegetative characters for studying domestication of this species. Prostrate growth might represent an advantage for harvesting and therefore it could be favoured by artificial selection. However, a clear distinction between these two characters was not observed in the field. The number of branches per individual was also recorded and was used for estimating fruit yield per individual as mentioned in the former chapter. However, it was not included in this analysis because it was considered that it is strongly related to the age of the plant.

Fruits.

9. Form of fruits. Spherical fruits were scored 1 and elongated fruits were scored 2.

This character is used by taxonomists in classification of species of the genus *Stenocereus,* and the two forms are found in this species. This character was considered to have possible meaning for artificial selection. People distinguish between the "boludo" (spherical) forms and the "alargado" (elongated) forms, and consider the "alargado" forms to be the most common fruit form in wild populations.

10. Peel colour. Four different colours distinguished by people were considered: red, designated 1; green-reddish, 2; green, 3; and yellow-orange, 4

11. Pulp colour, Six different colours distinguished by people were considered: red, designated 1; pink, 2; purple, 3; yellow, 4; orange, 5; and white, 6.

Colours have been characters traditionally selected by mesoamerican domesticators in many plants. In this case people distinguish "xoconochtli" according to different colours, mainly pulp colours, but commonly by combinations of peel and pulp colour (i.e. variant red with red peel and variant red with green peel, and others). As mentioned in the chapter of ethnobotany, colours of xoconochtli fruits have different human cultural values and they seem to be important features selected in the domestication process.

12. Flavour of the pulp. Four flavours recognized by people were considered: sour, 1; sweet and sour, 2; sweet, 3; and insipid, 4.

As mentioned, sweet flavours in xoconochtli have traditionally higher value than other flavours. Therefore, this character is very important to analyze domestication processes in this plants.

13. Total number of areoles per fruit.

14. Number of areoles per cm^2 in fruits. This feature was measured by using a card with holes of 2 cm^2. Cards were put always in the equatorial line of fruits. All complete or incomplete areoles included in the squared holes were counted and then divided by 2.

Artificial selection in other Cactaceae like prickly pear *(Opuntia ficus-indica),* has been directed to diminish or eliminate spines in fruits (Colunga *et al.* 1986). This could be equally true for "xoconochtli".

15. Thickness of the peel. This character was measured through a calliper always in the equatorial line of the fruits. As mentioned, people consider xoconochtli variants with thick peel are better to resist rotting.

16. Size of fruits. This feature was estimated by approaching a model to calculate the volume of spheric and ellipsoid bodies. The model considered was: $2(2 \pi r^2/h/3)$ where **r** was the radius, calculated as 1/2 of the maximum diameter of the fruits, and h is the height of semi-spheric or semi-ellipsoid bodies, calculated as 1/2 of the maximum length of the fruits. The resulting estimated volume is given in cm^3.

17. Total weight of fruits.

18. Weight of peel

29. Weight of the edible portion

20. Proportion of water in the edible portion. This was measured by weighting samples

after dried and then dividing by the weight of the whole edible portion.

21. Proportion of edible portion in fruits. This was calculated as the ratio of the weight between pericarp and the edible portion (flesh and seeds).

All these characters are related to the amount of edible matter, which generally has a high meaning in artificial selection of all edible plants.

22. Total number of seeds per fruit.

23. Mean size of the seeds, estimated through a mean weight of individual seeds (in mg) per fruit and then per individual. This parameter was obtained by weighing a sample of 100 seeds per fruit and dividing by 100 to obtain the individual seed weight.

24. Total weight of seeds per fruit.

25. Proportion of seeds in the edible portion. This character was estimated by the ratio of the total weight of seeds and the total weight of the edible portion.

It was considered important to explore such characteristics of seeds because in this and other species of the genus *(Pachycereus weberii,* for example) seeds are edible separately from flesh, after roasting, and their size is considered an attribute of quality by people. As revealed in the ethnobotanical studies, seeds have also an important economic value. For all these reasons, it was considered that a certain selection for increasing amount of seed mass would be possible at some point in the history of manipulation of this species.

METHODS OF DATA ANALYSIS

A Basic Data Matrix (BDM) was constructed with the the morphological characters studied considered as the variables, and the individuals considered as Operational Taxonomic Units (OTU). For quantitative characters, mean values and standard deviation per individual were considered in the analysis. Each individual was labelled according to the population to which it belongs. However, in the analysis the identity of individuals was considered independently of their population.

Individuals were classified based on the variables measured through multivariate statistical analyses. For these analyses, the basic data matrix was standardised because of the presence of different types of variables in the matrix as well as differences in scales of the variables. Standardization was carried out through the Numerical Taxonomy and Multivariate Analysis System (NTSYS-PC) programme version 1.8 developed by Rohlf (1993) by using the linear transformation **y'=(y-a)/b** where **y'** is the standardised value, y the variable mean value, a the average of values for this variable in all individuals, and b their standard deviation.

A Cluster Analysis (CA) was performed by calculating a similarity matrix between individuals through the Euclidean Distance coefficient and then processing this matrix through the Unweighted Pair Groups Method of Analysis (UPGMA) (Sneath and Sokal, 1973). Differences in composition of observed and expected groups (if individuals were not different) were tested by a Chi-square test. Principal Component Analysis (PCA) was performed on a correlation matrix between characters calculated by using the Pearson correlation coefficient (Sneath and Sokal, 1973). Through these statistical methods it was possible to recognize similarity and differences between populations in terms of multivariate morphological variation of individuals. Through PCA, variables which contribute most to the total variation were identified. NTSYS-PC was used to perform such analyses.

Through Discriminant Analysis (DA) the null hypothesis was tested that there are no significant differences between the nine populations studied, or between the three groups of populations defined according to the forms of management (wild, managed *in situ* and cultivated). The characters with higher discriminatory value were identified. This analysis was performed through the Statistical Graphics System (STATGRAPHICS) programme. 15 quantitative characters among the most relevant for explaining variation were considered in this analysis.

One-way Analyses of Variance were performed for each quantitative character considered independently from the rest. These analyses were carried out in order to visualize particular status of variation of each character among populations and to test significance of differences of particular characters between them. These analyses were performed through STATGRAPHICS.

Morphological diversity in populations.

A measure and comparison of levels of morphological diversity within and between populations of *Stenocereus stellatus* was considered to be useful to analyze whether or not artificial selection has altered the patterns of variation existing in natural populations, and to what extent. Univariate analyses of variance, give information on particular states of variance of quantitative characters, but it was considered useful to have information of morphological variance from a multivariate approach and including qualitative characters.

For this estimation, the Simpson's index was used. Simpson's index, derived from probability theory, and applied to synecological studies also to measure species diversity. This index measures the probability of picking two organisms at random that are different species, and is defined as:

$$D=1-\sum(pi)^2$$

where ***pi*** is the proportion of individuals of species i in the community, and S is the number of species. Based on this index Nei (1987) has developed indexes to estimate heterozygosity ***(He)*** and haplotypic diversity (***h***). ***pi*** was considered as the proportion of total individuals sampled in a population presenting the ***i***th feature, and S was substituted by ***n***, the number of states per character considered.

For calculating this index, some transformations to the Basic Data Matrix were necessary. Particularly, it was necessary to convert quantitative characters into multistate qualitative variables, dividing the whole range of the quantitative character into discrete classes, and giving a value to each class. From the univariate analyses of variance, quantitative intervals for assigning qualitative states were defined as those intervals comprised between the lowest limit of a given interval and the lowest limit of the following interval that is significantly different. The lowest and the highest values of the intervals comprised in the whole sample were considered as the lowest and the highest limits of the lowest and the highest intervals respectively. In this way, it was possible to obtain frequencies for particular classes

3. RESULTS

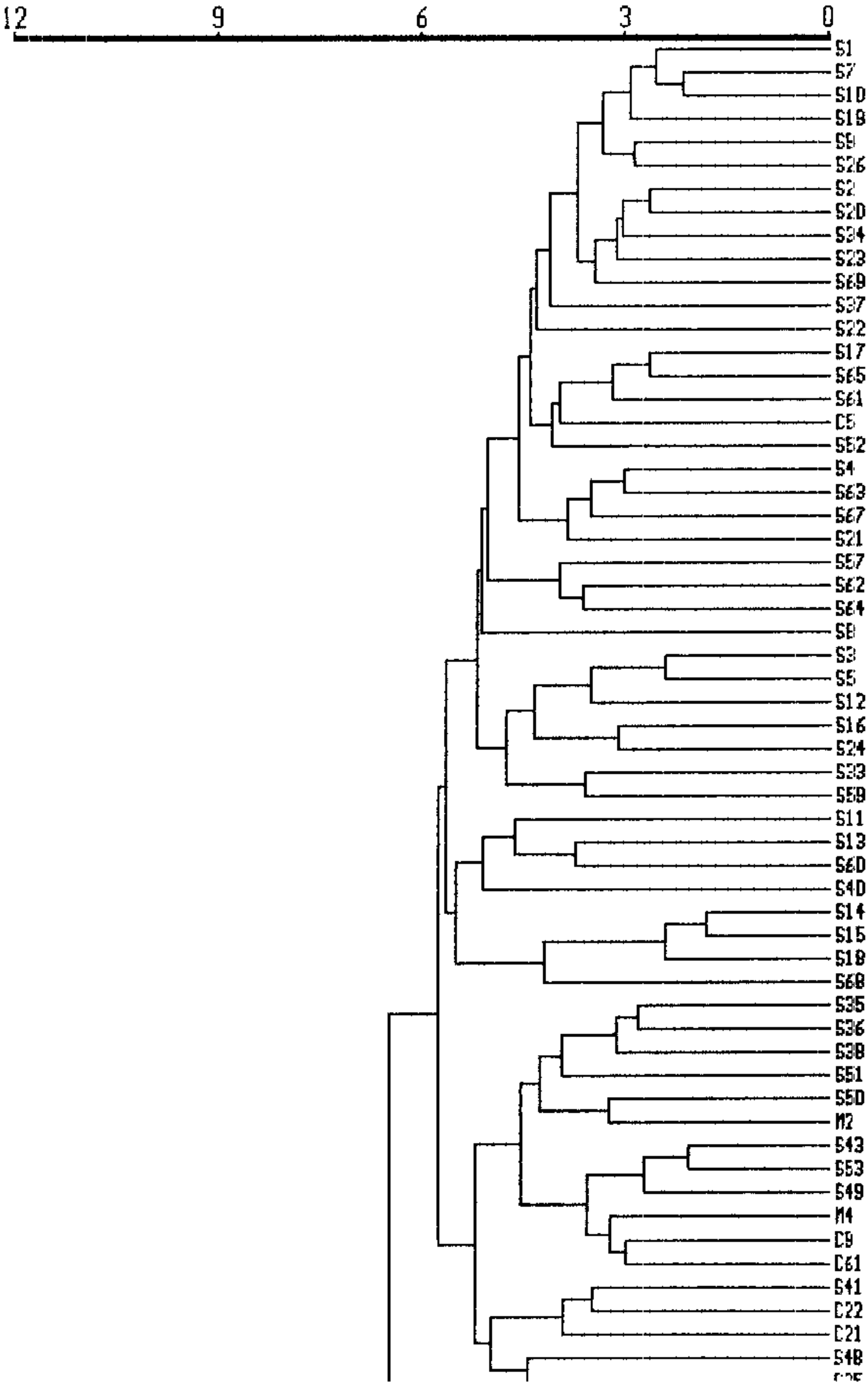
MEASURES OF MORPHOLOGICAL FEATURES OF *STENOCEREUS STELLATUS*

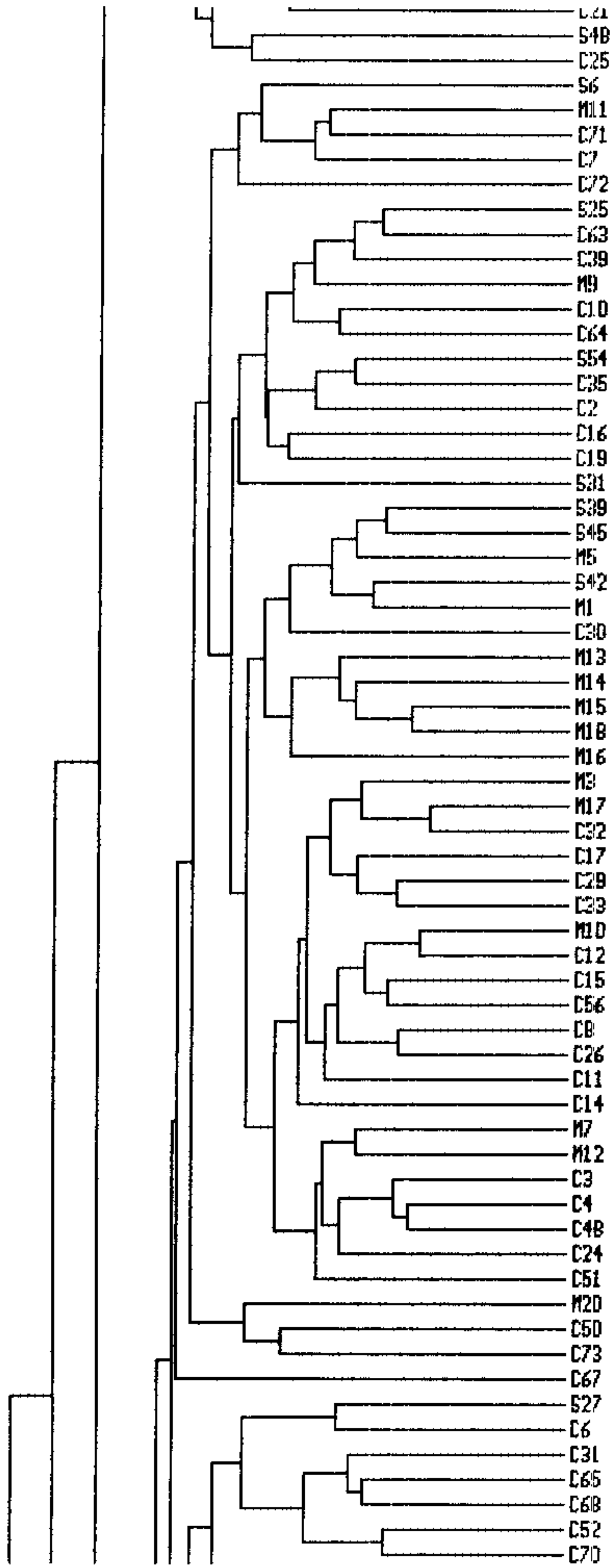
A 25 per 165 basic data matrix was constructed. The 25 characters were those described above and the 165 individual plants were those showed in the last column of Table 1. As suggested by Sneath and Sokal (1973), preliminary multivariate analyses includied standard deviations of the quantitative data. However, these values made very small contributions to explaining variation, i.e. that they varied at random, so they were removed in further analyses. The characters "fruit size", "fruit weight" and "edible portion weight" presented correlations higher than 0.9. The characters "fruit weight" and "edible portion weight" were therefore removed for the analyses. The resulting 23 X 165 basic data matrix was the matrix considered for the analysis presented in this chapter.

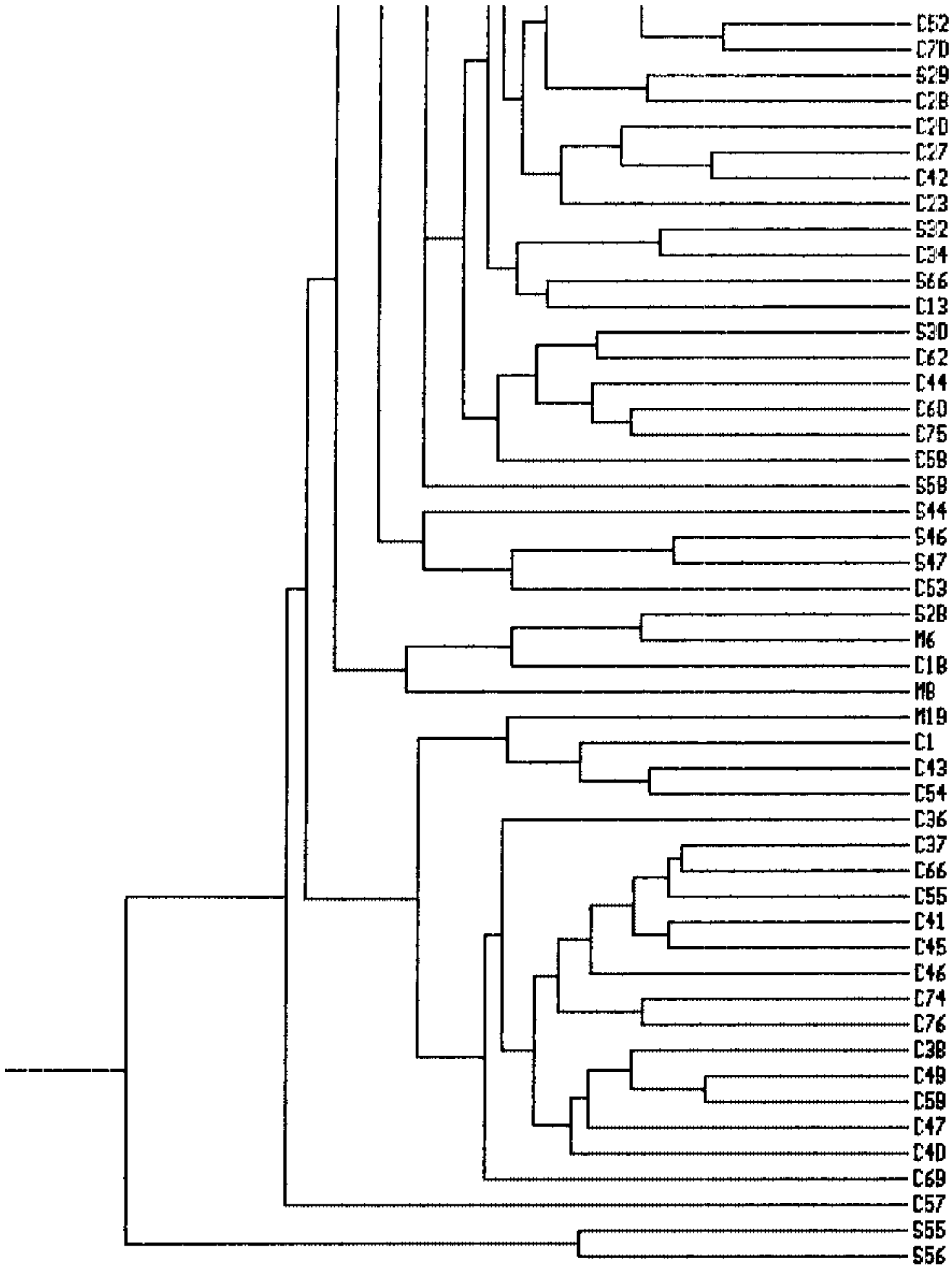
CLUSTER ANALYSIS

Figure 1 is the phenogram which resulted from Cluster Analysis. Five main groups of individuals can be observed. Group I is composed by two individuals from the wild population of San Lorenzo which separate from the rest at a dissimilarity level 10.417. Group 11. separates clearly from the rest at the level 8.295. It is composed by 19 cultivated individuals and only one individual from a managed *in situ* population. Eighteen of the cultivated individuals are from Chinango while only one individual is from Metzontla. This last individual is the only "xoconochtli aventurero" from Metzontla which presented the biggest fruits of the sample from Metzontla. The individual managed *in situ* is from Chinango.

Figure 1. Cluster Analysis




S48
C25
S6
M11
C71
C7
C72
S25
C63
C39
M9
C10
C64
S54
C35
C2
C16
C19
S31
S39
S45
M5
S42
M1
C30
M13
M14
M15
M18
M16
M3
M17
C32
C17
C29
C33
M10
C12
C15
C56
C8
C26
C11
C14
M7
M12
C3
C4
C48
C24
C51
M20
C50
C73
C67
S27
C6
C31
C65
C68
C52
C70


C52
C70
S29
C28
C20
C27
C42
C23
S32
C34
S66
C13
S30
C62
C44
C60
C75
C58
S58
S44
S46
S47
C53
S28
M6
C18
M8
M19
C1
C43
C54
C36
C37
C66
C55
C41
C45
C46
C74
C76
C38
C49
C59
C47
C40
C69
C57
S55
S56

Group III separates clearly from the other groups at a level of dissimilarity of 7.095. It is composed of 58 individuals, 50 wild individuals (86% of the group), six cultivated individuals (10% of the group) and two from managed *in situ* populations (4% of the group). This group includes the majority (72.5%) of the wild individuals in the sample.

The central part of the phenogram contains two groups. Group IV separates at level 5.447 and is composed of 53 individuals, 31 cultivated (58.5% of the group), 15 individuals from managed *in situ* populations (28.3% of the group) and 7 wild individuals (13.2% of the group). 75% of all the individuals from managed *in situ* populations are included in this groups.

Group V is composed by 32 individuals. Twenty are cultivated (62.5% of the group), two individuals are from populations managed *in situ* (6.2% of the group) and ten are wild individuals (31.3% of the group). Cultivated individuals included in this group constitute the 26.3% of all cultivated individuals sampled while managed *in situ* and wild individuals of this group constitute the 10% and 14.5% of all managed *in situ* and wild individuals included in this study

Table 2 summarizes the composition of each of these groups and the proportion of wild, managed *in situ* and cultivated individuals sampled comprised en each group. Table 3 shows the distribution of individuals of each populations among the different groups resulted from Cluster Analysis.

Table 4 shows that individuals from wild, managed in situ and cultivated populations are not distributed randomly between the groups. Group III contains more wild and fewer managed *in situ* and cultivated trees than expected if distributions were at random, whereas Group II includes fewer wild and more cultivated than expected. And finally, group IV is formed by fewer wild and more cultivated and managed *in situ* individuals than expected.

PRINCIPAL COMPONENT ANALYSIS

Figure 2 shows the first versus the second principal components and Figure 3 the first versus the third principal components. The first principal component separates cultivated individuals, which occupy mainly the right side of the plot, from wild individuals, which occupy mainly the left side of the plots Most individuals managed *in situ* occupy the central part of the plots.

Table 5 shows the eigenvalues resulting from the analysis, indicating that about 53% of the variation is explained by the first three principal components, mainly the first one Table 6 shows the eigenvectors for the first three principal components. Fruit size, density of spines on Fruits, peel weight and the total weight of seeds per fruit explain most of the variation in the first principal component. Peel thickness is the most important character in the second principal component. In the third principal component, the highest values correspond to the number of ribs and number of spines per areole, but these values are relatively low.

TABLE 2. COMPOSITION OF GROUPS OF INDIVIDUALS RESULTED FROM CLUSTER ANALYSIS.

GROUPS	I	II	III	IV	V
Total number of trees	2	20	58	53	32
% of trees sampled	1.2	12.1	35.2	32.1	19.4
Wild trees	2	0	50	7	10
% of the group	100.00	0.0	86.2	13.2	31.3
% of wild trees sampled	2.9	0.0	72.5	10.1	14.5
Managed *in situ* trees	0	1	2	15	2
% of the group	0.0	5.0	3.5	28.3	6.3
% of managed *in situ* trees sampled	0.0	5.0	10	75	10
Cultivated trees	0	19	6	31	20
% of the group	0.0	95.0	10.3	58.5	62.5
% of cultivated trees sampled	0.0	25.0	7.9	40.8	26.3

TABLE 3. % OF INDIVIDUALS FROM EACH POPULATION BELONGING TO EACH GROUP RESULTED FROM CLUSTER ANALYSIS

Population	G	R	O	U	P
	I	II	III	IV	V
Zapotitlán	0.0	0.0	95.8	4.2	0.0
Chinango-W	0.0	0.0	22.2	22.2	55.6
Sn. Juan Raya	0.0	0.0	100.0	0.0	0.0
Sn. Lorenzo	11.1	0.0	50.00	22.2	16.7
Coxcatlán	0.0	0.0	84.6	0.0	15.4
Metzontla-M	0.0	0.0	16.7	66.7	16.6
Chinango-M	0.0	12.5	0.0	87.5	0.0
Metzontla-C	0.0	3.9	19.2	57.7	19.2
Chinango-C	0.0	36.0	2.0	32.0	30.0

TABLE 4. OBSERVED AND EXPECTED FREQUENCIES OF INDIVIDUALS MANAGED IN DIFFERENT FORM WITHIN GROUPS RESULTED FROM CLUSTER ANALYSIS. (X^2=99.2088 WITH 13 D.F. SIG. LEVEL 2.33147E-[15]

Groups		Individual trees		
		Wild	Managed in situ	Cultivated
	Obs.	2	0	0
I	Exp.	1	0	1
	X^2	1.00	0.00	1.00
	Obs.	0	1	19
II	Exp.	9	2	9
	X^2	9.00	0.500	11.11
	Obs.	50	2	6
III	Exp.	24	7	27
	X^2	28.167	3.571	16.333
	Obs.	7	15	31
IV	Exp.	22	6	25
	X^2	10.227	13.500	1.440
	Obs.	10	2	20
V	Exp.	13	4	15
	X^2	0.692	1.000	1.667

TABLE 5. EIGENVALUES RESULTED FROM PRINCIPAL COMPONENT ANALYSIS.

PRINCIPAL COMPONENT	EIGENVALUE	PERCENT	CUMULATIVE
1	7.832514	34.0544	34.0544
2	2.582286	11.2273	45.2817
3	1.791454	07.7889	53.0707

DISCRIMINANT ANALYSIS

Table 7 shows that discriminant scores resulted from the first and second discriminant functions in the three groups of populations are significantly different. This means that the three groups of populations analyzed according to their management by people are significantly different in morphology. The classification resulting from Discriminant Analysis is presented in Table 8 and it can be visualized also in the plot of Figure 4. This classification indicates that about 75% of individuals of each group are different from individuals of the other two groups and the remaining individuals share morphological similarity with individuals of the other two groups standardized and unstandardized discriminant function coefficients for characters analyzed are shown in Table 9. This table indicated that total weight of seeds per fruit, peel thickness and weight as well as density of spines in fruits are the most important characters in the first discriminant function while the proportion of edible portion in fruits, fruit size, peel thickness and seed size are the most important characters in the second discriminant function.

TABLE 6. EIGENVECTORS RESULTED FROM PRINCIPAL COMPONENT ANALYSIS,

CHARACTER	PC1	PC2	PC3
Length of the highest branch	0.354	0.067	0.336
Diameter of the highest branch	0.661	-0.199	-0.421
Number of ribs	-0.139	0.061	-0.684
Width of ribs	0.630	-0.194	0.107
Rib depth	0.707	-0.313	0.156
Number of spines per areole	-0.124	0.120	-0.651
Size of principal spines	0.227	0.034	-0.205
Distance between areoles	0.409	-0.090	0.471
Fruit form	0.273	-0.139	-0.029
Peel colour	0.517	-0.125	-0.152
Pulp colour	0.556	-0.266	0.229
Flavour	0.405	0.090	-0.057
Total number of areoles in fruits	0.199	-0.070	0.126
Number of areoles/cm2 in fruits	-0.816	-0.130	0.199
Peel thickness	-0.321	-0.813	0.087
Fruit size	0.912	-0.058	0.037
Fruit peel weight	0.810	-0.303	0.066
Proportion of water in fruits	0.725	0.548	0.139
Proportion of edible portion	0.721	0.611	-0.084
Total number of seeds per fruit	0.629	-0.470	-0.220
Individual seed weight	0.735	-0.000	-0.152
Seed total weight per fruit	0.838	-0.326	-0.192
Seeds weight/edible portion weight	-0.568	-0.695	-0.163

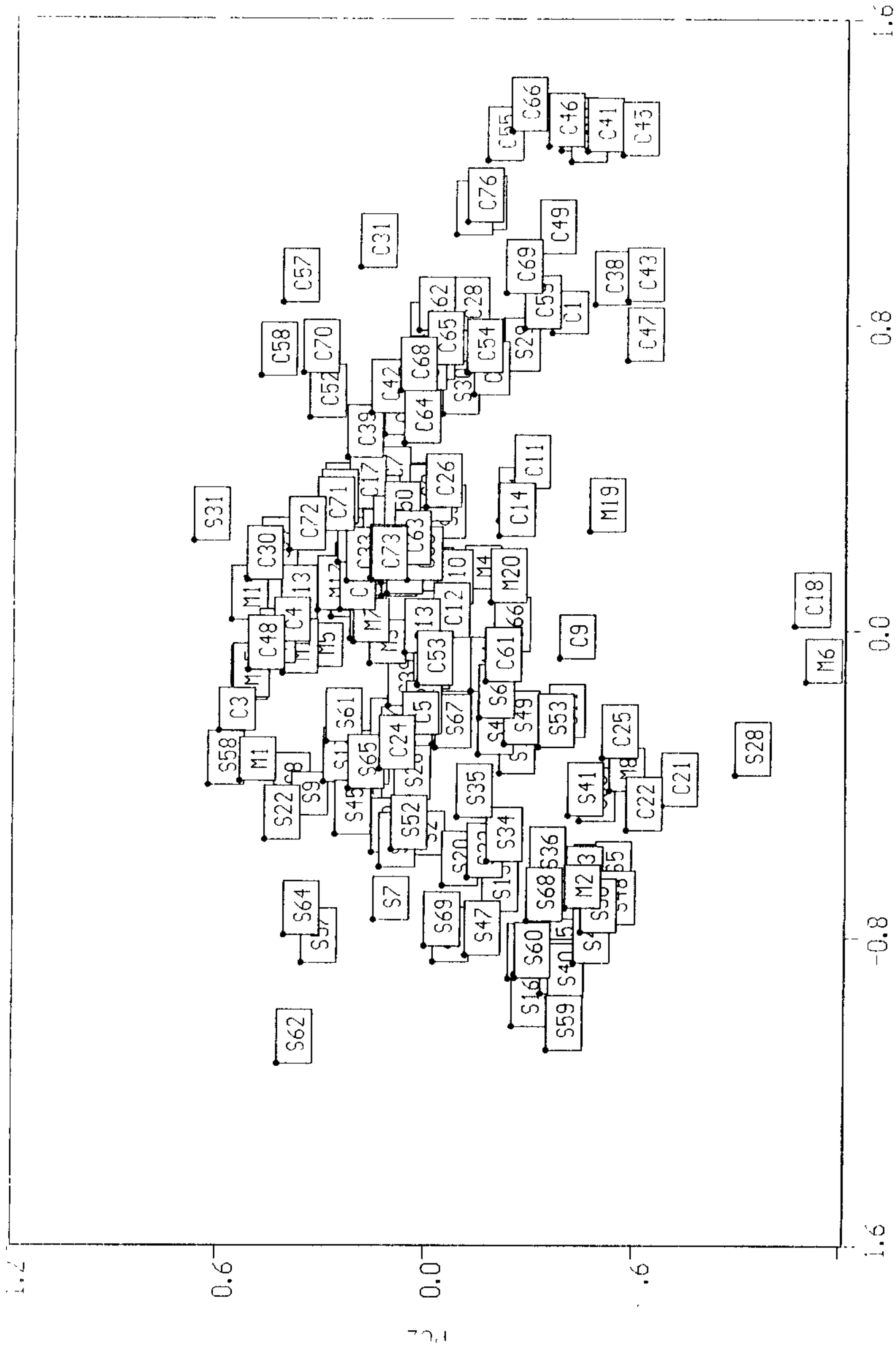


Figure 2. Projection of the xoconochtli individual plants in the space of the two first principal components (S=wild; M=managed *in situ* and C=cultivated individual plants).

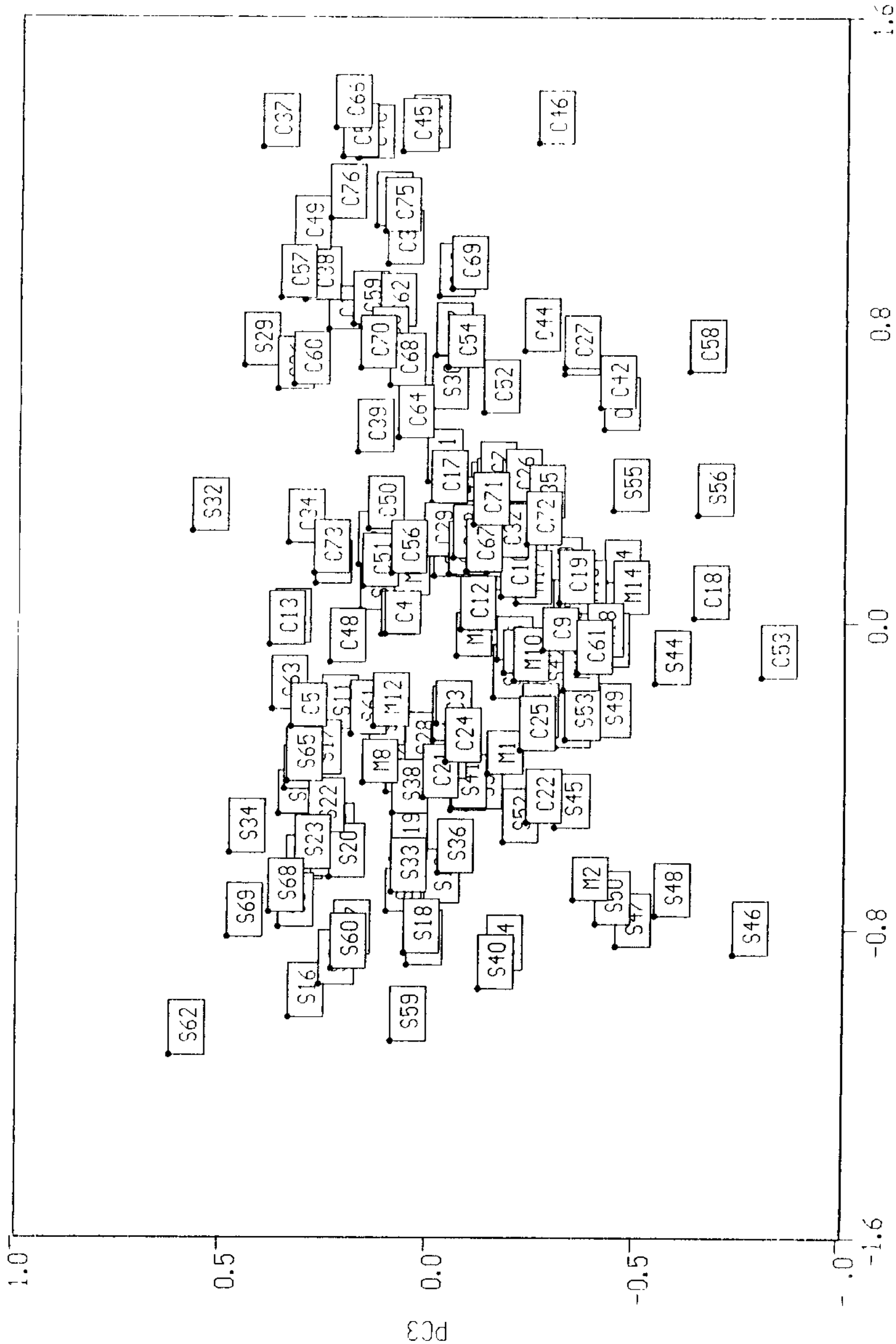


Figure 3. Projection of xoconochtli individual plants in the space of the first and third principal components (S=wild; M=managed in silts and C=cultivated individual plants).

Tables 10 to 12 present the results of Discriminant Analysis when the nine populations were compared. Table 10 shows that the two first discriminant functions explain 81.26% of the variation and that there exist significant differences in morphology between the populations analysed. Table 11 shows the classification of individuals that resulted from this analysis. This table indicates that wild populations possess a high percentage of individuals unique for their correspondent populations while in managed *in situ* and cultivated populations there are more individuals sharing morphological similarity with individuals of other populations. That is, there is a higher level of identity in wild populations compared with managed *in situ* and cultivated populations. Similarity among geographic regional populations seems to be important. Thus, cultivated individuals from Metzontla are similar, mainly, to individuals managed in situ in the same area, and cultivated individuals from Chinango are similar mainly to wild and managed *in situ* individuals from Chinango. But geographic affinities are not the only factor for explaining morphological similarity. Thus, there are individuals from each of the nine populations similar lo individuals from other populations in different geographic and environmental conditions. Plot of Figure 5 is a graphic representation of the classification of individuals from different populations according to this analysis.

Table 12 shows the discriminant function coefficients for the two first discriminant functions. It indicates that proportion of edible part of fruits as well as number and width of ribs are the most relevant characteristics in the first discriminant function while seed and fruit size are the most relevant characters in the second discriminant function.

TABLE 7. DISCRIMINANT ANALYSIS FOR WILD, MANAGED *IN SITU* AND CULTIVATED POPULATIONS OF *STENOCEREUS STELLATUS*.

Discriminant Function	Eigenvalue	Relative Percentage		Canonical Correlatio
1	1.3288797	85.67		0.75539
2	0.2222143	14.33		0.42640
Functions Derived	**Wilks Lambda**	**Chi-Square**	**DF**	**Sig. Level**
0	0.3513222	162.13799	30	0.00000
1	0.8181871	31.10295	14	0.00536

TABLE 8. CLASSIFICATION OF INDIVIDUALS OF WILD, MANAGED *IN siru* AND CULTIVATED POPULATIONS ACCORDING TO DISCRIMINAT ANALYSIS

Actual Group	Predicted Group							
	Wild		Managed *in situ*		Cultivated		Total	
	count	%	count	%	count	%	count	%
Wild	51	73.91	10	14.49	8	11.59	69	100.00
Managed *in situ*	3	15.00	15	75.00	2	10.00	20	100.00
Cultivated	5	6.58	15	19.74	56	73.68	76	100.00

TABLE 9. DISCRIMINANT FUNCTION COEFFICIENTS RESULTING FROM DISCRIMINANT ANALYSIS (STD=STANDARDIZED USTD=UNSTANDARDIZED).

Character	Discriminant Functions			
	1		2	
	USTD	STD	USTD	STD
Diameter of the highest branch	0.07676	0.12784	-0.05044	-0.08400
Number of ribs	0.13525	0.16809	0.18522	0.23019
Width of ribs	0.62984	0.34720	1.44075	0.79423
Rib depth	0.13122	0.05274	-0.78770	-0.31657
Number of spines per areole	-0.04364	-0.10239	0.22616	0.53061
Number of areoles/cm2 in fruits	-0.55203	-0.42102	-0.08260	-0.06300
Peel thickness	-6.07451	-0.56823	9.35063	0.87469
Fruit size	-0.01544	-0.34807	-0.04723	-1.06501
Peel weight	0.08130	0.56715	0.06937	0.48390
Proportion of water in pulp	-1.37550	-0.07256	-7.21592	-0.38064
Proportion of edible portion	-0.26168	-0.02789	14.6956	l .56605
Total number of seeds per fruit	-0.00058	-0.18886	-0.00182	-0.59515
Individual seed weight	-0.68651	-0.16496	-3.32955	-0.80004
Total weight of seeds per fruit	1.24333	0 57073	1.41997	0.65181
Seeds weight/edible portion weight	0.48451	0.01891	-2.22093	-0.08668

TABLE 10 DISCRIMINANT ANALYSIS FOR THE NINE POPULATIONS OF *STENOCEREUS STELLATUS* STUDIED.

Discriminant function	Eigenvalue	Relative percentage	Canonical correlation
1	3.3038409	61.03	0.87616
2	1.0951656	20.23	0.72299
3	0.4093250	7.56	0.53893
4	0.2813058	5.20	0.46856
5	0.1840638	3.40	0.39427
6	0.0632874	1.17	0.24397
7	0.0475321	0.88	0.21301
8	0.0291260	0.54	0.16823

Functions derived	Wilks Lambda	Chi-square	DF	Sig. level
0	0.0452480	470.53055	120	0.0000
1	0.1947404	248.68536	98	0.0000
2	0.4080134	136.26121	78	0.0000
3	0.5750235	84.10835	60	0.0217
4	0.7367809	46.43063	44	0.3724
5	0.8723956	20.74987	30	0.8955
6	0.9276072	11.42232	18	0.8755
7	0.9716983	4.36390	8	0.8228

TABLE 11. CLASSIFICATION OF INDIVIDUALS OF THE NINE POPULATIONS OF *STENOCEREUS STELLATUS* STUDIED ACCORDING TO DISCRIMINANT ANALYSIS

Predicted groups		Zap	Chin-W	S.J.R	S.L.	Cox	Metz-M	Chin-M	Metz-C	Chin-C
Zap	Count	20	1	1	0	1	0	0	0	0
	%	83.33	11.11	20.00	0.00	7.69	0.00	0.00	0.00	0.00
Chin- W	Count	1	6	0	0	0	2	0	1	6
	%	4.17	66.67	0.00	0.00	0.00	16.67	0.00	3.85	12.00
S.J.R.	Count	2	1	4	1	0	0	0	1	1
	%	8.33	11.11	80.00	5.56	0.00	0.00	0.00	3.85	2.00
S.L.	Count	0	0	0	12	0	1	0	1	1
	%	0.00	0.00	0.00	66.67	0.00	8.33	0.00	3.85	2.00
Cox	Count	1	0	0	0	12	0	0	0	0
	%	4.17	0.00	0.00	0.00	92.31	0.00	0.00	0.00	0.00
Met-M	Count	0	0	0	1	0	5	0	4	5
	%	0.00	0.00	0.00	5.56	0.00	41.67	0.00	15.38	10.00
Chin-M	Count	0	0	0	1	0	2	7	3	5
	%	0.00	0.00	0.00	5.56	0.00	16.67	87.50	11.54	10.00
Met-C	Count	0	0	0	3	0	1	0	15	2
	%	0.00	0.00	0.00	16.67	0.00	8.33	0.00	57.69	4.00
Chin-C	Count	0	1	0	0	0	1	1	1	30
	%	0.00	0.00	0.00	0.00	0.00	8.33	12.50	3.85	60.00
TOTAL	Count	24	9	5	18	13	12	8	26	50
	%	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

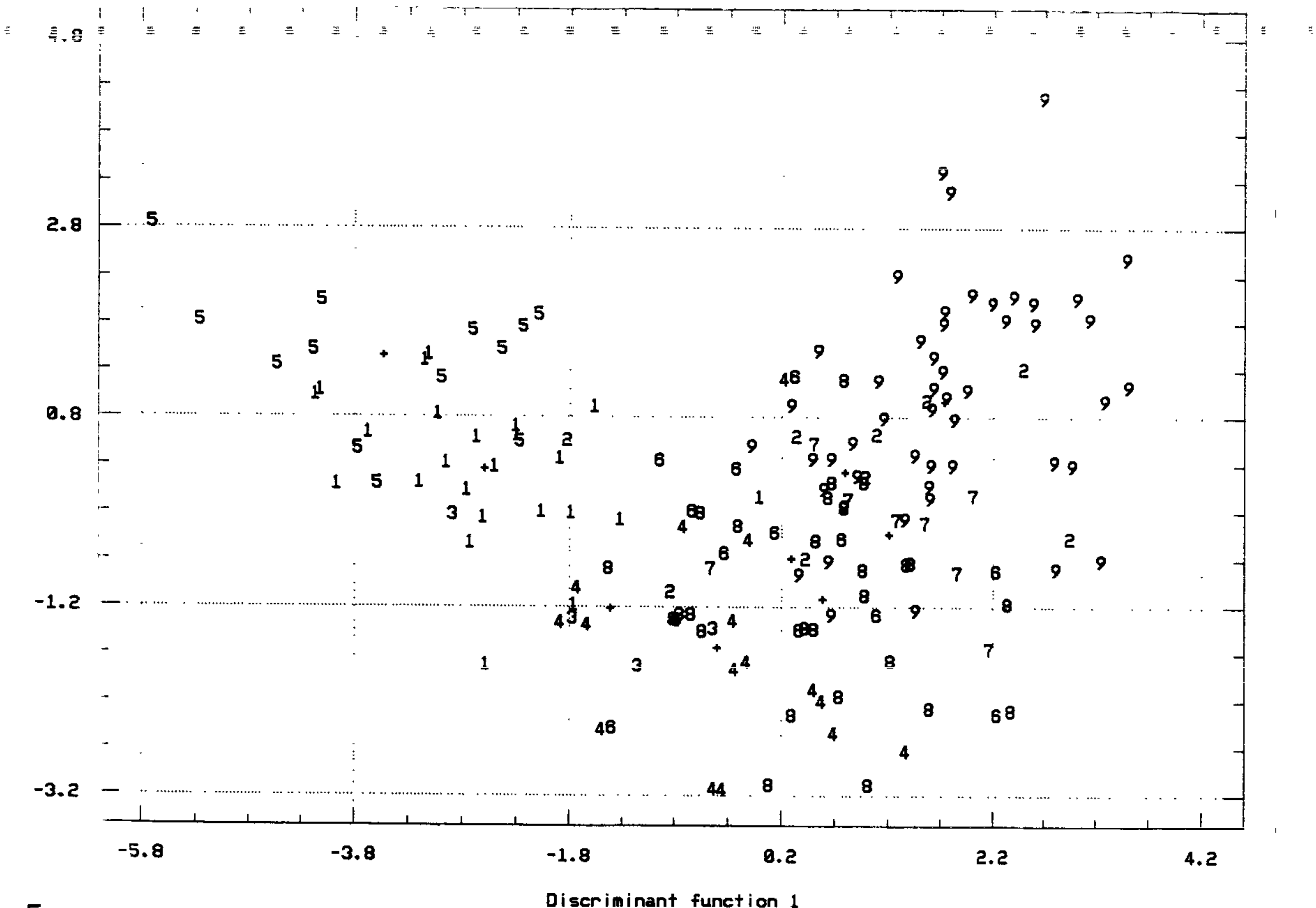


Figure 5. D iminant Function Analysis of xoconochtli individual plants according to populations studied (1=Zapotitlán; 2=Chinango-Wild; 3=San Juan Raya; 4 an Lorenzo; 5=Coxcatlán; 6=Metzontla-Managed *in situ*; 7=Chinango-Managed *in situ*; 8=Metzontla-Cultivated and 9=Chinango-Cultivated pc tations).

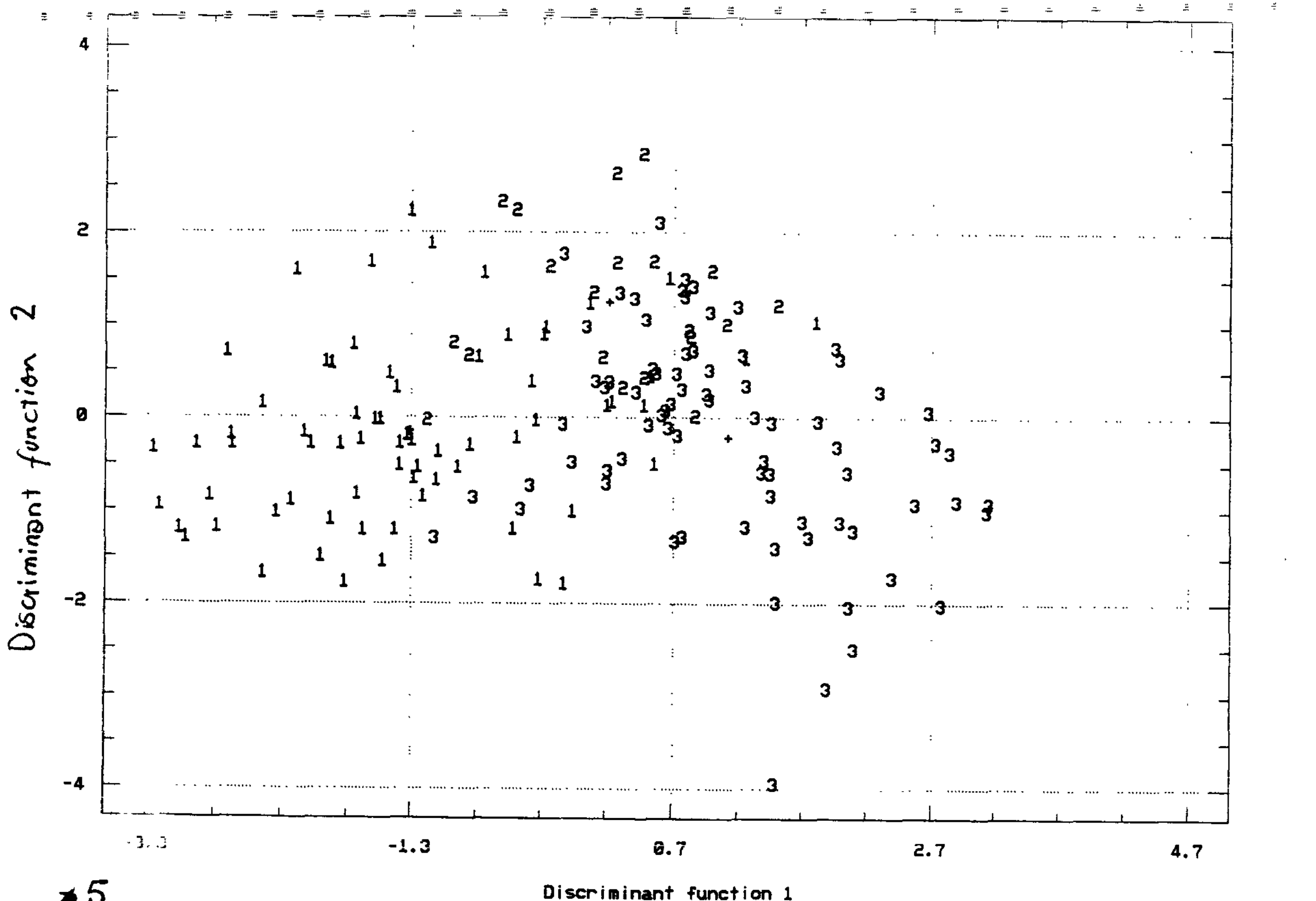


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Figure 30. Dis[illegible]nat Function Analysis classification of xoconochtli individual plants according to forms of management (1=wild; 2=managed *in situ* and 3=cultiva[illegible]opulations)

TABLE 12 COEFFICIENTS FOR THE TWO FIRST DISCRIMINANT FUNCTIONS RESULTED FROM THE DISCRIMINANT ANALYSIS OF THE NINE POPULATIONS OF *STENOCEREUS STELLATUS* STUDIED (USTD=UNSTANDARDISED, STD=STANDARDISED).

Character	Discriminant Function 1		Discriminant Function 2	
	USTD	STD	USTD	STD
Diameter of the highest branch	0.13183	0.18599	-0.19366	-0.27322
Number of ribs	0.57855	0.64021	-0.34203	-0.37849
Width of ribs	1.20887	0.60248	-0.42894	-0.21378
Deepth of ribs	0.49074	0.18268	0.62615	0.23309
Number of spines per areole	-0.02973	-0.06521	-0.09126	-0.20015
Number of areoles/cm2 in fruits	-0.54345	-0.38749	0.39611	0.28243
Peel thickness	2.59597	0.23665	-0.71380	-0.06507
Fruit size	-0.00503	-0.09762	0.02677	0,51920
Peel weight	0.05064	0.33061	0.02968	0.19377
Proportion of water in pulp	-5.25782	-0.25924	1.05275	0.05191
Proportion of edible portion	9.37566	0.91422	2.90719	0.28348
Total number of seeds	-0.00099	-0.31528	0.00092	0.29143
Individual seeds weight	-0.80019	-0.17984	-2.56357	-0.57616
Total seeds weight per fruit	0.55156	0.24592	-0.21670	-0.09662
Seeds weight/edible portion weight	4.14996	0.14839	-7.71845	-0.27599

ONE-WAY ANALYSES OF VARIANCE

One-way Analyses of Variance summarized in Table 13 , showing the populations that significantly differ in each character. From these results, it is possible to do the following observations:

1) Length of branches is significantly different only between San Lorenzo and Chinango-M and Chinango-C, being shorter in San Lorenzo and Chinango-M. The shortest branches were registered in Chinango-M and the longest in San Juan Raya. The highest variance occurs in wild and managed *in situ* populations (with the exception of Zapotitlán and San Lorenzo) and the lowest occurs in the cultivated populations.

2) The thinnest branches were registered in Zapotitlán, Coxcatlán and San Juan Raya and are significantly different to the rest. The thickest branches were registered in Chinango-M. As observed in branch length, the lowest variance in diameter were registered in cultivated populations as well as in Zapotitlán and San Lorenzo.

3) Xoconochtles from Coxcatlán have the lowest number of ribs (7 to 9) while those: from San Lorenzo have the highest number (10 to 12). There are significant differences between these extremes. Xoconochtles from the rest of the populations are intermediate in this character but there are significant differences between Zapotitlán, and the managed *in situ* and cultivated populations. The lowest variance occurs in Zapotitlán and the cultivated populations.

4) Ribs of xoconochtles from Chinango and Metzontla are wider and deeper than those of the rest of the populations. The lowest variance occurs in cultivated populations, as well as in Zapotitlán and San Lorenzo.

5) Number of spines per areole in xoconochtles from San Lorenzo and Chinango-M is significantly higher than in xoconochtles from Zapotitlán and Chinango-C. The lowest variance occurs in the cultivated populations and Zapotitlán and San Lorenzo.

6) Size of principal spines differed to be significantly only between xoconochtles from .Zapotitlán and San Lorenzo. The smallest spines were registered in San Juan Raya and the biggest in San Lorenzo. The lowest variance occurs in Zapotitlán and cultivated populations.

7) The shortest distance between areoles was registered in San Lorenzo. The lowest variance occurs in Zapotitlán and cultivated populations.

8) There is a general high variance in total number of areoles in fruits. The lowest variance was registered in Zapotitlán and cultivated populations. There are significantly fewer areoles in San Lorenzo and Metzontla-C than in Chinango-C but the rest of the populations are not significantly different with these populations and among them.

9) Density of spines, measured as number of areoles per cm^2 presented interesting significant differences between populations. In general terms, density is low in fruits of cultivated trees, intermediate in managed *in situ* and high in fruits of wild trees. The highest density of spines in fruits was registered in Coxcatlán and the lowest among cultivated trees in Chinango. The lowest variance was registered in Zapotitlán, San Lorenzo and cultivated populations.

10) Fruit peel was significantly thicker in Zapotitlán and San Lorenzo and significantly thinner in Chinango-M (where the thinnest peels were recorded) and Chinango-C. The rest of

the populations are intermediate in the range of variation, without significant differences with the populations mentioned or among them. The thickest peels occurred among fruits from San Juan Raya. The lowest variation was recorded in Zapotitlán, San Lorenzo and cultivated populations.

11) Fruits of cultivated individuals from Chinango were significantly bigger than those from the rest of the populations. Among the rest of the populations, there are significant differences only between Zapotitlán and Metzontla-C with smaller and bigger fruits respectively. The lowest variance was recorded in Zapotitlán and the cultivated populations.

12) There are significant differences in peel weight between fruits of cultivated xoconochtles from Chinango and those from the rest of the populations. The rest of the populations do not differ significant in this character among themselves.

13) Proportion of water in fruits is higher in xoconochtles from the three populations from Chinango. However, there are significant differences only between Chinango-C and the populations outside Chinango region. The lowest proportion of water in fruits was recorded in xoconochtles from San Juan Raya.

15) Proportion of edible part was significantly higher in managed *in situ* and cultivated populations from Chinango. Populations from Metzontla and Chinango-C present intermediate ranges being different to Zapotitlán population. The lowest proportion of edible matter in fruits 'was registered among individuals from San Juan Raya.

16) The significantly highest number of seeds was registered among cultivated individuals from Chinango. It was intermediate in the other two populations from Chinango and the two populations from Metzontla. And it was low in the rest of populations from the Tehuacán Valley.

17) Seeds were significantly bigger in cultivated individual trees, significantly smaller in Coxcatlán and intermediate in size in the rest of the populations.

18) Total weight of seeds per fruit was equally significantly higher among cultivated populations, lower among Zapotitlán and Coxcatlán populations and intermediate among the rest of the populations.

19) However, the relation between seed weight and edible portion weight was lower in

TABLE 13.MULTIPLE RANGE ANALYSIS FOR MORPHOLOGICAL CHARACTERS BY POPULATIONS (95% TUKEY HSD).

Population	Zapotitlán	Chinango-W	S.J.Raya	S.Lorenzo	Coxcatlán	Metzontla-M	Chinango-M	Metzontla-C	Chinango-C
Level	1	2	3	4	5	6	7	8	9
Branch length				(9)					(4)
Branch diameter	(2,4,6,7,8,9)	(1,5)	(9)	(1,5)	(2,4,6,7,8,9)	(1,5)	(1,5)	(1,5)	(1,5)
Number of ribs	(4,5)			(1,5,8,9)	(1,4,6,7,8,9)	(5)	(5)	(4,5)	(4,5)
Rib width	(2,6,7,8,9)	(1,4,5)		(2,8,9)	(2,6,7,8,9)	(1,5)	(1,5)	(1,4,5)	(1,4,5)
Rib deepness	(2,7,8,9)	(1,5)		(9)	(2,8,9)	(9)	(1)	(1,5,9)	(1,5,6,9)
Spines per areole	(4,7)	(4,7)		(1,2,9)			(1,2,9)		(4,7)
Principal spine size	(4)			(1)					
Distance between areoles	(4)	(4)		(1,2,5,8,9)	(4)	(9)	(9)	(4)	(4,6,7)
Num. of areoles in fruits				(9)				(9)	(4,8)
Areoles/ cm^2 in fruits	(6,7,8,9)	(5,9)	(9)	(8,9)	(2,6,7,8,9)	(1,5,9)	(1,5,)	(1,4,5)	(1,2,3,4,5,6)
Peel thickness	(7,9)		(7)	(7)			(1,3,4)		(1)
Fruit size	(8,9)	(9)	(9)	(9)	(9)	(9)	(9)	(1,9)	(1,2,3,4,5,6,7,8)
Peel weight	(9)	(9)	(9)	(9)	(9)	(9)	(9)	(9)	(1,2,3,4,5,6,7,8)
Water in pulp	(9)		(9)	(9)	(9)	(9)		(9)	(1,3,4,5,6,8)
Prop. of edible part	(2,7,8,9)	(1)	(7,9)	(7,9)	(7,9)	(9)	(1,3,4,5)	(1,9)	(1,3,4,5,6,8)
Total number of seeds	(8,9)		(9)	(9)	(9)			(1)	(1,3,4,5)
Individual seed weight	(8,9)	(5)	(5)	(5.8,9)	(1,2,3,4,6,7,8,9)	(5)	(5)	(1,4,5)	(1,4,5)
Total weight of seeds	(6,8,9)		(9)	(8,9)	(8,9)	(1,9)	(9)	(1,4,5)	(1,3,4,5,6,7)
Seeds/edible portion	(9)		(9)	(7,9)	(9)	(9)	(4)	(9)	(1,3,4,5,6,8)

Chinango managed in situ and cultivated populations and higher in the rest of the populations

Table 14 shows pairise comparisions of similarity between populations, calculated from the proportion of morphological characters that do not show significant differences between that pair of populations. These values can be considered as estimates of similarity between populations. Figure 6 is a phenogram resulting from a Cluster Analysis of this similarity. It is possible to appreciate that the cultivated population from Chinango is the most different of all populations in morphology. This population differenciates to the rest at level 0.507, The wild population from Coxcatlán is also different to the rest of the population at level 0.784. The rest of the population are similar at level 0.853 and then they form trhee clusters similar at level 1.00. Zapotitlán, Chinango-W and San Juan Raya in the first cluster; San Lorenzo and Metzontla-M in the second and Chinango-M and Metzontla-C in the third. In this analysis similarity seems to be independent of geographic location.

TABLE 14. PROPORTION OF SIMILAR MORPHOLOGICAL CHARACTERS AMONG POPULATIONS STUDIED.

Population	Zap.	Chin-W	S.J.R.	S. Lzo.	Cox	Met-M	Chin-M	Met-C	Chin-C
Zap.	1.000	0.789	1.000	0.737	0.947	0.789	0.632	0.526	0.316
Chin-W	0.789	1.000	1.000	0.842	0.789	1.000	0.947	1.000	0.842
S.J. R.	1.000	1.000	1.000	1.000	0.947	1.000	0.895	1.000	0.526
S. Lzo.	0.737	0.842	1.000	1.000	0.789	1.000	0.842	0.684	0.158
Cox.	0.947	0.789	0.947	0.789	1.000	0.737	0.684	0.632	0.316
Met-M	0.789	1.000	1.000	1.000	0.737	1.000	1.000	1.000	0.526
Chin-M	0.632	0.947	0.895	0.842	0.684	1 000	1.000	1.000	0.737
Met-C	0.526	1.000	1.000	0.684	0.632	1.000	1.000	1.000	0.632
Chin-C	0.316	0.842	0.526	0.158	0.316	0.526	0.737	0.632	1.000

MORPHOLOGICAL DIVERSITY BETWEEN POPULATIONS

Table 15 shows the ranges of quantitative characters and their corresponding qualitative states. Table 16 summarises frequencies of character states per population as well as their corresponding diversity indices. It is possible to appreciate from Table 16 that the highest value of mean morphological diversity corresponds to the wild population of Chinango while wild populations from the Tehuacán Valley had lower mean morphological diversity. Morphological diversity in managed *in situ* and cultivated populations from the Tehuacán Valley is higher than in wild populations of the area while in La Mixteca Baja region the population managed *in situ* is considerable less diverse than the wild and the cultivated population is almost as high in morphological diversity as the wild population.

Figure 6. Phenogram resulted from Cluster Analysis of morphological similarity between populations of *Stenocereus stellatus* studied (1=Zapotitlán; 2=Chinango-Wild; 3=S an Juan Raya; 4=San Lorenzo; 5=Coxcatlán; 6=Metzontla-Managed in *situ;* 7=Chinango-Managed *in situ;* 8=Metzontla-Cultivated and 9=Chinango-Cultivated populations).

TABLE 16. FREQUENCIES OF CHARAC'T'ER STATES IN POPULATIONS

Character	State	Zapotitlán x	Zapotitlán H	Chinango-W x	Chinango-W H	Sn. Juan Raya x	Sn. Juan Raya H	San Lorenzo x	San Lorenzo H	Coxcatlán x	Coxcatlán H	Metzontla-M x	Metzontla-M H	Chinango-M x	Chinango-M H	Metzontla-C x	Metzontla-C H	Chininango-C x	Chininango-C H
Branch length	1	0.625		0.556		0.200		0.778		0.385		0.750		1.00		0.265		0.450	
	2	0.375	0.469	0.444	0.493	0.800		0.222	0346	0.615	0.473	0.250	0.374	0.000	0.000	0.735	0.390	0.550	0.495
						0.320													
Branch diam.	1	0.958		0122		0.600		0.222		1.000		0.333		0.125		0.615		0.149	
	2	0.042	0.080	0.778	0.346	0.400		0.778	0.346	0.000	0.000	0.667	0.445	0.875	0218	0.835	0.277	0.851	0.254
						0.480													
Num. of ribs	1	0.292		0.444		0.400		0.000		0.846		0.167		0.125		0.085		0.222	
	2	0.708	0.587	0.556	0.493	0.600		1.000	0.000	0.154	0.260	0.833	0.278	0.875	0.218	0.915	0.155	0.778	0.345
						0.480													
Rib width	1	0.917		0.222		0.800		0.556		1.000		0.250		0.125		0.119		0.142	
	2	0.083	0.153	0.778	0.346	0.200		0.444	0.493	0.000	0.000	0.750	0.374	0.875	0.218	0.881	0.210	0.858	0.244
						0.320													
Rib deepness	1	0.875		0.333		0.400		0.500		0.769		0.500		0.250		0.319		0.066	
	2	0.125		0.222		0.600		0.500		0 231		0.250		0.625		0.485		0.308	
	3	0.000	0218	0.444	0.642	0.000		0.000	0.500	0.000	0.356	0.250	0.624	0.125	0.530	0.196	0.625	0.626	0.509
						0.480													

TABLE 16. (...CONTINUATION)

Character	State	Zapotitlán		Chinango-W		S. Juan Raya	Sn.Lorenzo		Coxcatlán		Metzontla-M		Chinango-M		Metzontla-C		Chinango-C	
		x	H	x	H		x	H	x	H	x	H	x	H	x	H	x	H
Spines/areole	1	0.833		1.000		0.800	0.278		0.539		0.167		0.125		0.569		0.765	
	2	0.167	0.278	0.000	0.000	0.200	0.722	0.401	0.461	0.497	0.833	0.278	0.875	0218	0.431	0.490	0.235	0.360
						0.320												
Spine size	1	1.000		0.556		1.000	0.889		0.539		0.667		0.625		0.777		0.483	
	2	0.000	0.000	0.444	0.493	0.000	0.111	0.198	0.461	0.497	0.333	0.445	0.375	0.468	0.223	0.346	0.517	0.499
						0.000												
Distance/areoles	1	0.500		0.556		0.600	1.000		0.539		0.750		0.750		0.388		0.311	
	2	0.500	0.500	0.444	0.493	0.400	0.000	0.000	0.461	0.497	0.250	0.374	0.250	0 374	0 612	0.475	0.689	0.429
						0.480												
Fruit form	1	0.667		0.444		1.000	0.611		0.461		0.833		0.875		0.692		0.570	
	2	0.333	0.455	0.556	0.493	0.000	0.389	0.475	0.539	0.497	0.167	0.278	0.125	0.218	0.308	0.426	0.430	0.491
						0.000												
Peel colour	1	0.750		0.444		0.400	0 167		0.932		0.750		0.750		0.481		0.325	
		0.208		0.556		0.600	0.667		0.077		0 167		0 250		0 362		0 225	
	3	0.042		0.000		0.000	0.167		0.000		0.083		0.000		^{0}0.131		0.450	
	4	0.000	0.392	0.000	0.493	0.000	0.000	0.500	0.000	0.142	0.000	0.402	0.000	0.374	0.027	0.620	0.000	0.641
						0.480												

TABLE 16 (...CONTINUATION)

Character	State	Zapotitlán		Chinango-W		S. Juan Raya		Sn. Lorenzo		Coxcatlán		Metzontla-M		Chinango-M		Metzontla-C		Chinango-C	
		x	H	x	H	x	H	x	H	x	H	x	H	x	H	x	H	x	H
Pulp colour	1	0.917		1.000		1.000		1.000		1.000		0.917		1.000		0.869		0.589	
	2	0.042		0.000		0.000		0.000		0.000		0.083		0.000		0.131		0.070	
	3	0.042		0.000		0.000		0.000		0.000		0.000		0.000		0.000		0 007	
	4	0.000		0.000		0.000		0.000		0.000		0.000		0.000		0.000		0.070	
	5	0.000	0.156	0.000	0.000	0.000		0.000	0.000	0.000	0.000	0.000	0.153	0.000	0.000	0.000	0.227	0.265	0.573
						0.000													
Flavour	1	0.500		0.556		1.000		0.500		0.692		0.000		0.125		0.000		0.000	
	2	0.333		0.333		0.000		0.389		0.154		0.833		0.375		0.650		0.132	
	3	0.000		0.111		0.000		0.000		0.000		0.083		0.375		0.119		0.868	
	4	0.167	0.611	0.000	0.568	0.000		0.111	0.587	0.154	0.473	0.083	0.292	0.125	0.686	0.231	0.457	0.000	0.229
						0.000													
Areoles/fruit	1	0.542		0.667		0.400		0.667		0.385		0.667		0.375		0.877		0.470	
	2	0.458	0.497	0.333	0.445	0.600		0.333	0.445	0.615	0.473	0.333	0.445	0.625	0.468	0.123	0.216	0.530	0.498
						0.480													
Areoles/cm2	1	0.042		0.111		0.600		0.111		0.000		0 .167		0 .125		742		0.775	
	2	0.333		0.111		0.400		0.556		0.461		0.750		0.875		0.238		0.212	
	3	0.625	0.496	0.111	0.333	0.000		0.333	0.568	0.539	0.497	0.083	0.402	0.000	0.218	0.019	0.391	0.013	0.335
						0.480													

TABLE 16 (..CONTINUATION)

Character	State	Zapotitlán x	Zapotitlán H	Chinango-W x	Chinango-W H	S. Juan Raya x	S. Juan Raya H	Sn. Lorenzo x	Sn. Lorenzo H	Coxcatlán x	Coxcatlán H	Metzontla-M x	Metzontla-M H	Chinango-M x	Chinango-M H	Metzontla-C x	Metzontla-C H	Chinango-C x	Chinango-C H
Peel thickness	1	0.167		0.222		0.200		0222		0.615		0.583		0.750		0.788		0.586	
	2	0.833	0.278	0.778	0.346	0.800		0.778	0.346	0.385	0.473	0.417	0.486	0.250	0.374	0.212	0.333	0.414	0.485
						0.320													
Fruit size	1	0.833		0.333		1.000		0.778		0.846		0.500		0.250		0.254		0.026	
	2	0.167		0.667		0.000		0.222		0.154		0.500		0.750		0.738		0.447	
	3	0.000	0.278	0.000	0.445	0.000		0.000	0.346	0.000	0.260	0.000	0.500	0.000	0.374	0.008	0.391	0.527	0.522
						0.000													
Peel weight	1	0.708		0.556		0.800		0.722		0.846		0.500		0.625		0.138		0.123	
	2	0.250		0.333		0.200		0.278		0.154		0 500		0.250		0.823		0.368	
	3	0.042	0.434	0.111	0.568	0.000		0.000	0.401	0.000	0.260	0.000	0.500	0.125	0.530	0.039	0.302	0.510	0.590
						0.680													
Water in pulp	1	0.750		0.333		1.000		0.833		0.846		0.750		0.750		0.477		0.232	
	2	0.250	0.374	0.667	0.445	0.000		0.167	0.278	0.154	0.260	0.250	0.374	0.250	0.374	0.523	0.499	0.768	0.356
						0.000													
Edible part	1	750		0.222		0. 800		0.611		0.615		0.250		0.125		0.115		0 000	
	2	0.208		0.444		0.200		0.278		0.077		0.417		0.250		0.600		0.358	
	3	0.042	0.392	0.333	0.642	0.000		0.111	0.537	0.308	0.520	0.333	0.652	0.625	0.530	0.285	0.546	0.642	0.459
						0.320													

TABLE 16 (...CONTINUATION)

Character	State	Zapotitlán		Chinango-W		S. Juan Raya		Sn. Lorenzo		Coxcatlán		Metzontla-M		Chinango-M		Metzontla-C		Chinango-C	
		x	H	x	H	x	H	x	H	x	H	x	H	x	H	x	H	x	H
Num. of seeds	1	0.708		0.333		1.000		0.556		0.615		0333		0.625		0.246		0.225	
	2	0.292	0.586	0.667	0.445	0.000		0.444	0.493	0.385	0.473	0.667	0.445	0.375	0.468	0.754	0.371	0.775	0.349
						0.000													
Seed size	1	0.500		0.111		0.800		0.278		0.769		0.083		0.125		0.000		0.036	
	2	0.458		0.333		0.200		0.389		0.231		0.583		0.500		0.269		0.318	
	3	0.042	0.538	0.556	0.568	0.000		0.333	0.661	0.000	0.356	0.333	0.542	0.375	0.593	0.731	0.394	0.646	0 481
						0.320													
Seeds weight/fruit	1	0.833		0.222		0.600		0.556		0.769		0.333		0.500		0.565		0.116	
	2	0.167		0.444		0.400		0.389		0.231		0.333		0.375		0 054		0 338	
	3	0.000	0.278	0.333	0.642	0.000		0.056	0.537	0.000	0.356	0.333	0.667	0.125	0.593	0.381	0.532	0.546	0 574
						0.480													
Seeds/edible part	1	0.458		0.778		0.200		0.278		0.539		0.583		1.000		0.804		0.987	
	2	0.542	0.497	0.222	0.346	0.800		0.722	0.599	0.461	0.497	0.417	0.486	0.000	0.000	0.196	0.316	0.013	0.026
						0 320													
MEAN H		**0.344**		**0.453**		**0.278**		**0.385**		**0.353**		**0.427**		**0.350**		**0.391**		**0.424**	
ADJUSTED H*		**0395**		**0.784**		**0.481**		**0.666**		**0.611**		**0.739**		**0.606**		**0.676**		**0.734**	

*Estimated by dividing mean H by the maximum mean value of H (0.578)

4. DISCUSSION

Multivariate statistical analyses demonstrated that wild, managed *in situ* and cultivated populations are different in morphology. The five wild populations analysed are located in different geographic areas with important environmental differences, however, nearly 80% of these individuals (86% according to Cluster Analysis and 75% according to Discriminant Analysis) are morphologically similar and significantly different: from the managed *in situ* and cultivated individuals. Individuals managed *in situ* also constitute a well defined group in terms of morphological affinities. Cluster Analysis grouped them mainly along with about 40% of the cultivated individuals and only two managed individuals were grouped with the main group of wild individuals (Figure 1 and Tables 2 and 3). Discriminant Analysis classified 75°/i of the managed *in situ* individuals in a defined "Managed *in situ"* group together with almost 15% of wild and near 20% of cultivated individuals (Table 8). Cluster Analysis distinguished a group of cultivated individuals from Chinango (almost 50% of the individuals from this population) that are strongly different from the remaining cultivated individuals, and other group that is similar to cultivated individuals from Metzontla and managed *in situ* individuals (Figure 1 and Tables 2 and 3). Discriminant Analysis classified 73.68% of cultivated individuals conforming the group "cultivated" together with 8 wild and 2 managed individuals (Table 8). There are some cultivated individuals that resulted to be similar to wild individuals. Cluster Analysis included 6 cultivated individuals in the main group of wild individuals (Tables 2 and 3) while Discriminant Analysis included 5 cultivated individuals within the group "wild". All these individuals, as informed by people, were brought to home gardens from wild populations. There are also some wild individuals similar to cultivated individuals. Cluster Analysis identified 17 from Chinango, San Lorenzo and Coxcatlán (Tables 2 and 3) and Discriminant Analysis identified 8 individuals. This indicates that although in a low frequency, cultivated-like phenotypes occur in wild populations.

Multivariate statistical analyses showed that there are differences between wild populations from the Tehuacán Valley (Zapotitlán, San Juan Raya, San Lorenzo and Coxcatlán)and the wild population from La Mixteca Baja (Chinango-W). Thus, Cluster Analysis (Table 3) grouped almost 90% of wild individuals from the Tehuacán Valley in group III while almost 80% of the wild individuals from La Mixteca Baja (Chinango-W population) were in groups IV and V. In a similar way, the Discriminant Analysis of populations showed that wild individuals from a given population of a geographic area are more similar to individuals from other populations of the same geographic area (Table 11). However, all these analyses showed that patterns of variation in managed in situ and cultivated individuals have a low correlation with geographic provenance. In addition, one way-analyses of variance of particular characters defined a classification of similar populations that resulted to be independent of their geographic location (Figure 5).

TABLE 15. QUALITATIVE STATES OF CHARACTERS DERIVED FROM SIGNIFICANTLY DIFFERENT INTERVALS OF QUANTITATIVE CHARACTERS.

Character	Inetrval	State	Intervale	Satate	Inetrvale	State
Branch length	174.48/324.78	1	324.79/414.96	2		
Branch diameter	9.81/12.74	1	12.75/15.81	2		
Num. of ribs	7.71/9.25	1	9,26/11.71	2		
Rib width	2.24/3.02	1	3.03/4.03	2		
Rib deepness	2.03/2.48	1	2.49/2.86	2	2.87/3.11	3
Spines/areole	10.74/14.77	1	14.78/18 30	2		
Principal spine size	0/0.26	1	0.27/0.53	2		
Distance /areoles	1.80/2.43	1	2.44/2.80	2		
Areoles per fruit	24.04/31.24	1	31.25/37.67	2		
Areoles/cm^2 per fruit	1.34/1.88	1	1.89/3.01	2	3.02/4.13	3
Peel thickness	0.19/0.33	1	0.34/0.54	2		
Fruit size	0.72/31.35	1	31.36/67.94	2	67.95/80.15	3
Peel weight	4.03---12.53	1	12.54/21.29	2	21.30/25.41	3
Water in pulp	0.74/0.86	1	0.87/0.90	2		
Edible portion	0.35/0.52	1	0.53/0.63	2	0.64/0.73	3
Num, of seeds	428.85/1008.75	1	1008.76/1444.96	2		
Seed size	0.54/0.86	1	0.87/1.17	2	1.18/1.39	3
Seeds weight/fruit	0.37/0.92	1	0.93/1.53	2	1.54/1.83	3
Seeds/edible part	0.02/0.07	1	0.08/0.13	2		

Morphological similarity between individuals from different geographic areas with important environmental differences as well as similarities of cultivated individuals that were brought from wild populations with individuals from wild populations suggest that morphological variation in this species has an important genetic component. The significant morphological differences between wild and managed *in situ* and cultivated populations suggest that phenotypic structure of populations has been influenced by human management. This last means that evolution of this species under domestication has achieved a significant morphological divergence from wild populations. This divergence is especially marked between wild individuals and individuals cultivated in home gardens where manipulation of plants by planting and replacing of variants is relatively intense. The divergence is also significant between wild and managed *in situ* populations, but not as marked as with cultivated in home gardens. This form of management is mainly directed to increase frequencies of good phenotypes existing in wild populations.

One-way analyses of variance demonstrated that exist significant differences between some populations in all characters analysed. However, the Principal Component and Discriminant Analysis showed that the most relevant characters for classifying groups of individuals according to the form of management were: 1) fruit: size (bigger among cultivated individuals); 2) density of spines in fruits (higher in fruits of wild individuals); 3) peel weight (heavier in fruits of cultivated individuals); 4) peel thickness (thicker in wild individuals) 5) total weight of seeds (higher in fruits of cultivated individuals) and 6) seed size (bigger in cultivated individuals).

Characters such as flavour and colour of fruit pulp, which are relevant in traditional classification of this species, did not appear relevant in the morphological analyses performed. In the case of pulp colour, this can be explained because of the low frequency of occurrence of colours different to red. This was reflected in the sample, in which 95% of individuals presented red pulp. In the case of flavour, a more objective method for measuring amounts of sugars in fruits could give more precise information.

Indices of morphological variation that were estimated reveal that, in general terms, there is a higher variation in La Mixteca Baja than in the Tehuacán Valley wild populations. Causes of these differences are not studied for the moment. The following chapters of this thesis examine morphological variation in relation to genetic variation and ecological aspects intervening in reproduction of this species. But more research is needed in this direction.

Contrasting with the low morphological diversity in wild populations, the cultivated population from the Tehuacán Valley (Metzontla-C) presented a relatively high morphological diversity. In Chinango, morphological diversity of this species in home gardens is also high. This can be explained because people use to cultivated several variants of this species in a same home garden and they commonly exchange propagation materials with other families of the 'village and introduce new materials from other villages.

Managed *in situ* population from Metzontla presented a higher morphological diversity than wild population of the Tehuacán Valley. In Chinango, where the wild population presented the highest index of morphological diversity, the managed *in situ* population presented a reduced diversity. In the first case, as mentioned in the former chapter, wild populations are scarce. This encourage people to take special care of managed in situ populations and even to introduce propagation materials from 'individuals cultivated in home gardens. In Chinango, as discussed in the former chapter, managed *in situ* populations play a secondary role in production of xoconochtli fruits. People in this area only tolerate good phenotypes and eliminate others.

Apéndice 4

MORPHOLOGICAL DIVERGENCE IN POPULATIONS OF STENOCEREUS STELLATUS (CACTACEAE) UNDER DOMESTICATION IN CENTRAL MEXICO

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(Artículo sometido a **Economic Botany)**

Casas, Alejandro (The University of Reading. Department of Agricultural Botany School of Plant Sciences. Whiteknights PO Box 221, Reading RG6 6AS, UK. Jardín Botánico, Instituto de Biología, Universidad Nacional Autónoma de México. Apartado Postal 70-614, México, D.F. 04510, México), **Javier Caballero** (Jardín Botánico, Instituto de Biología, Universidad Nacional Autónoma de México. Apartado Postal 70-614, México, D.F'. 04510, México), **Barbara Pickersgill** (The University of Reading. Department of Agricultural Botany. School of Plant Sciences. Whiteknights PO Box 221, Reading RG6 6AS, UK), **Alfonso Valiente-Banuct** (Centro de Ecología, Universidad Nacional Autónoma de México. Apartado Postal 70-275, México, D.F. 04510, México) and **José Antonio Soriano** (Centro de Ecología, Universidad Nacional Autónoma de México. Apartado Postal 70-275, México, D.F. 04510, México). MORPHOLOGICAL DIVERGENCE IN POPULATIONS OF STTNOCEREUS STELLATUS (CACTACEAE) UNDER DOMESTICATION IN CENTRAL MEXICO. Patterns of morphological variation under domestication are assessed in the columnar cactus Stenocereus stellatus. This species is distributed in arid and semi-arid lands of Central Mexico where indigenous peoples have interacted with it, probably for more than 4000 years. It is a multipurpose plant, mainly used for its edible fruits. Morphological variation is analysed among individuals from nine populations of the Tehuacán Valley and La Mixteca Baja region: five wild populations whose useful parts are occasionally gathered by people; two populations managed in situ through a selective sparing of desirable phenotypes and the removal of undesirable phenotypes during clearance of natural vegetation for agriculture; and two populations of individuals cultivated in home gardens by indigenous people. Multivariate statistical analyses, including Cluster

Analysis, Principal Component Analysis and Discriminant Analysis showed a significant morphological divergence between populations, related in part to environmental differences but mainly to the extent of human management. This illustrates how domestication is changing patterns of morphological variation of this species through cultivation in home gardens but also through forms of management of wild populations in situ. This information is discussed in relation to domestication in situ of other plants in Mesoamerica.

INTRODUCTION

Stenocereus stellatus (Pfeiffer) Riccobono is a columnar cactus from arid and semi-arid lands of Central Mexico, particularly the Tehuacán Valley and parts of the Balsas river basin in the states of Puebla, Guerrero, Oaxaca and Morelos (Figure 1). It is a multipurpose species, mainly used as human food with fruits as the most important edible parts (Casas et al. in press). In the area of distribution, S. stellatus may occur in cultivation and also in wild populations as part of tropical deciduous forests and thom-scrub forests in different environmental conditions. Altitudes range from 1500 to 2000 m; annual precipitations between 300 and 800 mm and annual mean temperatures from 17 to 24^0C. The area is today inhabited by about 10 different indigenous ethnic groups (Casas et al. in press), who probably have interacted with S. stellatus for more than 4000 years, according to archaeological information obtained by MacNeish (1967) and Smith (1967) in caves from the Tehuacán Valley. It is therefore possible to analyze in this area the processes of domestication of S. stellatus in different cultural and environmental situations.

In the wild as well as in cultivation, Stenocereus stellatus may propagate vegetatively. However, sexual reproduction is also carried out constituting an important source of morphological and genetic variation. During August and September, the season when fruits of this species are ripe, it is possible to appreciate in rural villages and traditional markets of the area of distribution a great morphological variability in fruits. They may have red or green peel with high or low spininess; size ranging from 3 to 9 cm in diameter; and red, pink, purple, yellow, orange or white flesh containing numerous black seeds.

Differences in environmental conditions may influence this variation, but it may also have a genetic basis. Such morphological variation is in part the result of a long time of natural evolution. But in part, it may also be the result of a long history of manipulation of these plants by humans. The distinction of the results of natural and artificial selection is a crucial problem for analyzing how domestication has operated and the degree of advance of this process. In this paper, an attempt to analyze this problem is presented based on the analysis of variation of morphological features that are meaningful for humans who use this plant species.

In a previous ethnobotanical study (Casas et al. in press), three general forms of interaction between indigenous people and Stenocereus stellatus were recognised. The first is gathering of products in the wild with apparently no significant impact on populations. The second also affects wild populations during clearance of vegetation for cultivation of maize. In this case, some phenotypes with desirable characteristics are spared while others are removed. This firm of interaction is called management in situ because it occurred in the area occupied by the original wild populations. The third form of interaction is cultivation, mainly in home gardens, where desirable phenotypes are vegetatively propagated and new variation is incorporated through tolerance of volunteer seedlings.

Casas et al. (in press), showed that fruits are the main useful part of this species and colour, flavour, amount of edible matter, peel thickness and spininess of fruits appeared to be significant characteristics distinguished by people, used for classification of variants, of this species and in assessing quality of products in the particular cultural context studied. These morphological features are the basis on which individuals are selected for use and for preferential propagation.

Management in situ and cultivation of this plant thus appears to involve artificial selection (Casas et al. in press). If this is true, these forms of plant manipulation might have changed in some extent patterns of morphological and genetic variation from wild populations. The role of artificial selection causing morphological and genetic divergence has been well documented for cultivation in the studies of plant domestication, though not for forms of management in situ. Examples of forms of management in situ have been described for a number of plant species in Mexico (Bye 1985 and 1993; Caballero 1994; Casas et al. 1994;

Casas & Caballero 1995 and 1996; Casas et al. 1996 and Casas et al. in press). In the case of the legume tree Leucaena esculenta, Casas & Caballero (1996) found that artificial selection has caused significant divergence between wild and managed in situ populations. These authors suggest that domestication in situ is an attractive model for explaining domestication of some plants, especially long-lived perennials. Unfortunately, occurrence of artificial selection and domestication in situ has been little or non documented for other plants.

The purpose of this study was to evaluate the effect of cultivation and management in situ in patterns of morphological variation among populations of Stenocereus stellatus In order to assess this information, morphological features that seem to be directly submitted to human selection were measured and analysed. But also other characteristics, apparently non selected by people, were considered in order to have a reference of patterns of morphological variation in different environmental conditions independently of human intervention. These studies were focused to analyse how individuals from different geographic areas and environments differ in morphology and also to analyse differences between individuals from wild populations and from populations submitted to different ways of management.

STUDY AREA

This study was carried out in two geographic areas: the Tehuacán Valley, Puebla and La Mixteca Baja region in Oaxaca. The Tehuacán Valley is a 10000 square kilometres region, located in the southeast of the state of Puebla and the northwest of the state of Oaxaca in Central Mexico (Figure I). Climate is and and semi-arid with an annual mean precipitation of 300 nun. Tropical deciduous forest and several types of thorn-scrub forest are present. La Mixteca Baja region forms part of the Balsas river basin and maintains important phytogeographic differences from the Tehuacán Valley. It is located south of the Tehuacán Valley, in the northwest of Oaxaca, the southeast of Puebla and the northeast of Guerrero states It is a mountainous region with altitudes ranging from 600 to 3000 meters above sea level and types of vegetation from thorn-scrub and tropical deciduous forests in the lower dry and warm lands to pine forests in the higher wet and temperate areas. Stenocereus stellatus is distributed in the thorn-scrub and tropical deciduous forests where annual mean precipitation is

600 to 800 mm.

POPULATIONS STUDIED

Three groups of populations of <u>Stenocereus</u> <u>stellatus</u> managed in different forms by people were selected in the Tehuacán Valley and La Mixteca I3aja region (Figure 2). General information on environmental and cultural conditions of these populations is summarized in 'Table 1. The first group is composed by five wild populations: 1) Zapotitlán, located within the area of the Botanical Garden "Helia Bravo-Hollis" at Zapotitlán de las Salinas, Puebla, 80 km southwest Tehuacán; 2) Chinango-Wild, located 40 km out of the southern limits of the Tehuacán Valley, within La Mixteca Baja, near the village of Santa Catalina Chinango., Oaxaca; 3) San Juan Raya, located in Rancho San Isidro, near the village San Juan Raya 20 Km west Zapotitlán; San Lorenzo, located in the plateau Mesa de San Lorenzo, a travertine area in the eastern limits of the City of Tehuacán; and 5) Coxcatlán, located in an alluvial valley 10 km southeast the village of Coxcatlán.

The second group is formed by two populations managed <u>in</u> <u>situ</u> 1) Metzontla-Managed, in the Tehuacán Valley, located in agricultural parcels with sandstone soils in an inter-mountain valley in the hills at north of the village of Los Reyes Metzontla, 20 Km south Zapotitlán; and 2) Chinango-Managed from La Mixteca Baja, located in agricultural plots near the wild population of Chinango described above.

The third group is composed by two samples of cultivated individuals in home gardens from 1) Los Reyes Metzontla (Metzontla-Cultivated) and from 2) Chinango (Chinango-Cultivated).

METHODS

SAMPLING OF POPULATIONS.

For purposes of sampling, an individual was considered as a unit of branches emerging together from the soil. For estimating density of population, all individuals were counted. However, because morphological comparisons included reproductive parts, only individuals at reproductive stage were sampled. A pilot study was carried out to measure the smallest size of plants producing buds, flowers or fruits. From this study it was considered that individuals may produce flowers when they are 90 cm or more in lenght. Individuals sampled were marked through metallic labels.

Sample size in wild and managed in situ populations was decided taking into account the espacial dimensions and density of populations. The area of wild populations was delimited through field observations of the limits of occurrence of Stenocereus stellatus. In Zapotitlán and Coxcatlán, limits of the populations were strongly associated to patches of soils derived from sandstones, while in Chinango-Wild, San Juan Raya and San Lorenzo populations were delimited by cleared areas surrounding the populations. The area of populations managed in situ was delimited by the patches of agricultural cleared areas where individuals of S. stellatus were tolerated. The dimensions of the surface occupied by the populations were then measured by metric strings and mapped in scaled paper. The total area of each population was estimated by adding the magnitudes of areas of regular geometric figures approached to the map of the population. It these populations, transects were considered adequate as sampling method in order to represent as much as possible, individuals from different environmental conditions within the population. The length of transects was decided in order to include the longest distance covered by the populations. Considering density of populations, transects were from 5 to 20 in wide.

In cultivated populations the unit of sampling was the home garden. In these units, people propagate vegetative plant materials from different sources of origin and different characteristics. People know which plants are the same clone. Different clones were identified by asking the householders. The number of individuals of each clone were counted for estimation of density of population but only different clones per homegarden were considered in the ,analysis of morphological variation. Home gardens were sampled at random. A number was given to each home garden in a village, and then a list of numbers was drew from a table of random numbers. 10% of the home gardens in a village were sampled (11 in Los Reyes Metzantla and 16 in Chinango).

In total, 165 individuals were included in this study, 69 of them from the five wild populations, 20 from the two populations managed in situ and 76 from home gardens of the two villages described above (Table 1).

MORPHOLOGICAL CHARACTERS ANALYZED.

Table 2 lists the characters analysed. These include binary and multistate qualitative characters as well as discrete and continuous quantitative characters. In the case of quantitative characters at least 3 units (branches, ribs, areoles, spines or fruits) were measured to obtain mean values.

Although length and diameter of the highest branch could be strongly influenced by age and environmental conditions, they were included in the analysis because they give information on size and vigour of the plant, characteristics commonly related to yields in other crops.

Number of ribs was counted always at the middle part of the branch. Width and deepness of ribs were measured also at the middle part of the branch. These characters are commonly used for classification of species of the genus Stenocereus (Bravo-Hollis 1978; Britton and Rose 1920).

Mean number of spines per areole; size of the principal spines, the central biggest spines in areoles, (estimated as the product of the maximum length of the spine and the diameter at the middle part of the spine) and distance between areoles were registered in areoles selected at random. These characters were evaluated in order to analyze whether domestication has affected natural mechanisms of defense of this plant.

Local people distinguish the "boludo" (spherical) and the "alargado" (elongated) shapes of fruits. They consider the "alargado" to be the most common fruit form in wild populations. These fruit forms were considered to have possible meaning for artificial selection.

Four different colours of peel, six different colours of pulp and four pulp flavours distinguished by people were considered in the analysis. Green colour in peel, pulp colours other than red and sweet flavours in fruits of S. stellatus have traditionally higher value than other colours and flavours.

The total number of areoles per fruit was counted. The number of areoles per cm^2 was measured by using a card with holes of 2 cm^2 in the equatorial line of fruits. All complete or incomplete areoles included in the squared holes were counted and then divided by 2. This character was considered in order to evaluate differences in spininess in fruits from wild and cultivated individuals as referred by people.

Thickness of the peel was measured through a calliper always in the equatorial line of the fruits. People consider xoconochtli variants with thick peel to be the most common in the 'wild. They resist rotting better than variants with thin peel and therefore they are sometimes selected for cultivation.

Size of fruits was estimated by measuring maximum diameter and length of fruits and then calculating the volume from the formula $\mathbf{2(2 \pi r^2/h/3)}$ where r was the radius, calculated as 1/2 of the maximum diameter of the fruits, and **h** is the height of a semi-spheric or semi-ellipsoid body, calculated as 1/2 of the maximum length of the fruits. The resulting estimated volume is given in cm^3.

Weight of peel was measured through a precision balance. Proportion of water in the edible portion was measured by weighing samples after dried and then dividing by the weight of the whole edible portion. Proportion of edible portion in fruits was calculated as the ratio of the weight between pericarp and the edible portion. All these characters are related to the amount of edible matter, which generally has a high meaning in artificial selection of all edible plants.

Total number of seeds per fruit was counted as well as their total weight. Mean size of the seeds was estimated through a mean weight of individual seeds (in mg) per fruit and then per individual. This parameter was obtained by weighing a sample of 100 seeds per fruit and dividing by 100 to obtain the individual seed weight. And finally, proportion of seeds in the edible portion was estimated by the ratio of the total weight of seeds and the total weight of the edible portion. It was considered important to explore such characteristics because seeds are edible separately from flesh, and their size is considered an attribute of quality by people (Casas et al in press).

METHODS OF DATA ANALYSIS

A basic data matrix (BDM) was constructed with the 23 morphological characters states for the 165 individuals considered as operational taxonomic units (0115). Numerical values of characters of this matrix were standardised by using the linear translónnalion **y'=(y-a)/b** where **y'** is the standardised value, **y** the variable value, **a** the average of values for this variable in all individuals, and **b** their standard deviation.

Euclidean distance coefficients were calculated between all pairs of individuals on the basis of the 23 characterised variables, and the resultant dissimilarity matrix subjected to cluster analysis (CA) by the unweighted pair group method (UPGMA) (Sneath and Sokal, 1973) in order to recognize similarity and differences between populations in terms of multivariate morphological variation of individuals. Principal Component Analysis (PCA) was performed on a correlation matrix between characters calculated by using the Pearson correlation coefficient (Sneath and Sokal, 1973). Through PCA, variables which contribute most to the total variation were identified. Standardaisation, CA and PICA were carried out using NTSYS-PC version 1.8 (Rohlf, 1993).

Through Discriminant Analysis (DA) the null hypothesis was tested that there are no significant differences between the three groups of populations defined according to the fonns of management (wild, managed in situ and cultivated). Fifteen quantitative characters among the most relevant for explaining variation, according to PCA, were considered in this analysis. The characters with higher discriminatory value were identified. This analysis was performed through the Statistical Graphics System (STATGRAPHICS) programme.

RESULTS

CLUSTER ANALYSIS

As can be seen from Figure 3, the phenogram resulting from Cluster Analysis show five main groups of individuals. Group I is composed of two individuals from the wild population of San Lorenzo. Group II contains 19 cultivated individuals (18 from Chinango, one from Metzontla) and one individual from the managed in situ population of Chinango.

Group III is composed of 50 wild individuals, six cultivated individuals and two from managed in situ populations. This group includes the majority of the wild individuals sampled.

The central part of the phenogram contains two groups. Group IV is composed of 53 individuals, 31 cultivated (40.8% of all the cultivated individuals sampled); 15 from managed in situ populations (75% of all the individuals managed in situ sampled) and only 7 wild individuals(10.1% of the total wild individuals sampled).

Group V is composed of 32 individuals. Twenty are cultivated individuals (26 3% of all cultivated individuals sampled), two individuals are from managed in situ populations (10% of all managed in situ individuals sampled) and ten are wild individuals (14.5% of all wild individuals sampled). Cultivated individuals included in this group constitute 26.3% of all cultivated individuals sampled while managed in situ and wild individuals of this group constitute the 10% and 14.5% of all managed in situ and wild individuals included in this study. Table 3 summarizes the composition of each of these groups and the proportion of wild, managed in situ and cultivated individuals sampled composing each group.

Table 4 shows information on provenance of individuals belonging to each group. It indicates that nearly one thirth of the cultivated individuals from Chinango conform the Group II. Itt also shows that most individuals from wild populations of the Tehuacán Valley are grouped in Group III along with nearly 20% of the cultivated individuals from Metzontla. The wild individuals from Chinango form part of Groups III, IV and mainly (55.6%) of Group Vin which 30% of the cultivated individuals from Chinango are also important. From this table it is also clear that Group IV is mainly composed by individuals from managed in situ populations and most of the cultivated individuals from Metzontla together with 32% of the cultivated individuals from Chinango.

PRINCIPAL COMPONENT ANALYSIS

Figure 4 shows the first plotted against the second principal components. The first principal component separates cultivated individuals, which occupy mainly the right side of the plot., from wild individuals, which occupy mainly the left side of the plots. Most individuals managed in situ occupy the central part of the plots.

Eigenvalues resulting from the analysis, indicating that about 53% of the variation is explained by the first three principal components, mainly the first one (34%). Table 5 shows the eigenvectors for the first three principal components. Fruit size, density of spines on fruits, peel weight and the total weight of seeds per fruit explain most of the variation in the first principal component. Peel thickness is the most important character in the second principal component. In the third principal component, the highest values correspond to the number of ribs and number of spines per areole, but these values are relatively low.

DISCRIMINANT ANALYSIS

Table 6 shows the discriminant scores resulted from the discriminant functions when groups were tested according to their form of management This table shows that the three groups of populations are significantly different. The classification resulting from Discriminant Analysis is presented in Table 7 and it can be visualized also in the plot of Figure 5 This classification indicates that about 75% of individuals of each group are different from individuals of the other two groups and the remaining individuals share morphological similarity with individuals of the other two groups. Standardized and unstandardized discriminant function coefficients for characters analyzed are shown in Table 8. This table indicated that total weight of seeds per fruit, peel thickness and weight as well as density of spines in fruits are the most important characters in the first discriminant function while the proportion of edible portion in fruits, fruit size, peel thickness and seed size are the most important characters in the second discriminant function.

DISCUSSION

Principal Component and Discriminant Analysis showed that the most relevant characters for classifying groups of individuals were: 1) fruit size (bigger among cultivated individuals); 2) density of spines in fruits (higher in fruits of wild individuals); 3) peel weight (higher amount in the bigger fruits of cultivated individuals); 4) peel thickness (thicker in wild individuals); 5) total weight of seeds (higher in fruits of cultivated individuals) and 6) seed size (bigger in cultivated individuals). All these characters are selected by people. In contrast, vegetative characters were not relevant in classification of individuals, probably because they were not significantly variable or they did not present regular patterns of variation.

Characters such as flavour and colour of fruit pulp, which are relevant in traditional classification of this species, did not appear relevant in the morphological analyses performed. In the case of pulp colour, this could be explained because of the low frequency of occurrence of colours other than red. This was reflected in the sample, in which nearly 90% of individuals presented red pulp. In the case of flavour, a more precise method for measuring arnounts of sugars could be required.

Multivariate statistical analyses classified individuals of Stenocereus stellatus in part according to their geographic provenanceac but mainly according to their form of management. The five wild populations analysed are located in areas with important environmental differences, however, nearly 75% of these individuals (72% according to Cluster Analysis and 75% according to Discriminant Analysis) are morphologically similar and significantly different from the managed in situ and cultivated individuals. However, Cluster Analysys showed that there are differences between wild populations from the two main geographic areas. Thus, Table 4 grouped almost 90% of wild individuals from the Tehuacán Valley' in group III while almost 80% of the wild individuals from La Mixteca Baja were in groups IV and V.

Most of individuals from managed in situ populations were grouped together in all the analyses, and generally they may considered also as a defined group. However, Cluster Analysis grouped them along with about 40% of the cultivated individuals while Discriminant Analysis classified 75% of them together with near 15% of the wild and 20% of the cultivated individuals (Table 7). This group of individuals seems to have diverged from the most common wild types but never as strongly as some cultivated individuals.

Discriminant Analysis classified 73.68% of cultivated individuals conforming also a defined group together with 8 wild and 2 managed individuals (Table 7). Cluster Analysis distinguished a group of cultivated individuals from Chinango (almost 50% of individuals from this population) that are strongly different from the remining individuals. These are individuals presenting marked domesticated characteristics such as the biggest sizes, the lowest fruit spininess and different pulp colours. However, another group of cultivated individuals from Chinango was similar to the cultivated individuals from Metzontla and individuals from the managed in situ populations.

Some cultivated individuals were similar to wild individuals. Cluster Analysis included

6 cultivated individuals in the main group of wild individuals ('Table 3) while Discriminant Analysis included 5 cultivated individuals within the group "wild". All these individuals, as informed by people, were brought to home gardens from wild populations. Equally, some wild individuals similar to cultivated individuals. Cluster Analysis identified 17 from Chinango, San Lorenzo and Coxcatlán (Tables 3 and 4) and Discriminant Analysis identified 8 individuals. This indicates that although in a low frequency, cultivated-like phenotypes occur in wild populations and vice versa.

From this information, it is important to notice that morphological similarity between some individuals was maintained even when they are from different geographic areas with important environmental differences. Equally, it is noticeable that some cultivated individuals that were introduced to home gardens from wild populations maintained their similarity with individuals from wild populations. And finally, it is also important to note that morphological variation among variants is expressed within a same home garden. All these elements permit to suggest that morphological variation analysed, especially characteristic of fruits, in this species has an important genetic component. This indicates that changes in patterns of morphological variation may be inherited and that domestication as an evolutionary process is occurring through manipulation of this plant by people.

The significant morphological differences between wild, managed in situ and cultivated populations suggest that patterns of variation have been influenced by human management. This means that evolution of this species under domestication has achieved a significant morphological divergence from wild populations. This divergence is especially marked between wild individuals and individuals cultivated in home gardens where manipulation of plants by planting and replacing of variants is relatively intense. The divergence is also significant between wild and managed in situ populations, but not as marked as with cultivated in home gardens. This form of management is mainly directed to increase frequencies of good phenotypes existing in wild populations.

A similar pattern of morphological divergence between wild, managed in situ and cultivated populations was found by Casas & Caballero (1996) in Leucaena esculenta. In that case, the strongest divergence occurred between wild and managed in situ populations but cultivation of L. esculenta in home gardens was not as important as in the case of Stenocereus stellatus. These two case studies illustrate how the intensity of manipulation of plants by humans may influence the degree of morphological divergence from wild populations.

The cases of Leucaena esculenta and Stenocereus stellatus also illustrate how changes in patterns of morphological variation in long-lived perennial plants have been carried out by Mesoamerican people not only through cultivation in home gardens but also through forms of management of wild populations in situ. Casas & Caballero (1996) suggest that domestication in situ is an attractive model by which to investigate this process in perennial plants, especially outbreeders such as L. esculenta because of the difficulties for fixation of desirable characters by direct sowing of seeds from desirable phenotypes. However, the case of Stenocereus stellatus suggests that the spectrum of plants domesticated in situ could be wider. Recent studies by the authors reveal that Stenocereus stellatus is also an outbreeder (unpublished information). However, fixation of desirable characters in this species by people is carried out mainly through vegetative propagation.

As mentioned, different forms of management in situ, including tolerance, enhancing and protection, have been described for other perennial plants and also for a number of annual plants in Mexico (Bye 1985 and 1993; Caballero 1994; Casas et al. 1994; Casas & Caballero 1995 and 1996; Casas et el. 1996; Casas et el. in press). Management in situ seems to be an extended pattern of plant manipulation in Mesoamerica and although occurrence of artificial selection and domestication in situ has been little documented, the cases analysed here suggest that plant domestication in situ could be and have been a common form of plant domestication in this cultural area.

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TABLE 1. GENERAL INFORMATION ON POPULATIONS OF STENOCEREUS STELLATUS SAMPLED

Population	Elevation (miters)	Annual mean temp. (°C)	Annual mean rain fall (mm)	Origin of soils	Habitat	Sampled area (m^2)	Density of pop. (individ./ha.)	No. of indiv. analysed	Labels
WILD									
Zapotitlán	1550	21.2*	450*	sandstones	thorn-scrub forest	1700	142	24	S1-S24
Chinango-W	1700	20.6*	720.5*	sandstones	tropical deciduous forest	3060	49	9	S25-S33
S. J. Raya	1800	20.9*	649.7*	limestones	thorn scrub-forest	6000	22	5	S34-S38
Sn. Lorenzo	1700	19.1*	590*	limestones	thom-scrub forest	5000	34	18	S39-S56
Coxcatlán	1000	23.8*	440.6*	alluvial	thom-scrub forest/ tropical deciduous forest	3000	567	13	S57-S69
MANAGED									
Metzontla-M	2000	17.2**	527.9**	limestones	agricultural area	1000	120	12	M1-M12
Chinango-M	1700	20.6*	720.5*	sandstones	agricultural area	4000	72.5	8	M13-M20
CULTIVATED									
Metzontla C	1900	17.2**	527.9**	aluvial	Home gardens	3125	780	26	C1-C26
Chinango-C	1600	20.6*	720.5*	aluvial	Home gardens	6500	94	50	C27-C76

*Based on García 1988 **Based on Valiente 1991

TABLE 2. MORPHOLOGICAL CHARACTERS ANALYSED

Characters	Num. of parts measured per ind.	Units of measurements
1. Length of the highest branch	1	cm
2. Diameter of the highest branch	1	cm
3. Number of ribs	5 branches	numeric
4. Rib width	3 ribs	cm
5. Rib deepness	3 ribs	cm
6. Number of spines per areole	5 areoles	numeric
7. Size of the principal spines	10 areoles	cm^2
8. Distance between areoles	5 pairs of areoles	cm
9. Fruit form	Single	1=spherical; 2-=elongated
10. Peel colour	Single	1=-red; 2=green-reddish; 3=green; 4=yellow
11. Pulp colour	Single	1-=red; 2= pink; 3=purple; 4-yellow; 5=orange; 6=white
12. Pulp flavour	Single	1=sour; 2=sweet-sour; 3=sweet; 4=insipid
13. Total number of areoles per fruit	3-5 fruits	numeric
14. Number of areoles per cm^2	3-5 fruits	numeric
15. Peel thickness	3-5 fruits	cm
16. Fruit size	3-5 fruits	cm^3
17. Peel weight	3-5 fruits	g
18. Proportion of water in fruit pulp	3-5 fruits	numeric fraction
19. Proportion of pulp	3-5 fruits	numeric fraction
20. Number of seeds per fruit	3-5 fruits	numeric
21. Mean *size* of seeds	100 seeds	mg
22 Total weight of seeds per fruit	3-5 fruits	g
23. Proportion of seeds in pulp	3-5 fruits	numeric fraction

TABLE 3. COMPOSITION OF GROUPS RESULTING FROM CLUSTER ANALYSIS

GROUPS	I	II	III	IV	V
Number of trees in groups	2	20	58	53	32
% of trees sampled	1.2	12.1	35.2	32.1	19.4
Number of wild trees	2	0	50	7	10
% of the group	100.00	0.0	86.2	13.2	31.3
% of wild trees sampled	2.9	0.0	72.5	10.1	14.5
Number of managed *in situ* trees	0	1	2	15	2
% of the group	0.0	5.0	3.5	28.3	6.3
% of managed *in situ* trees sampled	0.0	5.0	10	75	10
Number of cultivated trees	0	19	6	31	20
% of the group	0.0	95.0	10.3	58.5	62.5
% of cultivated trees sampled	0.0	25.0	7.9	40.8	26.3

TABLE 4. PERCENT OF INDIVIDUALS FROM EACH POPULATION BELONGING TO EACH GROUP RESULTED FROM CLUSTER ANALYSIS

Population	G I	R II	O III	U IV	P V
Zapotitlán	0.0	0.0	95.8	4.2	0.0
Chinango-W	0.0	0.0	22.2	22.2	55.6
Sn. Juan Raya	0.0	0.0	100.0	0.0	0.0
Sn. Lorenzo	11.1	0.0	50.00	22.2	16.7
Coxcatlán	0.0	0.0	84.6	0.0	15.4
Metzontla-M	0.0	0.0	16.7	66.7	16.6
Chinango-M	0.0	12.5	0.0	87.5	0.0
Metzontla-C	0.0	3.9	19.2	57.7	19.2
Chinango-C	0.0	36.0	2.0	32.0	30.0

TABLE 5. EIGENVECTORS RESULTED FROM PRINCIPAL COMPONENT ANALYSIS.

CHARACTER	PCI	PC2	PO
Length of the highest branch	0.354	0.067	0.336
Diameter of the highest branch	0.661	-0.199	-0.421
Number of ribs	-0.139	0.061	-0.684
Width of ribs	0.630	-0.194	0.107
Rib deepness	0.707	-0 313	0.156
Number of spines per areole	-0.124	0.120	-0 651
Size of principal spines	0.227	0.034	-0.205
Distance between areoles	0.409	-0.090	0.471
Fruit form	0.273	-0.139	-0.029
Peel colour	0.517	-0.125	-0.152
Pulp colour	0.556	-0.266	0.229
Pulp flavour	0.405	0.090	-0.057
Total number of areoles per fruit	0.199	-0.070	0.126
Number of areoles/cm^2	-0.816	-0.130	0.199
Peel thickness	-0.321	-0.813	0.087
Fruit size	0.912	-0.058	0.037
Peel weight	0.810	-0.303	0.066
Proportion of water in fruit pulp	0.725	0.548	0.139
Proportion of pulp in fruits	0.721	0.611	-0.084
Number of seeds per fruit	0.629	-0.470	-0.220
Mean size of seeds per fruit	0.735	-0.000	-0.152
Total weight of seeds per fruit	0.838	-0.326	-0.192
Seeds weight/edible portion weight	-0.568	-0.695	-0.163

TABLE 6. DISCRIMINANT ANALYSIS FOR WILD, MANAGED *IN SITU* AND CULTIVATED POPULATIONS OF *STENOCEREUS STELLATUS*.

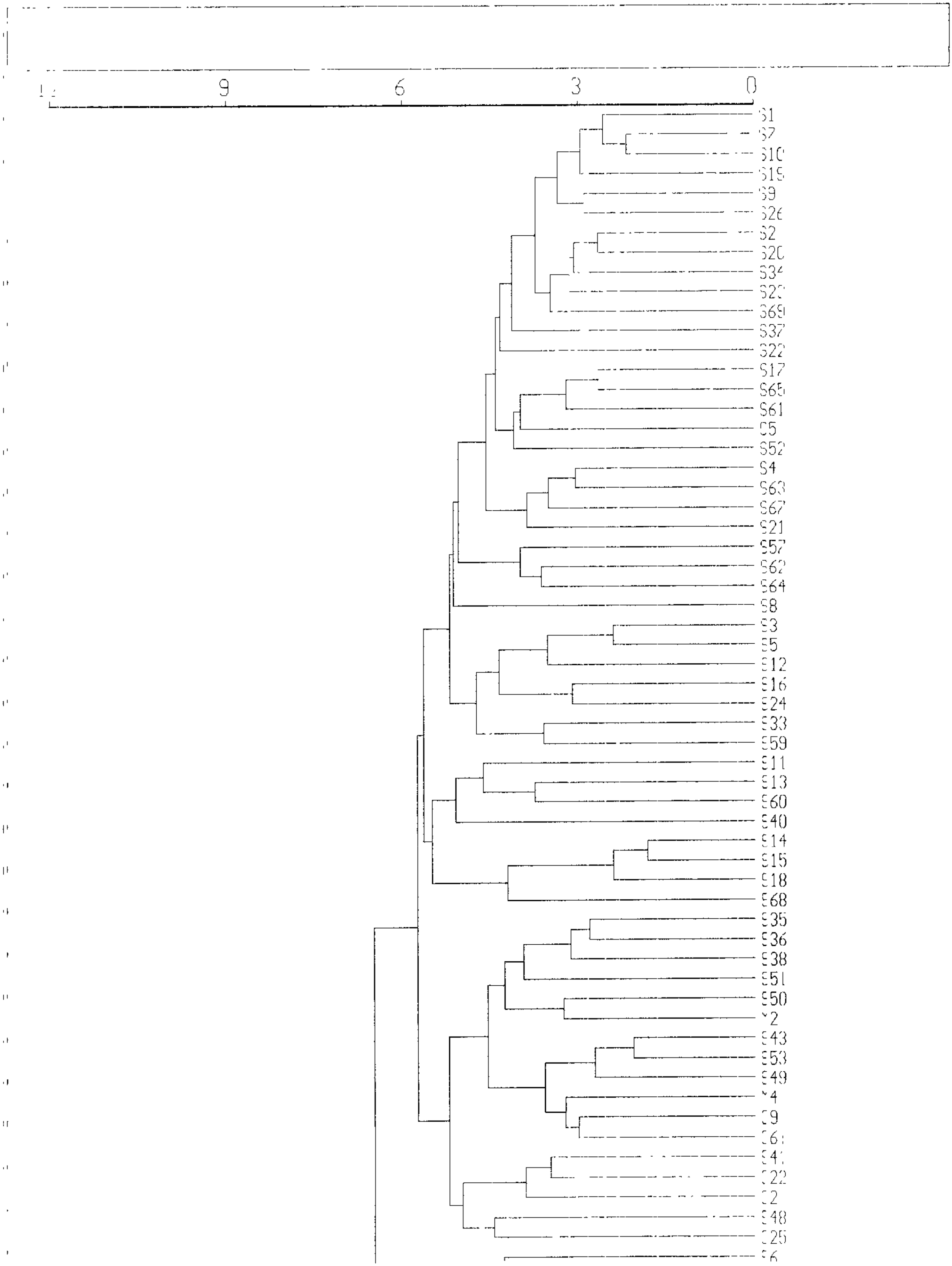
Discriminant Function	Eigenvalue	Relative Percentage	Canonical Correlation	
1	13288797	85.67	0.75539	
2	0.2222143	14.33	0.42640	
Functions Derived	**Wilks Lambda**	**Chi-Square**	**DF**	**Sig. Level**
0	0.3513222	162.13799	30	0.00000
1	0.8181871	31.10295	14	0.00536

TABLE 7. CLASSIFICATION OF INDIVIDUALS OF WILD, MANAGED *IN SITU* AND CULTIVATED POPULATIONS ACCORDING TO DISCRIMINANT ANALYSIS

Actual	Predicted Group							
Group	Wild		Managed *in situ*		Cultivated		Total	
	count	%	count	%	count	%	count	%
Wild	51	73.91	10	14.49	8	11.59	69	100.00
Managed *in situ*	3	15.00	15	75.00	2	10.00	20	100.00
Cultivated	5	6.58	15	19.74	56	73.68	76	100.00

TABLE 8. DISCRIMINANT FUNCTION COEFFICIENTS RESULTING FROM DISCRIMINANT ANALYSIS (STD=STANDARDIZED USTD=UNSTANDARDIZED).

Character	Discriminant Functions			
	1		2	
	USTD	STD	USTD	STD
Diameter of the highest branch	0.07676	0.12784	-0.05044	-0.08400
Number of ribs	0.13525	0.16809	0.18522	0 23019
Width of ribs	0.62984	0.34720	1.44075	079423
Rib depth	0.13122	0.05274	-0.78770	-0.31657
Number of spines per areole	-0.04364	-0.10239	0.22616	0.53061
Number of areoles/cm2 in fruits	-0.55203	-0.42102	-0.08260	-0.06300
Peel thickness	-6.07451	-0.56823	9.35063	0.87469
Fruit size	-0.01544	-0.34807	-0.04723	-1.06501
Peel weight	0.08130	0.56715	0.06937	0.48390
Proportion of water in pulp	-1.37550	-0.07256	-7.21592	-0.38064
Proportion of edible portion	-0.26168	-0.02789	14.6956	1.56605
Total number of seeds per fruit	-0.00058	-0.18886	-0.00182	-0.59515
individual seed weight	-0.68651	-0.16496	-3.32955	-0.80004
Total weight of seeds per fruit	1.24333	0.57073	1.41997	0.65181
Seeds weight/edible portion weight	0.48451	0.01891	-2.22093	-08668



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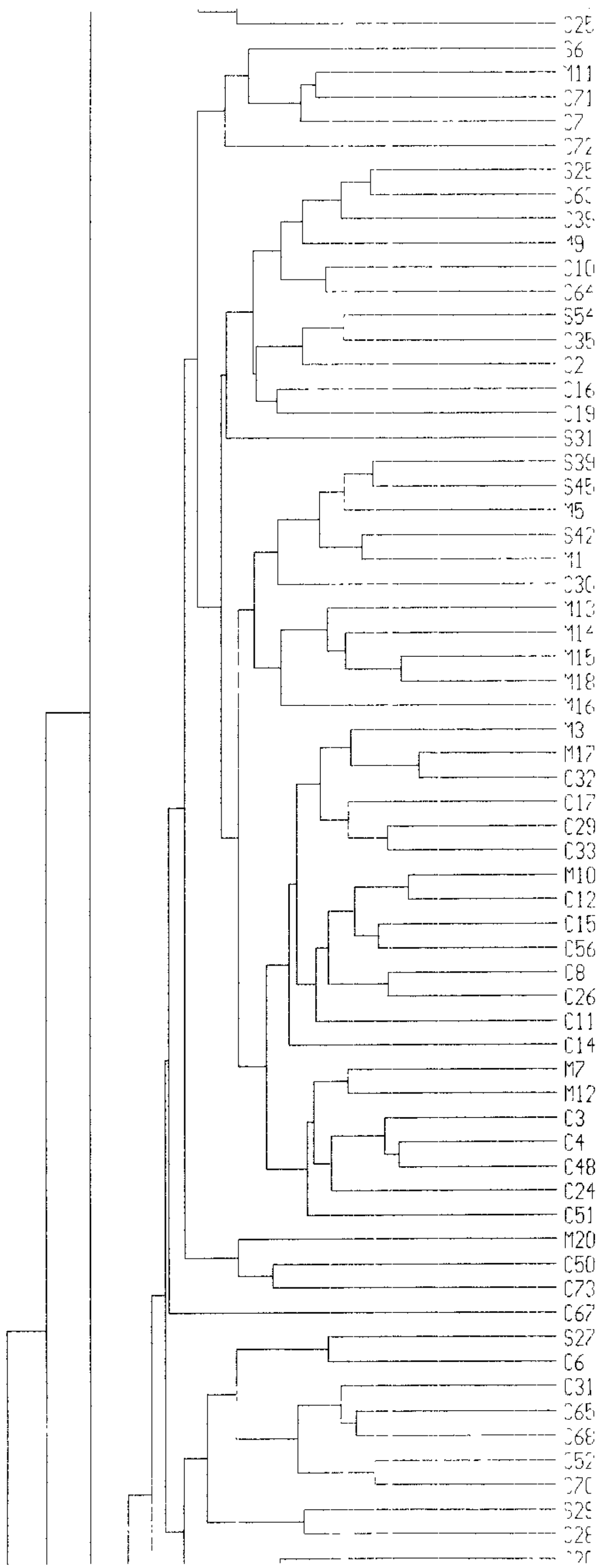

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C26
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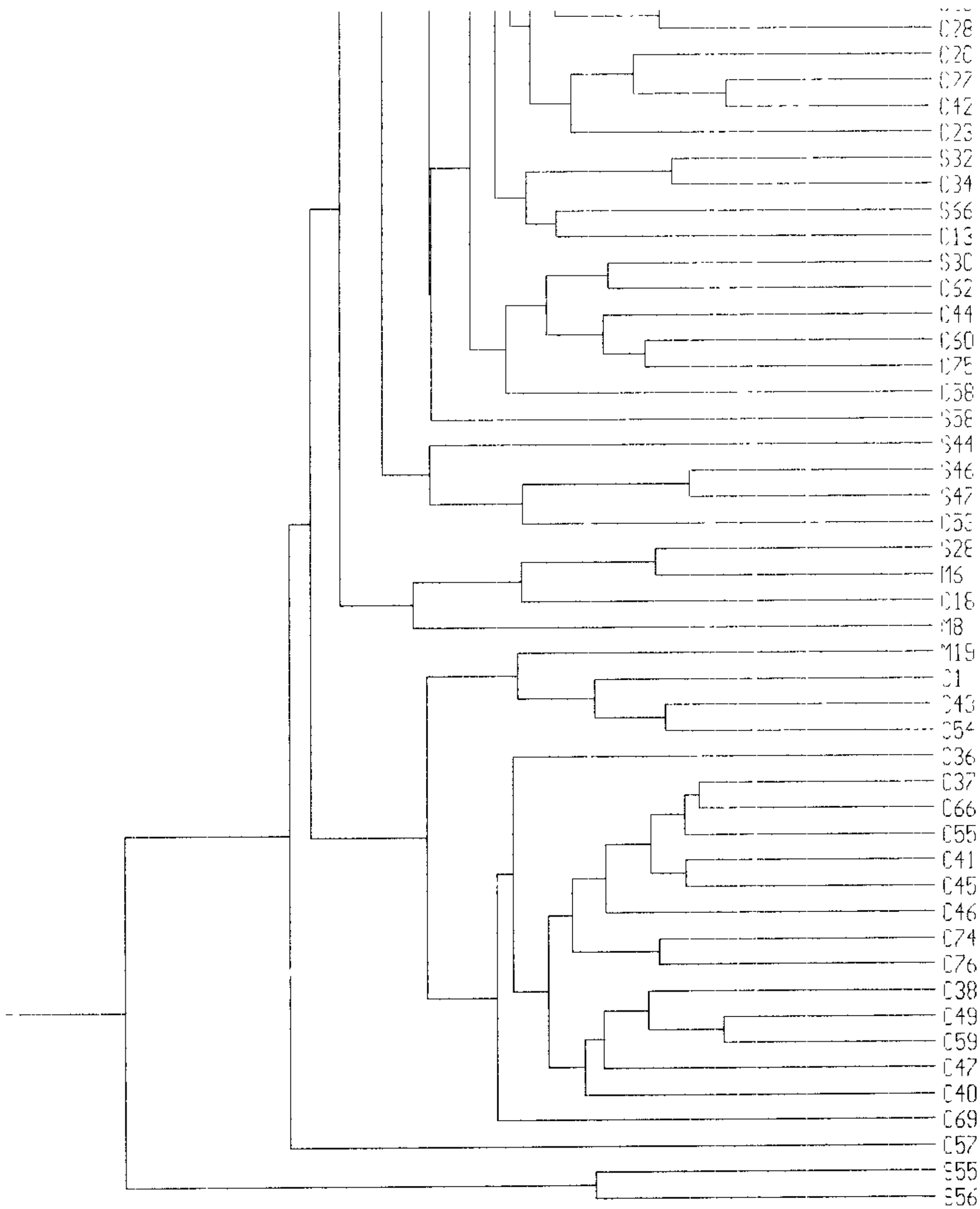
C31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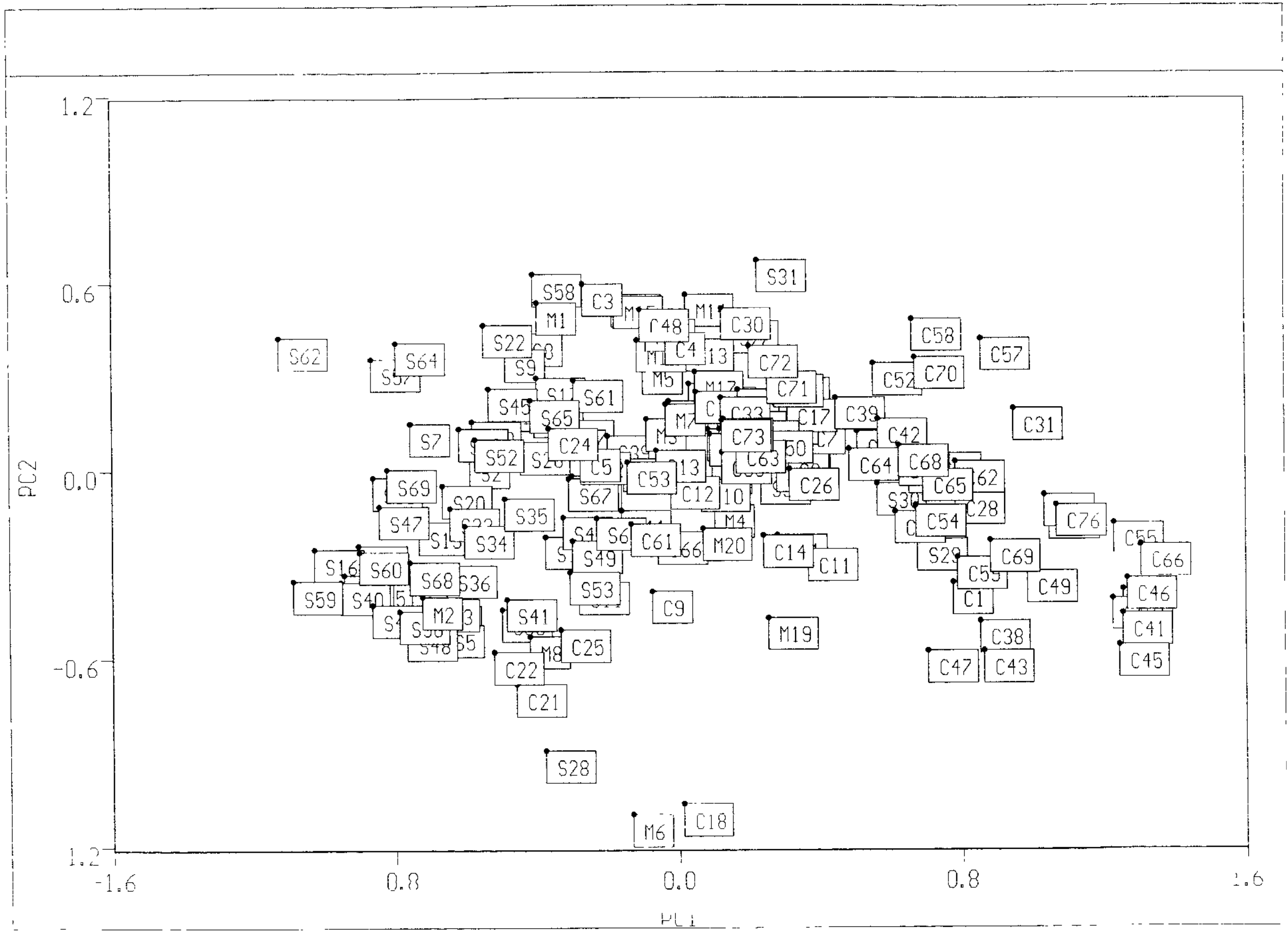

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S35
M4
C54
C76
S47
S34
S6
C61
M20
C14
C11
S29
C69
C55
C66
S16
S60
S49
S59
S40
S68
S36
S53
C9
C59
C49
C46
C1
M2
S41
M19
C41
C38
C25
M8
C47
C43
C45
C22
C21
S28
C18
M6

Apéndice 5.

GENETIC VARIATION IN POPULATIONS OF *Stenocereus stellatus*

1. INTRODUCTION.

In evolutionary processes, natural or artificial, phenotypes may be submitted to selection pressures, and their frequencies may change as result of such pressures. But because phenotypic expression of characters is regulated by both environmental and genetic factors, a real evolutionary change is considered only when phenotypic changes are inherited, that is, when changes involve genotypes. Domestication is an evolutionary process and, therefore, only genotypic changes caused by artificial evolutionary pressures can be considered as real domestication.

For analysing domestication processes, therefore, it seems to be not enough to know how human selection pressures may cause changes in frequencies of morphological features in populations. It is also necessary to evaluate consequences of these processes in the genotypic structure of populations. However, because changes in phenotypic frequencies are not necessarily associated to changes in genotypic frequencies, not always these last changes are directly observable. Generally, some studies are recquired first to characterise genetic component of phenotypic features. A possible way to evaluate if phenotypic differences are due to environmental or genetic causes is by growing together individuals with different morphological features (i.e. common glass house or reciprocal transplantation experiments) If phenotypic expression of such characters is consistently different, it can be assumed that morphological differences are caused by genetic differences. In short life cycle organisms such as bacteria, flies or annual plants this type of experiments are viable and it is possible to get information in short time. But in long life cycle plant species, obtaining information through this kind of methods could take a long time, especially when variation of reproductive structures is analysed. In some organisms it has been possible to identify alleles associated to morphological features. In those cases, genotypic frequencies can be analysed by directly counting phenotypic frequencies. But because this approach is based on observation of segregation of characters in progenies, it could also take long time when long life cycle organisms are studied.

Analyses of presence and absence of phenotypes in different and in similar environments, may help to evaluate the degree of influence of environment on variation of particular morphological features in long lived perennials. However, biochemical markers such as proteins and molecular markers such as DNA seem to be valuable sources of information for amore precise evaluation of genetic constitution of organisms, phenotypic plasticity and genotypic changes in populations caused by evolutionary processes.

At present it is possible to identify molecular markers as being genes regulating the expression of particular morphological features. However, isolation and characterization of genes contributing to variation in particular phenotypic features, involves still a very hard work, and information is available only for few species (Avise, 1994). Isozymes or fragments of DNA more commonly analyzed do not directly account evolutionary processes of particular morphological features. They are presumed to be a random sample of the genome and a significant portion of the genome is probably not expressed and, consequently, not exposed to selection. Furthermore, the spectacular morphological changes sometimes achieved by domestication, generally concern a very small portion of the genome. Therefore, by analyzing genetic markers at random, answers cannot be pretended on how artificial evolutionary processes have affected frequencies of genotypes related to morphological features desirable for humans. Nevertheless, the study of biochemical and molecular markers has contributed greatly to understanding of evolution not by direct association with selected phenotypic characters but by randomly sampling the amount of genetic variation both neutral and selected. These markers account for the characterization of genetic variation in populations, the raw matter of evolutionary processes, and changes caused on it by evolutionary factors. In studies of domestication of plants, these markers have supported the "traditional endeavour of crop evolution studies" (Gepts, 1993): 1) identification of the wild ancestor of crop plants, 2) study of the *status* of organization of genetic diversity in crop species and 3) analysis of introgression between wild and cultivated plants.

Through biochemical and molecular markers it is possible to study random samples of alleles and to analyse the *status* of genetic variation within and among populations. The amount and kind of genetic variation in a population are potentially affected by a number of factors, such as selection, migration, mutation, genetic drift and the mating system (Hedrick, 1983). These factors may increase or reduce the genetic variation depending upon the particular situation while combination of two or more of these factors can generate virtually any amount or pattern of genetic variation (Hedrick, 1983). Through domestication, human manipulation of plants may influence one or more of these factors. Thus, comparisions of patterns of genetic variation among wild and domesticated populations may be useful to visualize particular evolutionary trends of genetic variation as well as factors influencing such trends under domestication. Comparisons of random genetic variation may also be useful to examine genetic similarities and differences between populations, that are important to analyse, phylogenetic relationships and evolutionary divergences. According to Gepts (1993), the major advantage of molecular and biochemical markers is their presumed neutrality which allows to distinguish those similarities that are due to common ancestry from similarities due to convergence.

Based on analysis of allozyme polimorphism, this study was aimed at comparing patterns of genetic variation in populations of *Stenocereus stellatus* from different environments and different forms of management. Different measures of genotypic and allelic variation were estimated and compared between populations in order to analyse possible geographic and human cultural effects on amounts and patterns of genetic variation. Genotypic and allelic frequencies were compared between individuals and populations in order to analyse genetic similarity and divergence between them. Patterns of genetic variation were compared with patterns of morphological variation as analysed in the former chapter in order to explore correlations between genetic and morphological similarity and divergence.

2. METHODS

SAMPLING OF POPULATIONS

The same populations analysed in the study of morphological variation were included in this analysis. Population sampling strategies were therefore as describede before. Preliminary laboratory testings suggested that fresh tissue of stems was the most convenient material for the study of isozyme polymorphysm. Considering this information, pieces of branches or complete young branches from each individual sampled were collected. Branches collected were transported to the Botanical Garden of the National University of Mexico (U.N.A.M.). There, they were immediately protected against pests and fungi by using methilic paration, a wide spectrum protector, and then they were left to dry parts affected by cuttings for avoiding bacterial and fungal infections. The plant material was maintained in this conditions in a greenhouse for at least three weeks. Then, branches were planted in pots containing sustrate composed by 30% clay, 40% slime and 30% organic soil. Plants in pots were also maintained in a greenhouse. In such conditions, samples from these plants were used for the present study but they were also preserved as a collection of living plants as a reference to this study and as a source of information for future research.

Not all sampled individuals were included in this study. Some populations were sub-sampled in order to analyse at most 30 individuals per population. Individuals from sub-sampled populations were chosen in progressive order as collected in order to obtain information on distribution of genotypes in the space and area covered by them. Mortality of branches collected was about 10 % generally, but mortality affected especially samples of some populations (particularly Metzontla and Chinango managed *in situ*, Coxcatlán and Chinango wild). For this reason some individuals expected were no considered in this analysis Table 1 indicates individuals per population inculded in this study. Labels included there correspod with those included in studies of morphological variation.

ISOZYME POLYMORPHISM ANALYSIS.

Extraction of samples.

Five different extraction buffers and destilled water were tested in order to select the one with the best results. Buffers tested were the one used by García de León (1985); one proposed by Hamrick (personal communication); the one used by Cheliak and Pitel (1984); one adapted by Fournier (personal communication) for extraction of samples from species of *Abies* and the one used by Goodall and Stoddard (1989) for the study of *Rhyzophora.* This last buffer achieved the best results and was used for the whole study.

Pieces of 1 cm of ribs of fresh plant material were used as samples. Samples were collected by using seassors from living material maintained in a greenhouse. During collectings, seassors were cleaned with destilled water first and then with 96% ethanol after cutting each sample. After collected, each sample was immediately put on labelled test tubes which were sealed with parafilm and then immesed in ice within a portable cooler box. The best results were obtained when, after collected, samples were freezed for 30 minutes at -76^{0}C before grounding. Freezed samples were grounded for 25 seconds in a homegenizer. Homogeneizer generates heat that caused dennaturalization of proteins. However, when grounding test tubes were immersed in ice and samples were freezed, these problems were solved. Extraction buffer (5 ml per sample) was added just before grounding each sample. These: proportions of amount of tissue and extraction buffer were important for good results. More tissue sample caused moucilage problems while more extraction buffer caused weak stoning of bands in gels. Samples so grounded were freezed again. After grounded, freezed samples were put in a box with ice in order to make slowly the process of melting. Proceeding so, an aqueous phase separated first and wicks could be loaded with this sample. This proceeding for separation of phases in cool helped to avoid problems with the mucillaginous phase without need of centrifugation. Loaded wicks were immediately freezed and stored at -76°C. Wicks so stored presented good enzyme activity even after two months.

Gel and electrode buffers.

Twelve different systems of gel and electrode buffers were experimented (Table 2). However, the best resolution resulted from Poulik system (Hakim-Elahi, 1976)

Enzyme systems analyzed.

Preliminary assays were carried out in order to test resolution of different enzymes. Enzymes resolved by Parker and Hamrick (1992), for the columnar cactus *Lophocereus* scholia, were considered first. These enzymes were: diaphorase (DIA), menadione reductase (MNR.), triosephosphate isomerase (TPI), esterase (FE), phosphoglucomutase (PGM). glutaunic oxalic transaminase (GOT), isocitrate dehydrogenase (IDH), phosphoglucoisomerase

TABLE 1. INDIVIDUALS PER POPULATION ANALYSED.

Population	Individuals	Total
Zapotitlán	2(S2); 3; 4(S3); 5(S4); 6; 7; 8 (S5); 9 (56);10(57); 11 (S8); 13 (S10); 14; 15 (S11); 16; 17; 18 (S12); 19 (S13); 20 (S14); 21 (S15);22 (S16); 23; 24 (S17); 25 (S18);26; 27; 28 (SW); 29 (S20); 30; 31 (S21); 33	30
Chinango-W	1 (S25); 3; 4; 5; 6; 8 (S26); 9; 10 (S27), 11(S28); 14; 15, 16 (S31); 17; 18 (S32)	14
S.J Raya	1; 2; 3; 4 (S34); 5; 6; 7 (S35); 8 (S36); 9; 10;11; 12 (S37); 13; 14; 16; 17; 18 (S38)	17
San Lorenzo	1 (S39); 2 (S40); 3 (S41); 4 (S42); 7; 8; 9;10 (S44); 11 (S45); 12; 13; 14; 15 (S46); 16 (S47); 17 (S48);18 (S49); 19 (S50); 20; 21 (S51); 22; 23; 24; 26 (S53); 27; 28(S54); 29 (S55); 30 (S56)	27
Coxcatlán	1; 2; 3; 4 (S57); 7 (S59); 8 (S60); 9 (S61); 10; 11(S62); 14; 15 (S63); 16 (S64); 18; 19; 20; 21; 23; 25; 27; 28; 29; 30; 31 (566);32;33;34;36;37	28
Metzontla-M	3 (M3); 6 (M6); 8 (M8); 9 (M9); 10(M10); 11 (Ml1)	6
Chinango-M	1; 3; 4; 5 (M13); 7 (M15); 8 (M16);9; 10 (M17); 11; 12; 15; 16; 17 (M19); 18 (M20); 22; 23	l6
Metzontla-C	1 (Cl); 2 (C2); 3 (C3); 4 (C4); 6 (C5); 7 (C6); 8 (C7); 9 (C8); 10 (C9); 11 (C10); 12 (C11); 13 (C12); 14 (C13); 15 (C14); 16 (C15); 17 (C16); 18 (C17);19 (C18); 20 (C19); 21 (C20); 22 (C21); 23 (C22); 24 (C23);25 (C24); 26 (C25); 27 (C26)	26 (260)
Chinango-C	1; 2 (C27); 4 (C28); 6 (C29); 9 (C32); 11 (C34); 13 (C36); 15 (C38); 16 (C39); 17 (C40); 18 (C41); 20 (C43); 21 (C44); 22 (C45); 24 (C47); 26 (C49); 27 (C50); 28 (C51); 29 (C52); 30 (C53); 33 (C56); 34; 37; 38 (C58); 39, 42 (C59); 43 (C60); 48 (C65); 49 (C66); 64 (C73)	30 (169)

(PGI), and malate dehydrogenase (MDH). Then, other enzymes, in total 25, were also tested (Table 2) The best results were obtained with 8 enzymes: acid phosphatase (ACPH); diaphorase (DIA); esterase (EST); malate dehydrogenase (MDH); menadione reductase

(MNR); nicotinamide adenine dinucleotide dehydrogenase (NADHDH); phosphoglucise isomerase (PGI) and rubisco (RUB). These enzymes were analysed for a total of 194 individuals from the nine populations studied. A total of 45 genotypes and 24 alleles were identiifyed and analysed.

General procedure.

General procedure was based on that suggested by García de León (1985), however particular modifications were carried out in several steps of the process. Stock solution of the extraction buffer was prepared and stored at -20°C, but it was always used within one week after preparation. The complementary solution was prepared and mixed with the stock solution just before grounding of samples. Extraction of samples was carried out one to three days before electrophoreses, although part of the wicks was stored considering that repetitions of electrophoresis could be recquired.Gel and electrode buffers were prepared one day before running the gels. Gels were prepared one day before running electrophoreses (late afternoon). For preparation of gels, 50 g of starch and 12 g of sucrose were suspended in 400 ml of gel buffer in a round bottom flask. Suspension was heated over a medium strong naked gas flame while constantly and vigorously swirling until small bubbles appeared. Then, the flask was connected immediately to a vacuum line for 20 seconds to degas the gel. The gels were rapidly poured into moulds, immediately removing inclusions or bubbles with a microspatule. After one hour at room temperature, the gels were put in a at 4^{0}C fridge for one hour and then covered with cling film and stored at room temperature over night. The gels were refrigerated one hour before loading samples.

For loading the gels, they were cut across the origin line. This extreme was considered the cathodal end. The two pieces of gels were separated 1 cm, and the wick insertion guide was aligned along the larger gel slice. Eppendorf tubes with freezed wicks were put in ice to maintain them at low temperatures while loding the gels. Wet wicks were handled always by using forceps which were washed and cleaned after loading each sample. Two wicks wet with bromophenol blue were placed at the extremes of the gels as markers of front migration. Three other wicks wet with sample from individual number 2 from Zapotitlán population were placed at the extremes and the middle of the gel as reference pattern in all gels.

The loaded gels were put in the tank. Each end of the gels was connected to the corresponding electrode reservoir using a sponge wad. The tank was put in refrigerator, covered with cling film and then connected to the power pack. A constant 40 mA current was applied making a record of the corresponding voltage. After 15 minutes, the wicks were removed, more time caused overstainning of bands. A plastic drinking straw was inserted between the cathodal end of the gels and the mould, to compress the two sections of the gels and to prevent gaps in the origin line. Then, the gels were replaced in the tank, and were covered with a bag containing freeze jellies. The gels were run at constant current (40 mA). The runs were ended when the front migrated 9 cm after 5 hours approximately.

Taking the gel out of the tank, the smaller pieces of gels were removed. Elastic bands were used to secure five spacers 1 mm thick on each side of the gels. A hacksaw was used to slice the gels, holding the tool so that the taut wire was pressing firmly against the two spacers on the cathodal side of the gels, cutting with one smooth, unhesitating movement. Removing another pair of spacers, and cleaning the wire with a moist tissue paper, operation was repeated four or five times in order to get the same number of slices per gel (the top slices were discarded). Small circles in the left and upper comer of the gels were made in order to identify the order of the samples. Slices were separated from each other carefully by using hands. Slices so separated were put immediately in labeled boxes containing stains, and specific directions on recipes were followed for each stain.

Staining activity was checked periodically, gently shaking the boxes. When adequate staining occurred, the stains were discarded, and the gels were rinsed two or three times with current water. Slices were fixed in 25-35 ml of 70% aqueous ethanol and stored in a refrigerator over night. Then, slices were wrapped in cling film labelled scored and photographed.for few months after information is recorded or immediately scored and photographed.

Data analysis

A comparison of genetic diversity between populations was carried out. Heterozygosity or gene diversity index **H** (Nei, 1987) was calculated per locus, and a mean of loci heterozygosity was calculated per population as a measure of the magnitude of isozyme polymorphism in populations. According to Nei (1987), this gene diversity index is defined by:

$$\mathbf{H=1-\sum xi^2}$$

where $\mathbf{x_i}$ is the frequency of the **i**th allele at a locus, and **m** is the number of alleles. In a sample, the unbiased heterozygosity can be estimated as:

$$\mathbf{H=2n(1-\sum xi^2/2n-l)}$$

where $\mathbf{x_i}$ is the frequency of the **i**th allele in the sample and **n** is the number of individuals sampled Heterozygosity was calculated through these usual ways, that is biased **(H)** and unbiased heterozygosity **(Hunb)** according to Nei (1978) and through "direct counting" the

TABLE 2. ENZYMES TESTED AND THEIR RESOLUTION IN DIFFERENT SYSTEMS OF GEI, AND ELECTRODE BUFFERS (0=NO ACTIVITY; 1=ACTIVITY BUT WEAK OR DISTORTED RESOLUTION; 2=REGULAR RESOLUTION; 3=BE) 1ER RESOLUTION).

Enzymes	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Acid phosphatase ACPH	-	-	-	-	2	-	-	-	-	-		3
Alcohol dehydrogenase ADH	1	-	-	-	-	0	-	-	0	-		2
Aldolase ALD	-	-	-	-	-	-	-	-	-	0	-	-
Anodic peroxidase APX	-	-	-	0	0	-	0	0	-	0		2
Diaphorase DIA	-	-	2	1	-	-	2	2	-	-		3
Esterase EST	-	-	-	2	-	2	-	2	1	-		3
Glucose-6-phosphate dehydrogenase G6PD	-	-	-	-	-	-	-	-	2	-		2
Glucose dehydrogenase GDH	-	-	-	2	-	-	2	-	-	-		1
transaminase GOT	-	0	0	0	-	0	-	0	-	-		0
Isocitrate dehydrogenase IDH	0	-	-	-	-	-	1	-	-	0		1
Leucine aminopeptidase LAP	-	-	-	2	-	0	-	0	0	-		0
Malate dehydrogenase MDH	1	-	-	-	2	2	-	-	-	-		3
Malin enzyme ME	-	0	-	1	0	0	-	-	-	-		1
Ivlenadione reductase MNR	-	2	2	-	-	-	-	2	-	2		3

proportion of individuals sampled that were actually heterozygous **(Hdc).** Mean number of alleles per locus and percentage of loci polymorphyc (according to frequency of the commonest allele lower than 0.95) were calculated per population. Genotypic frequencies expected from Hardy-Weinberg equilibrium were calculated and compared with those observed in populations. CM-square tests were carried out to analyse deviations. Fixation Index (**F**) and **D** coefficient were calculated in order to analyse heterozygote deficiency or excess per locus and per population. Calculations were carried out through the programme BIOSYS-1 release 1.7 (Swofford & Selander, 1989).

Genetic identity and dissimilarity among populations.

A Basic Data Matrix of presence-absence of genotypes per individual was constructed in order to analyse genetotypic similarity between individuals. A similarity matrix between individuals was then calculated throug the Simple Matching Coefficient (Rohlf, 1993) This matrix was then analysed by the UPGMA. NTSYS programme version 1.8 (Rohlf, 1993) was used. A second Basic Data Matrix of allele frequencies was constructed with the different populations as columns, and the different alleles as rows. Through this matrix, genetic similarity was analysed between populations. A symmetric genetic dissimilarity matrix was calculated by using the genetic distance coefficient developed by Nei (1972). This coefficient is defined as:

$$d_{ij} = -\ln \frac{\sum_k X_{ki} \; X_{kj}}{\sum_k X^2_{ki} \; X^2_{kj}}$$

where $\mathbf{xk_i}$ and $\mathbf{xk_j}$ are frequencies of a given **k** allele in **i** and **j** populations. Calculation of this matrix was performed by using NTSYS programme version 1.8 (Rohlf, 1993). An unbiased genetic dissimilarity matrix according to Nei (1978) was also calculated through BIOSYS-1 release 1.7. These matrices were used to carry out a Cluster Analysis in order to obtain a UPGMA phenogram to visualize genetic similarities and differences between populations. An ordination analysis was also performed by calculating a double centre matrix through which the symmetric genetic dissimilarity matrix was transformed to scalar product form (Rohlf, 1993). Eigenvectors from the double centred matrix were then computed as principal coordinates axes. Cluster Analysis and Principal Coordinates Analysis were also carried out by NI SYS programme.

Comparisions between genetic and morphological variation

Based on the same model to estimate heterozygosity, an unbiased Genotypic Diversity Index (**GDI**) was also estimated per population. In this case $\mathbf{x_i}$ is the frequency of the **i**th genotype for a particular locus, and **m** is the number of genotypes. As mentioned before, a similar unbiased Phenotypic Diversity Index (**PHDI**), also based on this model, was calculated per population in Chapter (IV). This PHDI was compared with genotypic and allelic diversity indices through a Regression analysis. Regression analysis was performed by STATGRAPHICS. Phenotypic frequencies per population were analysed in a same way as allelic frequencies through the Nei dissimilarity coefficient, a UPGM analysis and a Principal Coordinates Analysis. These analyses were performed by NTSYS programme.

3. RESULTS

GENETIC VARIABILTY

Tables 3 to 11 show genotypes resulted for individuals of populations studied and Tables 12 and 13 summarise information on genotypic and allele frequencies as well as mean Genotypic Diversity Index (GDI) and Heterozygosity (H) resulted per locus and per population. Table 14 summarises information on different estimations of genetic variability at loci studied in all populations. Table 15 summarises information on deviation from Hardy-Weinberg per locus per population. Table 16 shows information on heterozygote deficiency or excess.

GENETIC SIMILARITY AMONG INDIVIDUALS AND POPULATIONS

Figure 1 is the UPGMA tree resulted from anlysis of genotypic similarity among individuals. Twelve groups of individuals can be identified. A summary of composition of each group is shown in Table 17. In this table, a number of deviations from expected random constitution of groups can be appreciated. Excesses and deficiencies indicating similarity and disimilarity of populations in each group.

UPGMA phenogram for biased and unbiased genetic dissimilarity matrices according to Nei (1972 and 1978) is shown in figure 2. Figure 3 is a tridimensional plot projecting populations on the space of the first three principal coordinates axes according to their genetic similarity.

COMPARISION OF MORPHOLOGICAL AND GENETIC VARIATION

Table 18 summarises information on heterozygosity and morphological diversity as discussed in the former chapter. Plots of Figures 4 and 5 are graphic representations of the regression analysis resulting from genotypic and allelic diversity respectively compared with phenotypic diversity. Figure 6 is a UPGMA tree resulted from analysis of phenotypic frequencies among populations and Figure 7 a tridimentional plot projecting populations on the space of the first three principal coordinates axes according to their phenotypic similarity.

TABLE 51 (...CONTINUATION)

Enzymes	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Nicotinamide adenine dinucleotide dehydrogenase NADH-DH	-	-	-	-	-	-	-	-	1			3
6 Phosphogluconate dehydrogenase 6PGD	-	-	-	-	0	-	-	-	-	2		2
Phosphoglucose isomerase PGI	-	2	2	-	-	-	2	2	-	-		3
Phosphoglucomutase PGM	0		2	-	-	-	0	-	-	-		1
Rubisco RUB	-	-	-	2	-	-	-	2				3
Shikimate dehydrogenase SKDH	-	-	2	-	-	-	0	-	-	0		0
Sorbitol SOR	-	-	-	-	-	-	-	-	-	0		-

Gel and electrode buffer systems:

I=System I, García de León (1985)

II=System II, García de León (1985)

III=System III, García de León (1985)

IV=System IV, García de León (1985)

V=System morpholine-citrate, Wendel & Weeden (1989)

VI=System 2, Soltis (19

VII=System 2, Tris-citrate, Miles *et al.* (1977)

VIII=Mtton

IX=R (May, 1992)

X=Histidine, Cheliak & Pitel (1984)

XI=System VII

XII=Poulik System, Hakim-Elahi (1976)

TABLE 3. GENOTYPES FOR DIFFERENT ENZYMES AMONG INDIVIDUALS FROM ZAPOTITLAN POPULATION

Individual	ACPH	DIA	EST	MDH	MNR	NADH DH	PGI	RUB
2(S2)	22	11	22	11	12	23	23	11
3	22	22	22	12	11	23	23	11
4(S3)	22	22	22	11	22	33	23	11
5(S4)	22	22	23	11	12	23	22	11
6	22	12	22	11	23	23	23	11
7	12	12	22	12	22	33	23	11
8(S5)	22	23	22	11	33	33	22	11
9(S6)	22	-	23	11	12	33	23	11
10(S7)	22	12	22	11	12	33	33	11
11(S8)	22	12	22	12	33	44	22	11
13(S10)	22	22	22	12	12	34	12	11
14	22	12	22	11	12	33	22	11
15(S11)	22	12	22	12	11	33	23	11
16	22	12	22	11	13	13	23	11
17	22	12	23	-	22	33	22	11
18(S12)	22	22	22	11	23	33	22	11
19(S13)	22	22	22	11	22	33	22	11
20(S14)	22	12	22	11	22	23	22	11
21(S15)	22	22	22	11	22	23	22	11
22(S16)	22	22	22	11	22	33	22	11
23	22	22	22	12	33	33	22	11
24(S17)	22	22	23	11	22	33	22	11
25(S18)	22	22	22	11	22	33	22	11
26	22	22	22	11	12	13	23	11
27	22	12	22	11	22	22	22	11
28(S19)	22	22	22	11	12	12	22	11
29(S20)	22	12	22	11	22	22	33	11
30	22	-	23	11	22	22	22	11
31(S21)	22	12	22	11	22	23	12	11
33	22	-	22	11	22	23	22	11

TABLE 4. GENOTYPES FOR DIFFERENT ENZYMES AMONG INDIVIDUALS FROM CHINANGO-WILD POPULATION

Individual	ACPH	DIA	EST	MDH	MNR	NADH DH	PGI	RUB
1(S25)	22	11	23	11	12	13	12	11
3	22	-	23	11	22	33	12	11
4	22	11	23	11	12	13	12	11
5	22	22	12	11	22	33	22	11
6(S26)	22	22	12	12	22	33	12	11
8	22	22	22	12	22	33	22	11
9	22	23	22	22	22	33	22	11
10(S27)	22	23	22	11	23	33	22	11
11(S28)	22	23	12	22	23	33	12	11
14	22	-	22	11	33	33	12	11
15	22	-	22	12	22	33	22	11
16(S31)	22	-	12	12	11	23	22	11
17	22	-	22	11	-	23	12	11
18(S32)	22	-	22	11	11	11	12	11

TABLE 5. GENOTYPES FOR DIFFERENT ENZYMES AMONG INDIVIDUALS FROM SAN JUAN RAYA POPULATION

Individual	ACPH	DIA	EST	MDH	MNR	NADH DH	PGI	RUB
1	22	33	22	11	22	33	22	11
2	22	23	23	11	12	23	22	11
3	22	23	22	11	12	13	22	11
4(S34)	22	12	22	11	12	33	23	11
5	11	22	22	11	22	13	23	11
6	22	23	22	11	22	33	23	11
7 (S35)	22	22	22	11	22	33	22	11
8(S36)	22	23	22	11	12	33	22	11
9	22	33	22	11	22	33	22	11
10	22	23	22	11	22	33	22	11
11	22	23	22	11	22	33	22	11
12(S37)	22	13	22	11	11	33	22	11
13	22	33	22	11	22	13	22	11
14	22	13	22	11	12	22	22	11
16	22	33	22	11	12	13	22	11
17	22	33	22	11	12	33	22	11
18(S38)	22	11	22	11	12	13	22	11

TABLE. 6. GENOTYPES FOR DIFFERENT ENZYMES AMONG INDIVIDUALS FROM SAN LORENZO POPULATION

Individual	ACPH	DIA	EST	MDH	MNR	NADH DH	PGI	RUB
1(S39)	22	22	23	11	22	33	23	11
2(S40)	22	22	22	11	12	13	22	11
3(S41)	22	12	22	11	12	13	22	11
4(S42)	22	12	22	11	22	13	22	11
7	22	12	22	11	22	23	23	11
8	22	22	22	12	22	[3	22	11
9	22	13	23	11	22	22	23	11
10(S44)	22	22	22	11	22	22	22	11
11(S45)	22	22	22	11	34	33	23	11
12	22	22	22	11	12	13	22	11
13	12	11	22	11	22	11	22	11
14	22	12	22	11	22	23	22	11
15(S46)	22	22	22	11	22	11	22	11
16(S47)	22	12	22	11	23	33	22	11
17(S48)	22	12	22	11	22	11	22	11
18(S49)	22	22	22	11	12	11	22	11
19(S50)	22	11	23	11	12	12	23	11
20	22	11	22	11	22	33	23	11
21(S51)	22	22	22	11	22	33	22	11
22	22	22	23	11	23	22	22	11
23	22	22	22	11	33	12	22	11
24	22	22	22	11	12	13	22	11
26(S53)	22	22	22	11	13	13	22	11
27	22	22	22	11	13	13	22	11
28(S54)	22	22	22	11	13	13	23	11
29(S55)	22	11	23	11	11	11	22	11
30(S56)	22	23	22	11	11	111	22	11

TABLE 7. GENOTYPES FOR DIFFERENT ENZYMES AMONG INDIVIDUALS FROM COXCATLÁN POPULATION

Individual	ACPH	DIA	EST	MDH	MNR	NADH DH	PGI	RUB
1	22	12	22	11	13	12	22	11
2	22	12	22	11	13	12	22	11
3	22	22	22	11	23	12	23	11
4(S57)	22	22	22	12	11	22	22	11
7(S59)	22	22	22	11	12	11	22	11
8(S60)	22	22	22	11	12	23	22	11
9(S61)	22	22	22	11	33	23	22	11
10	22	22	22	11	22	-	22	11
11(S62)	22	22	23	11	11	-	22	11
14	22	22	23	11	13	-	22	11
15(S63)	22	22	22	11	22	13	23	11
16(S64)	22	13	22	11	22	22	22	11
18	22	23	22	11	22	22	22	11
19	22	23	23	11	22	23	22	11
20	22	23	22	11	33	22	22	11
21	22	23	22	11	22	23	22	11
23	22	22	22	11	23	-	23	11
25	22	23	22	11	33	23	22	11
27	22	22	22	11	33	33	22	11
28	22	22	22	11	33	33	22	11
29	22	22	22	11	22	33	22	11
30	22	22	22	11	22	33	22	11
31(S66)	22	22	23	11	23	23	22	11
32	22	22	22	12	23	-	22	11
33	22	22	22	11	33	33	22	11
34	22	22	22	12	22	13	22	11
36	22	12	22	11	22	13	22	11
37	22	22	22	11	22	22	22	11

TABLE 8. GENOTYPES FOR DIFFERENT ENZYMES AMONG INDIVIDUALS FROM METZONTLA-MANAGED *IN SITU* POPULATION

Individual	ACPH	DIA	EST	MDH	MNR	NADH DH	PGI	RUB
3(M3)	22	33	-	11	13	12	23	11
6(M6)	22	13	-	11	11	12	23	11
8(M8)	22	23	11	11	12	22	22	11
9(M9)	22	33	12	11	22	l2	22	11
10(M10)	22	33	22	12	12	12	22	11
11(M11)	22	12	22	11	13	11	23	11

TABLE 9. GENOTYPES FOR DIFFERENT ENZYMES AMONG INDIVIDUALS FROM CHINANGO-MANAGED *IN SITU* POPULATION

Individuals	ACPH	DIA	EST	MDH	MNR	NADH DH	PGI	RUB
1	22	23	23	11	11	22	22	11
3	22	33	22	11	11	22	22	11
4	22	22	22	11	13	23	12	11
5 (M13)	12	23	22	11	23	33	22	11
7 (M15)	22	22	22	11	22	33	22	11
8 (M16)	22	22	22	11	23	23	12	11
9	22	23	22	11	33	33	12	11
10 (M17)	22	22	22	12	13	23	12	11
11	22	23	22	12	23	33	22	11
12	22	33	22	11	13	33	22	11
15	22	23	22	12	13	33	22	11
16	22	23	22	12	33	33	22	11
17 (M19)	22	33	22	11	23	23	22	11
18 (M20)	22	22	22	11	22	33	22	11
22	22	33	22	11	13	23	12	11
23	22	33	22	11	13	33	22	11

TABLE 10. GENOTYPES FOR DIFFERENT ENZYMES AMONG INDIVIDUALS FROM METZONTLA-CULTIVATED POPULATION

Individuals	Num. of individuals	ACPH	DIA	EST	MDH	MNR	NADH DH	PG1	RUB
1(C1)	2	22	22	22	11	33	33	23	11
2(C2)	3	22	24	22	11	23	33	23	11
3(C3)	1	12	24	22	11	22	23	22	11
4(C4)	6	11	24	24	11	22	33	22	11
6(C5)	8	22	14	23	11	23	23	23	11
7(C6)	2	22	33	23	11	33	33	22	11
8(C7)	2	22	33	22	11	23	33	22	11
9(C8)	36	22	23	33	11	23	33	22	11
10(C9)	2	22	23	23	11	33	33	23	11
11(C10)	28	22	23	22	11	23	23	23	11
12(C11)	11	22	33	22	11	23	24	23	11
13(C12)	8	22	33	22	12	22	23	22	11
14(C13)	8	22	33	22	11	22	22	22	11
15(C14)	4	22	33	22	11	23	24	22	11
16(C15)	8	22	33	22	11	33	33	22	11
17(C16)	23	22	33	22	11	23	23	22	11
18(C17)	43	22	12	13	11	23	24	23	11
19(C18)	1	22	11	22	11	22	33	23	11
20(C19)	1	22	33	13	12	22	23	23	11
21(C20)	11	22	33	33	11	12	12	23	11
22(C21)	1	22	33	11	11	33	22	22	11
23(C22)	4	22	23	11	11	23	22	22	11
24(C23)	7	22	33	23	11	33	33	22	11
25(C24)	5	22	33	23	11	22	22	22	11
26(C25)	9	22	12	23	11	23	22	22	11
27(C26)	26	22	12	13	11	12	12	22	11

TABLE 11 GENOTYPES FOR DIFFERENT ENZYMES AMONG INDIVIDUALS FROM CHINANGO-CULTIVATED POPULATION

Individual	Num. of individuals	ACPH	DIA	EST	MDH	MNR	NADH DH	PGI	RUB
1	1	12	23	-	11	23	13	22	11
2(C27)	1	22	23	-	11	33	23	23	11
4(C28)	10	22	22	-	11	33	33	23	11
6(C29)	1	22	13	22	11	22	23	22	11
9(02)	1	22	13	23	11	22	13	23	11
11(C34)	1	22	34	23	11	34	12	23	11
13(C36)	5	22	33	22	11	22	22	22	11
15(C38)	1	22	23	22	11	22	12	22	11
16(C39)	4	22	22	22	11	33	33	22	11
17(C40)	1	22	22	23	11	24	33	22	11
18(C41)	5	22	33	22	11	22	22	22	11
20(C43)	5	12	22	22	11	23	33	22	11
21(C44)	11	22	14	22	12	22	11	23	11
22(C45)	3	22	22	22	11	22	23	22	11
24(C47)	12	22	22	22	11	22	22	23	11
26(C49)	18	22	22	23	11	22	11	23	11
27(C50)	11	22	12	33	11	22	22	23	11
28(C51)	24	22	12	33	11	24	22	22	11
29(C52)	4	12	22	23	11	22	-	22	11
30(C53)	1	22	22	22	11	34	-	23	11
33(C56)	2	22	23	22	11	22	-	22	11
34	4	22	33	11	11	33	-	23	11
37	1	22	23	11	11	23	-	22	11
38(C58)	1	22	-	11	11	33	-	23	11
39	2	22	13	12	12	13	-	23	11
42(C59)	31	22	22	22	11	11	-	22	11
43(C60)	1	22	23	22	12	13	-	22	11
48(C65)	1	22	22	22	11	13	-	22	11
49(C66)	2	22	22	23	11	11	-	23	11
64(C73)	4	22	22	13	11	11	-	23	11

TABLE 12. GENOTYPIC FREQUENCIES AND GENOTYPIC DIVERSITY INDICES (GDI) FOR LOCI OF DIFFERENT ENZYMES IN POPULATIONS STUDIED

Enzyme	Genotype	Zapotitlán	Chinango-Wild	San Juan Raya	San Lorenzo	Coxcatlán	Metzontla-Managed	Chinango-Managed	Metzontla-Cultivated	Chinango-Cultivated	MEAN
ACPH	11	0.000	0.000	0.059	0.000	0.000	0.000	0.000	0.039	0.000	0.011
	12	0.033	0.000	0.000	0.037	0.000	0.000	0.063	0.039	0.100	0.030
	22	0.967	1.000	0.941	0.963	1.000	1.000	0.937	0.923	0.900	0.951
	GDI	0.0651	0.000	0.1133	0.0734	0.0000	0.0000	0.1218	0.0451	0.1117	0.059
DIA	11	0.037	0.250	0.059	0.148	0.000	0.000	0.000	0.039	0.000	0.059
	12	0.444	0.000	0.059	0.222	0.107	0.167	0.000	0.115	0.069	0.131
	13	0.000	0.000	0.118	0.037	0.036	0.167	0.000	0.000	0.103	0.051
	14	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0^{0}.039	0.034	0.008
	22	0.482	0.375	0.118	0.556	0.714	0.000	0.313	0.039	0.448	0.338
	23	0.037	0.375	0.353	0.037	0.143	0.167	0.375	0.154	0.207	0.205
	24	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.115	0.000	0.013
	33	0.000	0.000	0.294	0.000	0.000	0.500	0.313	0.500	0.103	0.190
	34	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.034	0.004
	44	0.000	0.000	0.000	0.000	0.000	1000	0.000	0.000	0.000	0.000
	GDI	0.5787	0.6992	0.7758	0.6286	0.4653	0.7266	0.6844	0.7138	0 6184	0.655

TABLE 12 (...CONTINUATION)

Enzyme	Genotype	Zapotitlán	Chinango-Wild	San Juan Raya	San Lorenzo	Coxcatlán	Metzontla-Managed	Chinango-Managed	Metzontla-Cultivated	Chinango-Cultivated	Mean
EST	11	0.000	0.000	0.000	0.000	0.000	0.250	0.000	0.077	0.111	0.049
	12	0.000	0.286	0.000	0.000	0.000	0.250	0.000	0.000	0.037	0.064
	13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.115	0.037	0.017
	14	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	22	0.833	0.500	0.941	0.815	0.857	0.500	0.937	0.462	0.518	0.707
	23	0.167	0.214	0.059	0.185	0.143	0.000	0.063	0.231	0.222	0.143
	24	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.039	0.000	0.004
	33	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.077	0.074	0.017
	34	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	44	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	GDI	0.2827	0.6450	0.1133	0.3077	0.2484	0.7143	0.1218	0.7340	0.6408	0.423
MDH	11	0.793	0.571	1.000	0.963	0.893	0.833	0.750	0.923	0.900	0.847
	12	0.207	0.286	0.000	0.037	0.107	0.167	0.250	0.077	0.100	0.137
	22	0.000	0.143	0.000	0.000	0.000	0-000	0.000	0.000	0-000	0.016
	GDI	0.3338	0.5922	0.0000	0.0734	0.1935	0.3033	0.3861	0.0681	0.0761	0.225

TABLE 12. (...CONTINUATION)

Enzyme	Genotype	Zapotitlán	Chinango-Wild	San Juan Raya	San Lorenzo	Coxcatlán	Metzontla-Managed	Chinango-Managed	Metzontla-Cultivated	Chinango-Cultivated	Mean
MNR	11	0.067	0.154	0.059	0.074	0.071	0.167	0.125	0.000	0.100	0.091
	12	0.267	0.154	0.471	0.222	0.071	0.333	0.000	0.077	0.000	0.177
	13	0.033	0.000	0.000	0.111	0.107	0.333	0.375	0.000	0.100	0.118
	14	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	22	0.467	0.462	0.471	0.444	0.393	0.167	0.125	0.269	0.400	0.355
	23	0.067	0.154	0.000	0.074	0.143	0.000	0.250	0.423	0.100	0.135
	24	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.067	0.007
	33	0.100	0.077	0Á00	0.037	0.214	0.000	0.125	0 231	0.157	0.951
	34	0.000	0.000	0.000	0.037	0.000	0.000	0.000	0.000	0.067	0.012
	44	0.000	0.000	0 000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	GDI	0.7027	0.7374	0.5687	0.7417	0.7698	0.7876	0.7732	0.5273	0.7241	0.704

TABLE 12. (...CONTINUATION)

Enzyme	Genotype	Zapotitlán	Chinango-Wild	San Juan Raya	San Lorenzo	Coxcatlán	Metzontla-Managed	Chinango-Managed	Metzontla-Cultivated	Chinango-Cultivated	Mean
NADH DH	11	0.000	0.071	0.000	0.222	0.036	0.167	0.000	0.000	0.111	0.067
	12	0.033	0.000	0.000	0.074	0.107	0.667	0.000	0.077	0.111	0.119
	13	0.067	0.143	0.294	0.333	0.107	0.000	0.000	0.000	0.111	0.117
	14	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	22	0.100	0.000	0.059	0.111	0.179	0.167	0.125	0.192	0.278	0.135
	23	0.267	0.143	0.059	0.074	0.214	0.000	0.313	0.231	0.167	0.163
	24	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.115	0.000	0.013
	33	0.467	0.643	0.588	0.185	0.179	0.000	0.563	0.385	0.222	0.359
	34	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.0004
	44	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004
	GDI	0.7050	0.5590	0.5770	0.7978	0.8842	0.5444	0.5874	0.7799	0.6609	0.677
PGI	11	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	12	0.067	0.571	0.000	0.000	0.000	0.000	0.313	0.000	0.000	0.106
	13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	22	0 567	0 429	0 824	0.741	0 893	0.500	0.687	0.615	0 533	0.643
	23	0.300	0.000	0.176	0.259	0.107	0.500	0.000	0.385	0.467	0.244
	33	0.067	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007
	GDI	0.5888	0.5082	0.2990	0.3913	0.1935	0.5455	0.4439	0.4891	0.4993	0.440

TABLE 12. (...CONTINUATION)

Enzyme	Genotype	Zapotitlán	Chinango-Wild	San Juan Raya	San Lorenzo	Coxcatlán	Metzontla-Managed	Chinango-Managed	Metzontla-Cultivated	Chinango-Cultivated	Mean
RUB	11	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	GDI	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
MEAN	**GDI**	**0.4071**	**0.4685**	**0.3059**	**0.3767**	**0.3443**	**0.4527**	**0.3898**	**0.4197**	**0.4164**	**0.398**

TABLE 13. ALLELE FREQUENCIES AND HETEROZYGOSITY (H) FOR LOCI OF DIFFERENT ENZYMES AMONG POPULATIONS STUDIED

Enzyme	Allele	Zapotitlán	Chinango-Wild	San Juan Raya	San Lorenzo	Coxcatlán	Metzontla-Managed	Chinango Managed	Metzontla-Cultivated	Chinango-Cultivated	Mean
ACPH	1	0.017	0.000	0.059	0.019	0.000	0.000	0.031	0.025	0.030	0.020
	2	0.983	1.000	0.941	0.981	1.000	1.000	0.969	0.975	0.970	0.980
	H	0.033	0.000	0.111	0.036	0.0000	0.0000	0.061	0.049	0.058	0.039
DIA	1	0.259	0.250	0.147	0.278	0.071	0.167	0.000	0.168	0.150	0.166
	2	0.722	0.563	0.324	0.685	0.839	0.167	0.500	0.311	0.695	0.534
	3	0.019	0.187	0.529	0.037	0.089	0.667	0.500	0.486	0.120	0.293
	4	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.035	0.008	0.012
	H	0.411	0.586	0.593	0.452	0.283	0.500	0.500	0.637	0.479	0.493
EST	1	0.000	0.188	0.000	0.000	0.000	0.375	0.000	0.153	0.052	0.085
	2	0.944	0.688	0.971	0.907	0.929	0.625	0.969	0.434	0.623	0.788
	3	0.056	0.125	0.029	0.093	0.071	0.000	0.031	0.402	0.326	0.126
	4	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.000	0.001
	H	0.105	0.477	0.057	0.168	0.133	0.469	0.061	0.627	0.504	0.289
MDH	1	0.885	0.625	1.000	0.981	0.946	0.875	0-875	0.983	0.955	0.903
	2	0.115	0.375	0.000	0.019	0.054	0.125	0 125	0 017	0 045	0 097
	H	0.204	0.469	0.0000	0.036	0.101	0.219	0.219	0.034	0.086	0.152

TABLE 13. (...CONTINUATION)

Enzyme	Allele	Zapotitlán	Chinango-Wild	San Juan Raya	San Lorenzo	Coxcatlán	Metzontla-Managed	Chinango-Managed	Metzontla-Cultivated	Chinango-Cultivated	Mean
MNR	1	0.231	0.125	0.294	0.241	0.161	0.375	0.313	0.069	0.245	0.228
	2	0.596	0.750	0.706	0.593	0.500	0.500	0.250	0.515	0.577	0.554
	3	0.173	0.125	0.000	0.148	0.339	0.125	0.438	0.415	0.090	0.206
	4	0.000	0.000	0.000	0.019	0.000	0.000	0.000	0.000	0.087	0.012
	H	0.561	0.406	0.415	0.569	0.609	0.594	0.648	0.557	0.591	0.550
NADH DH	1	0.058	0.125	0.147	0.426	0.174	0.500	0.000	0.069	0.296	0.196
	2	0.231	0.000	0.088	0.185	0.413	0.500	0.281	0.419	0.583	0.300
	3	0.654	0.875	0.765	0.389	0.413	0.000	0.719	0.400	0.121	0.482
	4	0.058	0.000	0.000	0.000	0.000	0.000	0.000	0.112	0.000	0.019
	H	0.513	0.219	0.386	0.633	0.629	0.500	0.404	0.647	0.558	0.499
PGI	1	0.038	0.250	0.000	0.000	0.000	0.000	0.156	0.000	0.000	0.049
	2	0.731	0.750	0.912	0.870	0.957	0.875	0.844	0.788	0.738	0.829
	3	0.231	0.000	0.088	0.130	0.043	0.125	0.000	0.212	0.262	0.121
	H	0.411	0.375	0.161	0.226	0.083	0.219	0.264	0.335	0.387	0.273
RUB	1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	H	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
MEAN	**H**	**0.280**	**0.316**	**0.215**	**0.265**	**0.230**	**0.313**	**0.270**	**0.361**	**0.333**	**0.287**

TABLE 14. GENETIC VARIABILITY AT 8 LOCI ANALYSED IN POPULATIONS STUDIED

Population	Mean sample size per locus	Mean no. of alleles per locus	Percentage of loci polymorphic	Mean H	Mean Hunb	Mean Hdc
Zapotitlán	26.8	2.5	75.0	0.280	0.285	0.256
Std.error	0.5	0.3	0.067	0.078	0.080	0.067
Chinango-W	8.8	2.1	75.0	0.316	0.338	0.313
Std. error	0.8	0.3	0.082	0.078	0.083	0.082
S.J. Raya	17.0	2.0	62.5	0.215	0.222	0.199
Std. error	0.0	0.3	0.079	0.078	0.081	0.079
S. Lorenzo	27.0	2.4	62.5	0.265	0.270	0.218
Std. error	0.0	0.3	0.066	0.089	0.091	0.066
Coxcatlán	26.1	2.1	62.5	0.230	0.234	0.183
Std. error	0.9	0.3	0.064	0.090	0092	0.064
Metzontla-M	4.5	2.0	75.0	0.313	0.354	0.313
Std. error	0.3	0.3	0.091	0.083	0.094	0.091
Chinango-M	16.0	2.0	62.5	0.270	0.278	0.250
Std. error	0.0	0.2	0.073	0.082	0 085	0.073
Metzontla-C	259.0	2.8	62.5	0.361	0 361	0.374
Std. error	0.0	0.4	0.113	0.104	0 104	0.113
Chinango-C	138.6	2.6	62.5	0.333	0.334	0.193
Std. error	10.6	0.4	0.057	0.086	0.087	0.062

TABLE 15. GENOTYPIC FREQUENCIES DEVIATION FROM HARDY-WEINBERG EQUILIBRIUM AMONG POPULATIONS STUDIED

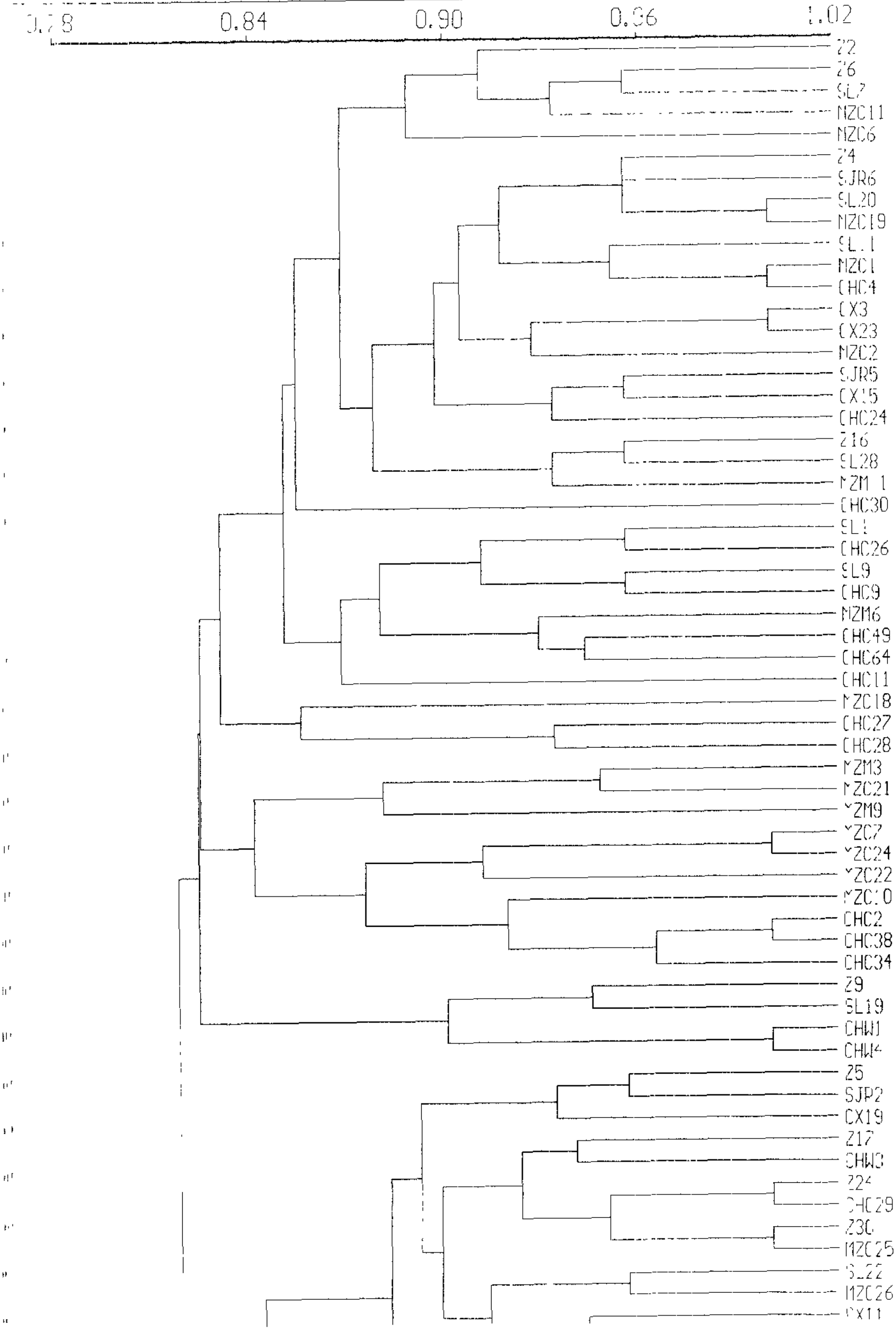
(*INDICATES SIGNIFICANT DIFFERENCES FROM CHI-SQUARE TEST)

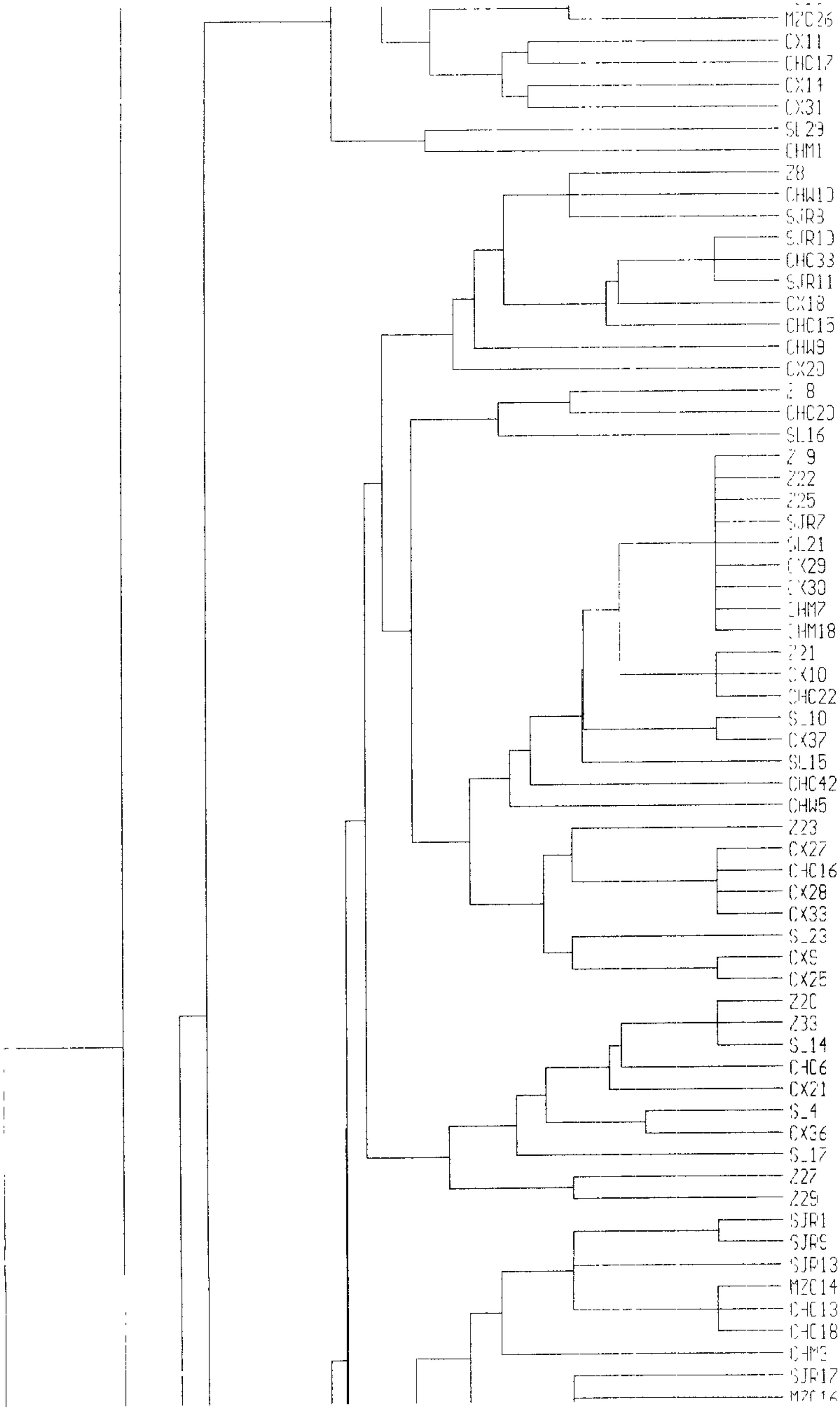
Locus	Zapot	Chinango W	S.J. Raya	San Lorzo	Coxcat	Metzon M	Chinan M	Metzon C	Chinan C
ACPH	-	*	-	-	-	-	*	-	-
DIA	-	*	-	-	-	-	-	*	*
EST	-	-	-	-	-	-	-	*	*
MDH	-	-	-	-	-	-	-	-	-
MNR	*	-	-	-	*	-	-	-	-
NADHDH	*	*	*	*	-	-	-	*	*
PGI	-	-	-	-	*	-	-	*	*
RUB	-	-	-	-	-	-	-	-	-

TABLE 16. COEFFICIENTS FOR HETEROZYGOTE DEFICIENCY OR EXCESS PER POLYMORPHIC LOCUS AMONG POPULATIONS

Locus	Hetrozygotes	Zapot	Chinan W	S.J. Raya	S. Lorzo	Coxca	Metz M	Chinan M	Metz C	Chinan C
ACPH	Observed	1	-	0	1	-	-	1	1	10
	Expected	1.000	-	1.939	1.000	-	-	1.000	12.698	9.731
	F	-0-017	-	1.000	-0.019	-	-	-0.032	0.921	-0.031
	D	0.000	-	-1.000	0.000	-	-	0.000	-0.921	0.028
DIA	Observed	13	3	9	8	8	3	6	165	58
	Expected	11.302	5.000	10.394	12.434	8.055	3.273	8.258	16.5.38	80.312
	F	-0.172	0.360	0.108	0.344	-0.011	0.000	0.250	3	0.276
	D	0-150	-0.400	-0.134	-0.357	-0.007	-0.083	-0.273	0.000	-0.278
									-0.002	
EST	Observed	3	5	1	5	4	1	1	12.0	33
	Expected	2.887	4.067	1.000	4.623	3.782	2.143	1.000	162.62	78.307
	F	-0.059	-0.311	-0.030	-0.102	-0.077	0.467	-0.032	9	0.577
	D	0.039	0.230	0.000	0.082	0.058	-0.533	0.000	0.261	-0.579
									-0.262	
MDH	Observed	6	2	-	1	3	1	4	9	14
	Expected	5.412	4.000	-	1.000	2.891	1.000	3.613	8.861	13.411
	F	-0.130	0.467	-	-0.019	-0.057	-0.143	-0.143	-0.018	-0.047
	D	0.109	-0.500	-	0.000	0.038	0.000	0.107	0.016	0.044
MNR	Observed	10	4	8	12	9	3	10	207	37
	Expected	14.882	3.467	7.273	15.642	17.364	2.714	10.710	144.59	91.861
	F	0.315	-0.231	-0.133	0.218	0.472	-0.263	0.036	8	0.596
	D	-0.328	0.154	0.100	-0.233	-0.482	0.105	-0.066	-0.434	-0.597
									0.432	
NADH DH	Observed	11	2	6	13	12	2	5	163	7
	Expected	13.588	1.867	6.758	17.415	14.778	2.286	6.677	168 01	57.780
	F	0.175	-0.143	0.085	0.239	0.170	0.000	0.227	4	0.878
	D	-0.190	0.071	-0.112	-0.254	-0.188	-0.125	-0.251	0.028	-0.879
									-0.030	
PGI	Observed	10	4	3	7	2	1	5	110	54
	Expected	10.902	3.200	2.818	6.208	1.956	1.000	4.355	86.309	40.039
	F	0.065	-0.333	-0.097	-0.149	-0.045	-0.143	-0.185	-0270	-0.355
	D	-0.083	0.250	0.065	0.128	0.023	0.000	0.148	0.267	0.349

Genotypic similarity among individuals

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CHC17
CX14
CX31
SL29
CHM1
Z8
CHW10
SJR8
SJR10
CHC33
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CHC15
CHW9
CX20
Z 8
CHC20
SL16
Z 9
Z22
Z25
SJR7
SL21
CX29
CX30
CHM7
CHM18
Z21
CX10
CHC22
SL10
CX37
SL15
CHC42
CHW5
Z23
CX27
CHC16
CX28
CX33
SL23
CX9
CX25
Z20
Z33
SL14
CHC6
CX21
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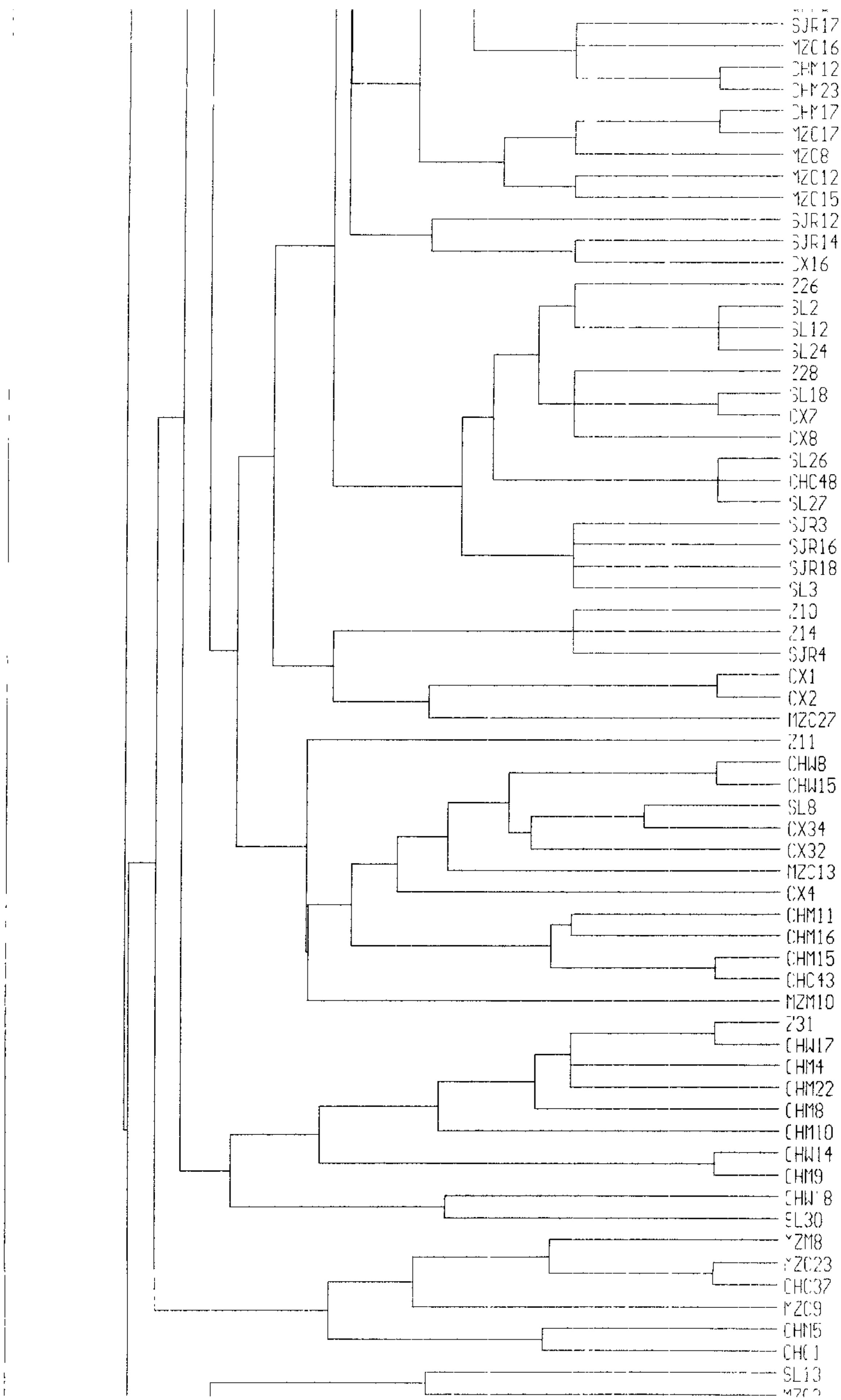
CHC18
CHM3
SJR17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MZC16
CHM12
CHM23
CHM17
MZC17
MZC8
MZC12
MZC15
SJR12
SJR14
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Z26
SL2
SL12
SL24
Z28
SL18
CX7
CX8
SL26
CHC48
SL27
SJR3
SJR16
SJR18
SL3
Z10
Z14
SJR4
CX1
CX2
MZC27
Z11
CHW8
CHW15
SL8
CX34
CX32
MZC13
CX4
CHM11
CHM16
CHM15
CHC43
MZM10
Z31
CHW17
CHM4
CHM22
CHM8
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CHM5
CHC1
SL13

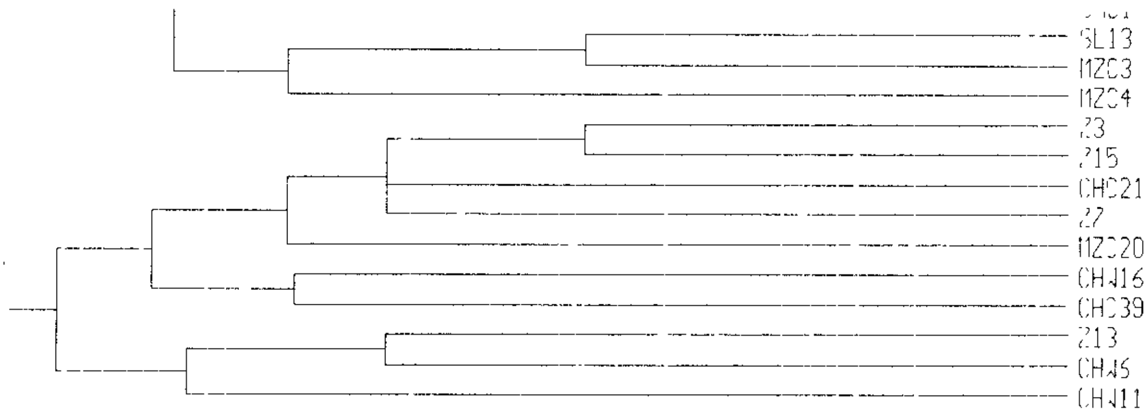
SL13
MZC3
MZC4
Z3
Z15
CHC21
Z7
MZC20
CHW16
CHC39
Z13
CHW5
CHW11

TABLE 17. COMPOSITION OF GROUPS RESULTED FROM **UPGMA** OF GENOTYPIC SIMILARITY AMONG INDIVIDUALS OF *STENOCEREUS STELLATUS*

Group	Indiv	Zapot	Chinan W	S.J. Raya	San Lorzo	Coxca	Metz M	Chinan M	Metz C	Chinan C	Total
I		5	2	2	7	3	4	0	11	13	47
	Exp.	7.27	3.39	4.12	6.54	6.78	1.45	3.88	6.30	7.27	
II	Obs.	4	1	1	2	4	0	1	2	2	17
	Exp.	2.63	1.23	1.49	2.37	2.45	0.53	1.40	2.28	2.63	
III	Obs.	2	2	3	1	2	0	0	0	3	13
	Exp.	2.01	0.94	1.14	1.81	1.88	0.40	1.07	1.74	2.01	
IV	Obs.	5	1	1	4	9	0	2	0	3	25
	Exp.	3.87	1.80	2.19	3.48	3.61	0.77	2.06	3 35	3.87	
V	Obs.	4	0	0	3	2	0	0	0	1	10
	Exp.	1.55	0.72	0.88	1.39	1.44	0.31	0.83	1.34	1.55	
VI	Obs.	0	0	6	0	1	0	4	6	2	19
	Exp.	2.94	1.37	1.67	2.64	2.74	0.59	1.57	2.55	2.94	
VII	Obs.	2	0	3	7	2	0	0	0	1	15
	Exp.	2.32	1.08	1.31	2.09	2.17	0.46	1.24	2.01	2.32	
VIII	Obs.	2	0	1	0	2	0	0	1	0	6
	Exp.	0.93	0.43	0.53	0.84	0.87	0.19	0.50	0.80	0.93	
IX	Obs.	1	2	0	1	3	1	3	1	1	13
	Exp.	2.01	0.94	1.14	1.81	1.88	0.40	1 07	1.74	2.01	
X	Obs.	1	3	0	1	0	0	5	0	0	10
	Exp.	1.55	0,72	0.88	1.39	1.44	0.31	0.83	1.34	1.55	
XI	Obs.	0	0	0	1	0	1	1	4	2	9
	Exp.	1.39	0.65	0.79	1.25	1.30	0.29	0.74	1.21	1.39	
XII	Obs,	4	3	0	0	0	0	0	1	2	10
	Exp.	1.55	0.72	0.88	1.39	1.44	0.31	0.83	1.34	1.55	
Total		30	14	17	27	28	6	16	26	30	194

TABLE 18. HETEROZYGOSITY (HI NB), GENOTYPIC DIVERSITY INDEX (GDI) AND PHENOTYPIC DIVERSITY INDEX (PHDI) AMONG POPULATIONS STUDIED

Population	H	GDI	PHDI
Zapotitlán	0.285	0.4071	0.3637
Chinango-Wild	0.338	0.4685	0.4797
San Juan Raya	0.222	0.3059	0.3092
San Lorenzo	0.270	0.3767	0.3962
Coxcatlán	0.234	0.3443	0.3670
Metzontla-Managed *in situ*	0.354	0.4527	0.4454
Chinango-Managed *in situ*	0.278	0.3893	0.3730
Metzontla-Cultivated	0.353	0.4197	0.3916
Chinango-Cultivated	0.365	0.4164	0.4252

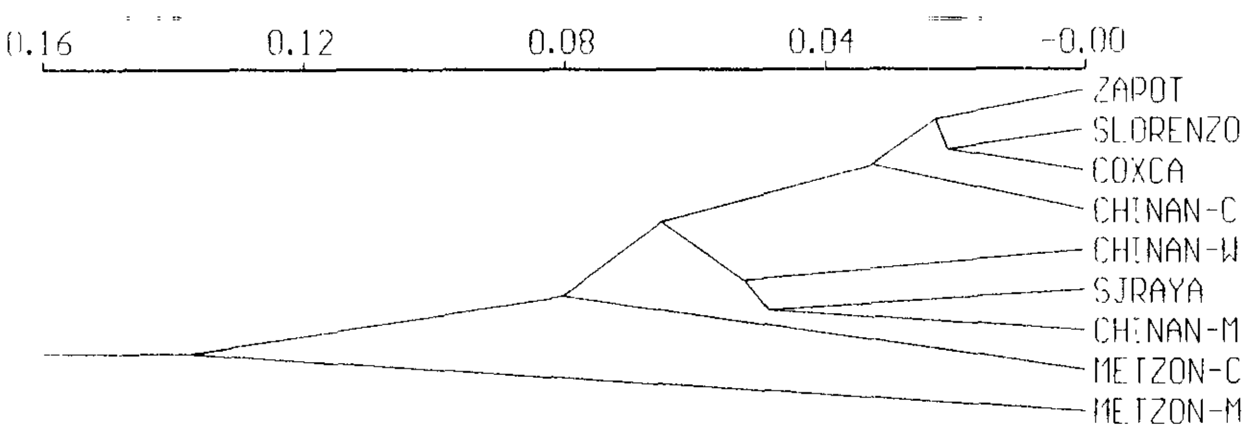

Figure 1. Phenogram resulting from UPGMA analysis of genetic dissimilarity between populations studied of *Stenocereus stellatus.*

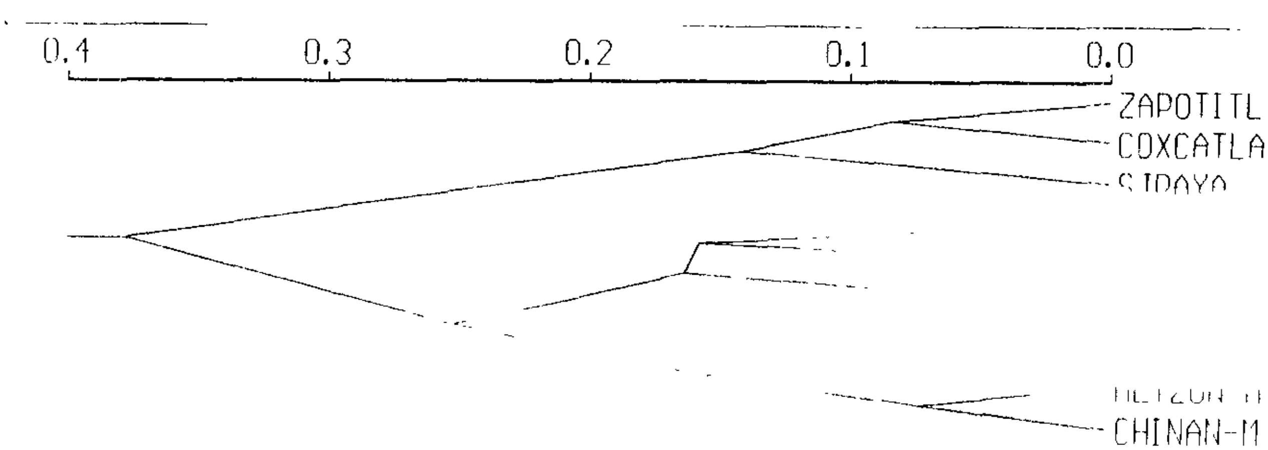

Figure 2. Phenogram resulting from UPGMA analysis of phenotypic dissimilarity between populations studied of *Stenocereus stellatus.*

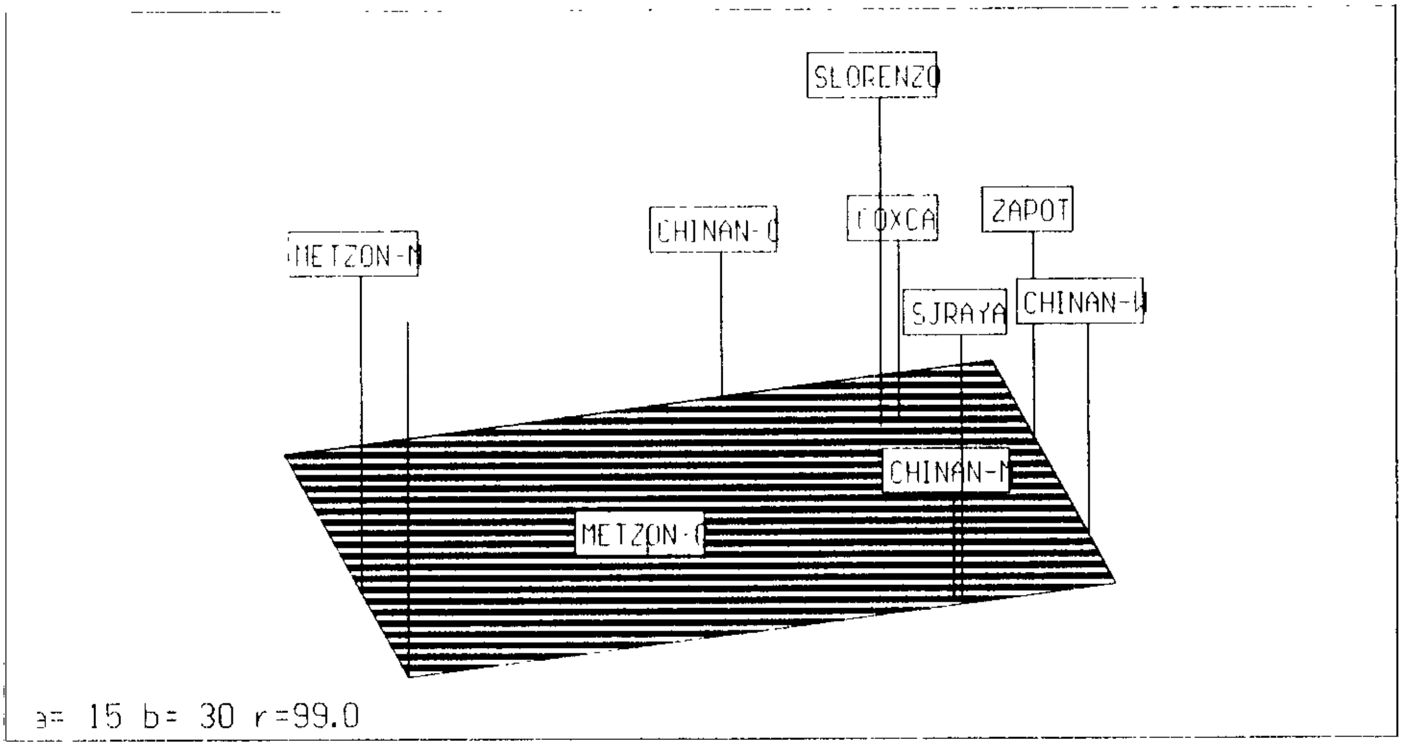

Figure 3. Populations of *Stenocereus stellatus* studied in the space of the first three principal coordinate axes of genetic dissimilarity analysis.

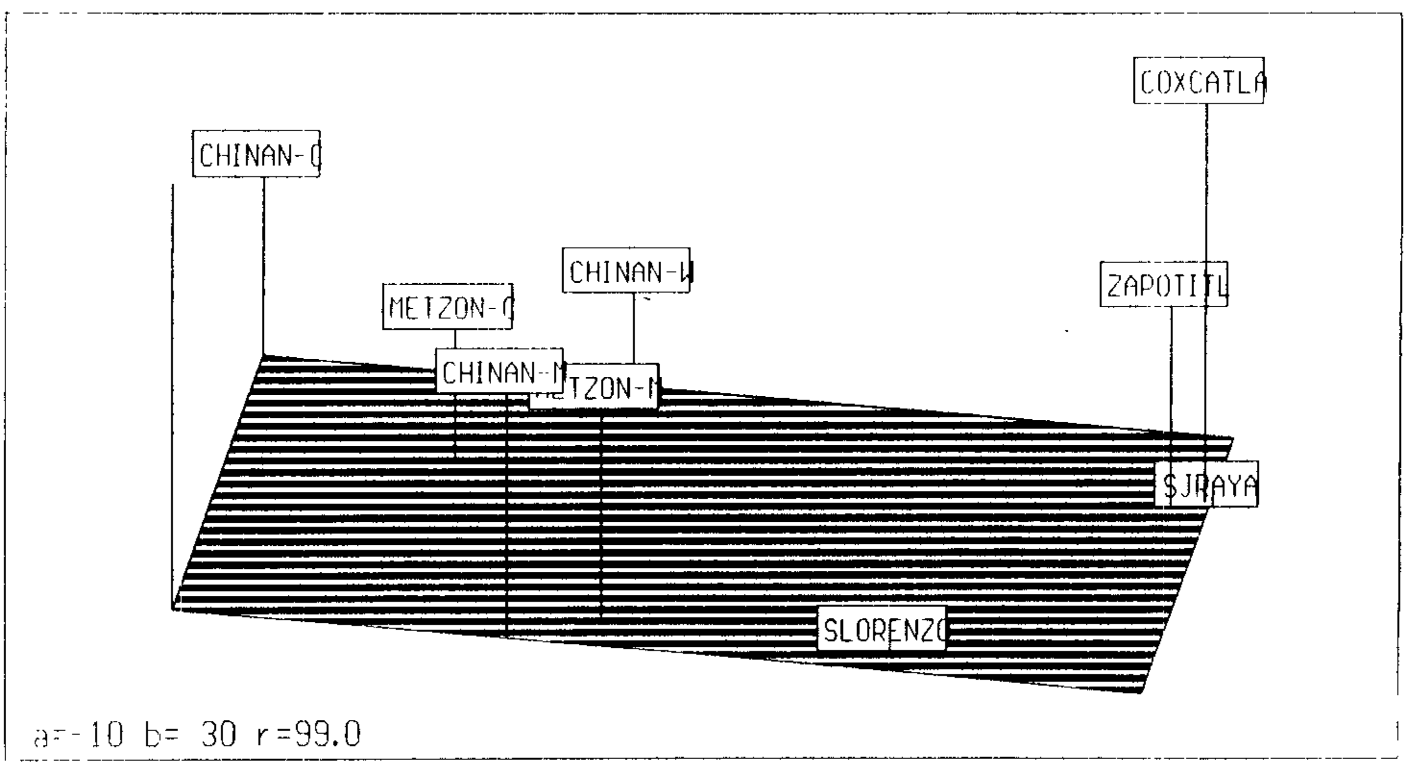

Figure 4. Populations of *Stenocereus stellatus* studied in de space of the first three principal coordinate axes of phenotypic variation analysis.

4. Discussion

The mean percentage of polymorphic loci (Table 14) for the species *Stenocereus stellatus* (66.67%) was higher to the mean value reported by Hamrick & Godt (1989) for temperate-tropical species (58.8%) and long lived woody perennials (64.7%) and also higher Chant that reported by Parker & Hamrick (1993) for the only one columnar cactus species studied in this direction *Lophocereus schotii,* (44.4%). Although proportion of polymorphic loci might change while more loci are included in the sample, this first approach reveals high levels of genetic variation existing in this plant species.

The mean number of allele per polymorphic locus (Table 14) for the species S. *stellatus* (2.28) was higher then that found by Parker & Hamrick (1993) in *L. schotii*, but less than the mean for other asexually/sexually reproducing species (2.59). This indicates that, as in *L. schotii,* in *S. stellatus* the maintenance of greater allozyme diversity within populations results from a high proportion of polymorphic loci rather than a high number of alleles per polymorphic locus. Among populations, the cultivated populations presented the highest number of alleles per locus (2.6 in Chinango cultivated and 2.8 in Metzontla cultivated), revealing that some alleles that are not present in the wild occur in cultivation contributing to increase genetic diversity by this means in cultivated populations.

Mean heterozygosities (0.287 forH, 0.297 for Hunb and 0.255 for Hdc) at species level resulted also high compared with mean heterozygosity found in *Lophocereus schotii* (0.159) but lower than the mean heterozygosity for polymorphic loci for that species (0.326). Clearly, the high values of heterozygosity obtained from this study are because RUB was the only rnonomorphic locus for all populations (Tables 13 and 14). Again, these estimations could be precised by sampling a higher number of loci, but present information suggests that levels of heterozygosity in this plant species are high.

At population level, the different genetic diversity estimations from this study generally reveal that this is relatively low in wild populations of the Tehuacán Valley and higher in the wild population from the Balsas river basin (Tables 13 and 14). Cultivated populations presented relatively high levels of genetic diversity in both areas. Manged in situ population the Tehuacán Valley presented relatively high genetic diversity while the one from the Balsas river basin showed relatively low levels. In the Tehuacán Valley, cultivated population presented higher levels of genetic diversity than the wild population while in the Balsas river basin genetic diversity was almost the same in the two populations. The managed *in situ* population from the Tehuacán Valley also showed higher levels of genetic diversity than the wild populations but in the Balsas river basin genetic diversity of managed *in situ* population was lower than in the wild population. Differences in genetic diversity between human influenced and wild populations are particularly strong in the Tehuacán Valley because of the low levels of diversity among wild populations. But also, levels of genetic diversity among human influenced populations from the Tehuacán Valley are higher than those estimated in the wild and cultivated populations from the Balsas river basin. A similar pattern can be appreciated in genotypic variation (GDI), although levels of variation on the wild population of the Balsas river basin and the managed *in situ* population from the Tehuacán Valley were higher than in cultivated populations (Tables 12 and 17).

From Table 14 it is possible to estimate partial means of heterozygosity among regions. Partial means of H and Hunb of the three populations of the Balsas river basin (0.306 and 0.317 respectively) are higher then those among the three populations of the Tehuacán Valley (0.277 and 0.288 respectively) while Hdc are approximately similar in both regions (0.252 in the Balsas river basin and 0.257 in the Tehuacán Valley).

The information above generally indicates that genetic diversity of *Stenocereus stellatus* in the Balsas river basin is higher than in the Tehuacán Valley and that human manipulation, particularly through cultivation but also through management *in situ* as found in the Tehuacán Valley, of this plant species has caused increasing of genetic diversity particularly by maintaining the high proportion of polymorphic loci occurring in the wild but also by maintaining alleles that are rare or abscent in wild populations.

Deviations from Hardy-Weinberg equilibrium occur in two of the loci analysed in all wild populations; no differences were found in managed *in situ* populations, but 5 of the 7 polymorphic loci analysed were significantly deviated from equilibrium in the cultivated populations. This information shows that artificial selection is strongly deviating allele frequencies from Hardy-Weinberg equilibrium, and this deviation is stronger than in wild populations. No deviations in managed *in situ* populations suggest that artificial selection in these populations is probably not important.

Biased and unbiased estimations of genetic dissimilarity showed similar patterns of genetic distance among populations (Figures 1 and 2). In general, these analyses showed three groups of populations with genetic similarity. One of them includes most of wild populations of the Tehuacán Valley (Zapotitlán, San Lorenzo and Coxcatlán) and the cultivated population from the Balsas river basin. In a second group, the remaining wild population from the Tehuacán Valley (San Juan Raya) is grouped similar to wild and managed *in situ* populations from the Balsas river basin. Cultivated and managed *in situ* populations from the Tehuacán Valley, in the third group, were similar between them but different to the rest of the populations.

According to this information, managed and cultivated populations from the Tehuacán Valley might form part of a different gene pool than the wild populations from the area, while the cultivated population from the Balsas river basin seems to be also different to the wild and managed populations of the area. These differences among populations of a same geographic area firstly indicate that gene flow between wild and cultivated populations and, in the Tehuacán Valley, also between wild and managed *in situ* populations is limited, suggesting that some: mechanisms of reproductive isolation may be occurring between those populations. This aspect is discussed in more detail in the next chapter. But this result has other important implications as discussed below.

Genetic similarity between wild populations from the Tehuacán Valley and the cultivated population of the Balsas river basin, on one hand, and between San Juan Raya population and the wild and managed *in situ* populations of the Balsas basin, on the other, could be explained by at least three hypotheses: 1) reproductive interaction between them, 2) immigration from one another or 3) a common origin. More evidence from genetic studies is still recquired to confirm this pattern of similarity and more evidence is still recquired from ecology to solve the questions arised from this first approach. However, based on the information available, some observations to these hypotheses can be made.

Thus, the first hypothesis seems to be unlikely. Distance between localities studied in the Tehuacán Valley and the Balsas river basin ranges from 60 to 90 Km. As discussed in the next chapter, bats seem to be the most relevant pollinators of flowers of *S. stellatus* and although this fact may give high mobility to pollen of this species, such range of distance seems to be out of any pollen interaction. Distances between wild and cultivated populations in the Tehuacán Valley range from 8 to 20 Km while in Chinango, in the Basas basin, distance is approximately 2 Km. Clearly, activity of pollinators seems to be more likely among populations of the same area. Immigration of seeds or vegetative plant material through birds and humans might be more likely than pollen travel. Especially because people use to carry propagules of interesting plants from one place to other. But these processes may occur more commonly within a same geographic area.

The hypothesis of a common origin could be a more plausible explaination. This hypothesis could mean 1) that populations from Chinango in the Balsas basin derived from wild populations of the Tehuacán Valley; 2) that the presumed "wild" populations of the Tehuacán Valley are not real wild populations and derived from wild, managed *in* situ or cultivated populations from the Balsas basin or 3) that all of them derived from an ancestral population somewhere else in the Tehuacán Valley or in the Balsas basin. The same could be said for the wild and managed *in situ* populations of Chinango and the wild populat ion from San Juan Raya in the Tehuacán Valley.

Considering the information available on genetic variation, it seems to be unlikely that populations of the Balsas basin with a higher genetic diversity had derived from wild populations of the Tehuacán Valley, with lower genetic diversity. Under this consideration, the contrary direction comprehended in the second assumption seems to be more likely However, the characteristics of the cultivated and managed *in situ* populations from Metzontla in the Tehuacán Valley indicates the possible existence of another branch of genetic variation with important levels of diversity whose wild relatives were not included in the sample and the Tehuacán Valley, therefore, cannot be discarded as an original source of variation. Under this consideration, the third assumption is also atractive, in this assumption neither the Tehuacán Valley nor the Balsas basin are discarded as possible scenarios of ancestral populations to the ones included in this study. Sampling of more populations in both areas could give more information to clarify this problem.

Nevertheless, whatever hypothesis results true one crucial question is when the presumed related populations separeted. In the case of the group conformed by wild populations from Tehuacán and the culativated population from the Balsas basin, the strong phenotypic divergence suggests that separation could occur before domestication caused such morphological differentiation. Probably during early stages of domestication of this species, probably before human presence in the Tehuacán Valley and the Balsas basin.

As mentioned in Chapter III, the oldest archaeological remains of *Stenocerus stellatus* in the Tehuacán Valley are from strata 4,500 years before present. This contrast with the time of human presence in the area that, according to MacNeish (1967) and Flannery (1986), could be about 12,000 years. Although identification and antiquity of archaeological remains have to be corroborated, in principle the information available indicates that humans inhabited the Tehuacán Valley more than 6,000 years before they started to use this plant species. As discussed previously, present populations of *Stenocereus stellatus* from San Lorenzo and Coxcatlán, near El riego and Coxcatlán caves where archaeological excavations were carried out, have densities of population of 34 and 567 individuals per hectare producing about 390 and 1,754 fruits per hectare respectively. Considering the relative abundance and the utilitarian advantages of this plant species, it is difficult to explain absence of archaeological remains in so long time strata

At present, wild populations of *Stenocereus stellatus* in the Tehuacán Valley appear to be part of natural vegetation in the area. They form part of communities characterised by presence of populations of other long-lived columnar cacti *(i. e. Neobuxbaumia tetetzo* and *Pachycereus weberi)* probably more than 300 years old. But the areas where they are settled are also abundant in archaeological remains (pottery, obsidian knives and buildings). This suggests that these "wild" populations of xoconochtli could have derived from ancient plantations and then getting naturalised after a certain time of abandonment, probably several centuries. The relatively reduced genetic variation in these populations could be caused by genetic drift as result of a founder effect under such situation. In this context, the population from San Juan Raya could have also derived from populations similar to the wild and managed *in situ* from the Balsas basin.

Analysis of genotypic similarity among individuals (Figure 2 and Tables 17 and 18) clustered individuals in twelve groups in which the three groups of populations defined by allelic frequencies shared absence or excessed or deficient presence, confirming the pattern of similarity among populations discussed above. However, from this analysis it results clear that not all individuals from a given population are exclusively similar to individuals of the same population or to individuals from other populations grouped together by allelic frequencies UPGMA. Thus, cultivated individuals from the Balsas basin are not exclusively similar to wild individuals from the Tehuacán Valley. Part of these individuals also share genotypic similarity with individuals of the wild and managed *in situ* populations of the area. This confirms the ethnobotanical information about the introduction of local wild plant material to home gardens. The same could be said for individuals from other groups of populations.

As shown in Table 18, in general terms, in populations with high levels of heterozygosity phenotypic diversity is higher than in populations with low levels of heterozygosity, although correlation of these parameters did not fit well (Figures 4 and 5). However, patterns of similarity among populations were different when phenotypic and allelic frequencies were analysed (Figures 1,2,3, 5 and 6). Thus, phenotypic frequencies grouped populations according to their form of management, with the only exception of Chinango wild population that was grouped together with the cultivated populations (Figures 5 and 6). These results suggest that morphological similarity in populations genotypically different as well as morphological dissimilarity in populations genotypicaly similar might be due in part: to direct influence of environmental factors regulating phenotypic expression but also in part to evolutionary convergence and divergence. Thus, while wild populations from the Tehuacán Valley have been submitted to natural environmental pressures, the cultivated population from the Balsas basin has been submitted to artificial selection resulting in a strong morphological divergence. For the contrary, although cultivated and managed *in situ* populations from the Tehuacán Valley and the Balsas basin are genetically different, and environments in the two geographic areas are also different, they are morphologically similar presumably because they are submitted to similar processes of artificial selection.

More evidence is still required to test hypotheses derived from this study. Number of loci sampled is small for the moment and this study therefore should be considered only as a first approach. Major efforts for future research should be directed to increase number of loci and number of populations in the sample. Molecular analysis of DNA polymorphism such as RFLPs, RAPDs or Minisatellite sequences could significantly increase the sample of loci and improve the information presented here. Equally, sampling of wild populations around Metzontla in the Tehuacán Valley and more localities in the hughe Balsas basin could fill important gaps of the present information

Apéndice 6
REPRODUCTIVE BIOLOGY OF *Stenocereus stellatus*

1.INTRODUCTION

It has been shown prevoiusly that although vegetative propagation commonly occurs among wild, managed *in situ* and cultivated populations of *Stenocereus stellatus,* considerable amounts of genetic and morphological variation exist among them. It has also been shown that different degrees of morphological and genetic divergence occur between populations., especially in relation to their form of management. In phylogenetic systematics, evolution is defined as the splitting of an evolutionary lineage into two separated ones (Stuessy, 1990; Raamsdonk, 1993). Information above, therefore, suggests that from a phylogenetic systematics point of view, an evolutionary process is occurring among populations studied and that, at least in part, this process is related to the form of management of this plant species by people of the area. In other words, domestication has been occurring in the xoconochtli.

Ethnobotanical studies showed that artificial selection is carried out mainly by keeping and enhancing through vegetative propagation, *in situ* and *ex situ,* desirable phenotypes and sometimes by eliminating the undesirable ones. This process, carried out by maybe several hundreds of years, seems to be the basic mechanism that maintains and develops the morphological and genetic divergence referred above. Through this mechanism, people are able to isolate within anthropogenic areas *(in situ* or *ex situ)* phenotypes that they prefer for use. However, presence of phenotypes exclusive of home gardens suggests that mechanisms of isolation of variants, other than artificial selection, have also been occurring, otherwise presence of these human-made phenotypes should also be common among wild populations. Existence of some phenotypes that occur exclusively in home gardens suggests also that part of the variation analysed has been generated or maintained by human influence and that other part, maybe the most, of the variation analysed has been generated and maintained by natural processes. However, nothing has been studied about sources of variation in this species. An analysis of mechanisms of both generation of variation and reproductive isolation barriers is therefore necessary for a comprehension of evolutionary changes, natural or artificial, of this species.

Amounts of variation in plant populations are strongly influenced by forms of reproduction. Thus, while vegetative propagation causes replication of particular genotypes, sexual reproduction reassorts genes for a new generation. Even more, in sexual reproduction, different breeding systems as well as methods of pollination and seed dispersal have a profound impact on how widely the genes of plants spread (Proctor, Yeo & Lack, 1996; Loveless & Hamrick, 1984; Hamrick & Godt, 1990). For instance, plants that are mainly self-pollinating have the most restricted pollen flow and there is less mixing of genes generally than in outcrossing plants while wind-pollinated plants generally mix genes greater than those pollinated by animals (Proctor, Yeo & Lack, 1996). Furthermore, the status of allele frequencies in natural populations can be regulated by selective pressures and survival of particular phenotypes at different steps of the life-cycle of plants, from the germination of seeds, the establishment of seedlings, their growt into vegetative adults and to flowering adults mating for new generations of individuals. Reproductive systems, therefore, not only mediates the genetic constitution of the next generation but also affects which alleles will survive. This chapter is a first approach to analyse the role of reproduction in the status of variation of populations of *S. stellatus.*

Stenocereus stellatus is reported in the literature presenting both sexual and asexual reproduction in nature (Bravo-Hollis, 1978; Benson, 1982). However, no formal studies on reproduction of this species have been published. From about 70 species of columnar cacti of the tribe Pachycereeae, reproductive biology of no more than 25 species has been studied in detail Among the most relevant studies, it can be mentioned those carried out in Northern Mexico and Arizona by McGregor *et al.* (1959) and by McGregor *et al.* (1962) with the saguaro *Carnegiea gigantea;* those by Alcorn *et al.* (1962) with the organpipe *Stenocereus thurberi;* and those by Fleming (1993) with *Pachycereus pringlei.* Also important are those studies by Soriano *et al.* (1991) and Sosa & Soriano (1992) with *Stenocereus gruels, Subpilocereus repandus* and *Pilosocereus tillianus* in Venezuela and those carried out in the Tehuacán Valley by Valiente-Banuet *et al.* (1995 a) with *Neobuxbaumia tetezo* and by Valiente-Banuet *et a1.* (1995 b) and Valiente-Banuet *etal.* (submitted) with other 15 species of columnar cacti.

Based on information available on reproductive biology of columnar cacti as well as on floral morphology, Valiente-Banuet *et al.* (1995 a) estimate that from the total number of species of columnar cacti, about 60% have flowers with chyropterophylous syndrome; 22% have diurnal anthesis and are pollinated by bees (6%), and hummingbirds (16%); 6% have a clear relationship with hawkmoth pollinators; and for 12% of the species (among them *Stenocereus stellatus),* anthesis time is unknown. For the Tehuacán Valley and the Balsas river Basin, Valiente-Banuet *et al.* (1995 a) recorded the highest richness of species of columnar cacti of Mexico and probably of the world. In this area, for 16 species studied, Valiente-Banuet *et al.* (1995 b) report 11 (69%) with nocturnal anthesis pollinated by bats and 5 (31%) with diurnal anthesis pollinated by bees and hummingbirds.

Considering the above, the general purposes of this study were to analyse some aspects of reproductive biology of *Stenocereus stellatus* in order to visualize: 1) biological processes interveining in conservation and reassortment of genetic variation in populations of this species. This, as a basis to analyse the state of phenotypic and genotypic variation as presented in former chapters; and 2) mechanisms of reproductive isolation between wild, managed *in situ* and cultivated populations, in order to analyse causes of phenotypic divergence between populations in different environmental and human cultural conditions. These two aspects were compared in wild, managed *in situ* and cultivated populations in order to analize possible modifications of natural mechanisms of reproduction by human intervention.

Concerning the first general objective, this study was particularly directed to obtain information on mechanisms of asexual and sexual reproduction. In the first case, to know how vegetative propagation occurs and to evaluate in which extent it occurs in wild, managed *in situ* and cultivated populations. In the case of sexual reproduction, this study aimed at knowing aspects of floral biology such as morphology of flowers, events occurring during anthesis, breeding systems and flower visitors, in order to know mechanisms of pollination as well as to confirm occurrence and evaluate proportion of in-breeding and out-breeding systems.

Concerning the second general objective, this study was restricted to analyse comparatively phenology of populations from different areas. Through this study, information on temporal behaviour of flowering and production of fruits in individuals and populations was searched. Comparisons of phenology between wild, managed *in situ* and cultivated populations were carried out in order to determine if artificial selection has been directed on the temporality of production of flowers and fruits and in which extent. In other plant species, domestication has affected phenology, favouring continuous flowering or synchronic patterns of flowering. This information was also directed to explore if any barrier for pollen exchange between wild and cultivated populations and between populations of diffrerent geographic areas.exists due to differences in temporality of blooming. Also, this study was directed to compare phenology of *Stenocereus stellatus* with that of *S. pruinosus* and *S. treleasi*, two species closely related, sometimes sympatric and with which interspecific hybridisation is suspected. This comparison was carried out in order to confirm if temporal pollen exchange is possible in nature between these species. A complete record of the flowering cycle for 1995 is included in this study.

2.METHODS.

CLONAL PROPAGATION

Based on direct observations in field, a description of mechanisms of vegetative reproduction in natural populations was made. This was complemented by information on genetic markers discussed in the former chapter in order to analyse proportions of clones in different populations. Spatial distribution of clones and area covered by them was visualized by mapping position of individuals within transects sampled as indicated in former chapters. Locations of individuals in the space were defined by measuring distance between each individual sampled through measuring tapes and by orientating direction from each other individual through a compass. Points of location were put in a map of the transect drawn on millimetre scaled paper. Based on this information, densities of genotypes per population were calculated. Relative importance of vegetative reproduction in populations was estimated as a rate between raw density of individuals, as calculated in Chapter 3, and density of genotypes.

FLORAL BIOLOGY

Floral morphology

A description of floral morphology was made. Two samples of 30 flowers each from two populations were considered in this description. The two populations studied were the wild population of Zapotitlán, in the Tehuacán Valley, and the cultivated population from Chinango in La Mixteca Baja region. Among populations studied, these two occur in different extremes of environmental and human cultural conditions. These populations were considered in the study in order to explore magnitude of variation in floral characters. Also, these descriptions were directed to explore syndromes of pollination which would be useful to corroborate or support information on systems of pollination and pollinators. Description of flowers included measures, carried out by using a calliper, of the following morphological characters:

1. Floral tube length. Distance comprised between the top of corolla and the point of insertion of the flower on areole.
2. Maximum diameter of corolla. Distance comprised between the extremes of opposite sepals.
3. Maximum diameter of floral tube light.

The first two characters account for the general form and size of flowers. Robustness of flowers is generally an important character taken into account to analyse pollination syndromes (Rowley, 1980). The third character was considered useful to visualize magnitude of the entrance of flower visitors which is important considering that bats, birds and bumble-bees were among possible visitors.

4. Volume of nectary. Diameter and height of nectaries were measured and volume was estimated by approaching a model to calculate volume of spheric or ellipsoid bodies $\mathbf{2(2\pi r^2h/3)}$, where **r** is 1/2 of the maximum diameter of nectaries and **h** their maximum height. This is a character related with amounts of nectar produced per flower and it is also correlated to the type of pollinator. In cacti, as in many plants, bee-pollinating flowers present small and hidden nectaries producing small amounts of concentrated nectar, while bird- and bat-

pollinating flowers present relatively big nectaries producing abundant and diluted nectar (Rowley, 1980).

5. Distance between top of nectaries and top of floral tube This character was considered also in order to explore role of flower visitors in pollination. For instance, some visitors such as hummingbirds or hawkmoths are able to take nectar from outside the flowers while others are forced to get into them.

6. Mean length of filaments of stamens. Ten filaments per flower chosen at random were measured.

7. Mean size of anthers. Estimated as the product of length by width of anthers of 10 stamens chosen at random.

These two characters, together with number of stamens are related to amount of pollen produced by flowers. Stamens in all flowers of this species are numerous and difficult to count. Therefore, these characters were considered as possible comparative units to analyse differences in pollen yield. Bat-pollinating flowers in cacti produce very abundant pollen, while bird- and hawkmoth-pollinating flowers produce moderately abundant and bee-pollinated flowers produce the least abundant pollen (Rowley, 1980).

8. Length of the style of pistil. Distance comprised between the top of ovary and the base of stigma. This character was considered in order to explore possible morphological mechanisms to prevent self-pollination in this species.

9. Length of stigma lobes.

10. Volume of ovary. Estimated in the same way as volume of nectary considering the maximum diameter and height of ovary.

These two characters were considered in order to explore their possible relation with differences in amounts of seeds and fruit size existing between these populations as analysed in Chapter 4. Length of stigma lobes could be related to efectiveness to catch pollen and volume of ovary with amount of ovules,

Univariate differences were tested through one-way Analyses of Variance while multivariate significant differences between populations were tested through a Discriminant Analysis. These analyses were carried out by using STATGRAPHICS programme.

Events occurring during anthesis.

Samples of five flowers were observed in three different populations in order to record timing of events occurring during anthesis. In particular, time of starting of anthesis, discharge of pollen from anthers, maximum turgency of stigma and closing of flowers. Observations were carried out in intervals of 30 minutes from 18:00 to 9:00 hours.

Amounts of nectar produced during anthesis was measured in a wild population (Zapotitlán) and a cultivated population (Chinango-C). Records were carried out over three flowers every hour from 22:00 p.m when flowers just opened to 6:00 a.m when flowers started to close. In each population, 27 flowers were covered with mosquito net exclusion bags before anthesis in order to avoid consumption of nectar by vistors. Three flowers were collected every hour and amounts of nectar measured and recorded by using calibrated capillary tubes and 3 ml hypodermic syringes.

Breeding systems.

Experiments were carried out in field, aimed at knowing occurrence and proportion of self-pollination and out-crossing in *Stenocereus stellatus* and occurrence and proportion of diurnal and nocturnal pollination. Based on methods developed by Valiente-Banuet *et al.* (1995 a) for studying breeding systems of *Neobuxbaumia tetetzo* in the same study area, the following experimental treatments were established in different populations: 1) automatic self-pollination; 2) manual self-pollination; 3) cross-pollination, 4) nocturnal pollination, 5) diurnal pollination, and 6) natural pollination.

At least ten flowers per treatment were included in each sample per population. Treatments were prepared by labelling and covering with exclusion bags flowering buds the afternoon just before blooming. Then, the treatments were managed by discovering and covering flowers as follows:

1. Automatic self-pollination. The development of excluded flowers were only followed until their abortion or until maturation of fruits produced by them.

2. Manual self-pollination. Excluded flowers were pollinated by hand with their own pollen. Paint brushes were used. This treatment was included in order to be sure that pollen got contact with estigmas.

3. Cross-pollination. Flowers were pollinated by hand with pollen from flowers of other individuals.

4. Nocturnal pollination. Flowers were exposed to nocturnal visitors by removing the bags from 21:00 to 05:00 hours (before blooming and just before sunrise respectively)

5. Diurnal pollination. Flowers were exposed to diurnal visitors from 06 00 Ito 9:00 hours (sunrise time and time after flowers closure).

6. Natural pollination. A sample of non excluded flowers was marked and followed until their abortion or maturation of fruits produced by them.

Number of aborted flowers and successful fruits as well as seeds produced by them in each treatment were counted. Numbers were compared between treatments. This was made in order to analyse effectiveness of diurnal and nocturnal visitors in pollination as well as to compare proportion of fruits and seeds produced through self and cross-pollination

Flower visitors and seed dispersors

Purposes in this part of the study were to identify which species visit flowers of "xoconochtli" and evaluate their relative importance in pollination. Several groups of animals were expected to visit flowers of this species. According to studies of Valiente-Banuet *et al.* (l 995 a) and Valiente-Banuet *et al.* (submitted) on pollination of *Neobuxbaumia tetetzo* and other columnar cacti, it was possible to expect species of birds, insects and bats as visitors. For this reason, different methods were used for traping flower visitors.

Bats, hawkmoths and birds were captured by mist-nets. Three nets were put in different points of populations the same day that experiments on breeding systems were carried out. Nets were put from 19:00 hours, before blooming time, to 9:00 hours, just after flowers closure, and were revised continually. Samples of pollen were collected from bodies of animals captured by using small squares of jelly fucsine. These squares were applied to the body of captured animals in order to trap pollen grains. Then, fucsine squares were mounted on a microscope slide and then melted by using a candle. Identification, counting and comparisions of amounts of pollen grains of *Stenocereus stellatus* transported species captured were carried out. For identification of pollen of *Stenocereus stellatus,* the Catalogue of Pollen of Plants from the Tehuacán Valley, which is in preparation by Valiente-Banuet *et al.,* was used.

A collection of insects visiting flowers of this species was done. They were captured when they were inside the flowers and then immobilized in a vial containing a piece of blotting paper with ethyl acetate as a killing agent. Then, insects were pinned on to entomological pins. Pollen was not sampled from bodies of insects captured.

Bats captured were kept in captivity until defecation in order to corroborate presence of pulp and seeds of *Stenocereus stellatus.* Birds were observed and identified when eating fruits of xoconochtli. Faeces of bats and birds from Zapotitlán and Chinango-C populations that were observed to have eaten fruits of this plant species were collected by Godinez and Valiente-Banuet from the Centre of Ecology, U.N.A.M., in order to test germination.

PHENOLOGY

Flowering buds and fruits growth.

Samples of 25 flowering buds in two different populations were followed through time, recording every trhee to ten days growth of flowering buds from appearence to anthesis and growth of fruits from anthesis to fruit maturation. These records were done in order to compare mean duration of flowering and maturation of fruits between a wild and a cultivated populations (Zapotitlán and Chinango-C respectively) where flowers and fruits maintain significant differences in several characters. Records of growth included length and diameter of flowering buds and fruits. Size of flowering buds was estimated by approaching a model to calculate volume of cylindrical bodies: $\mathbf{S=\pi r^2 h}$ where **S** is de size of flowering buds in cm^3, **r** is 1/2 of the diameter and **h** the length of buds measured. Size of fruits was estimated by approaching a model to calculate volume of spheric and ellipsoid bodies as done for studies in morphological variation.

Dynamics of flowering and fruit production in populations

Individuals and populations studied were the same sampled for morphological and genetic variation studies referred in former chapters. Based on methods suggested by Dafni (1992), part of the study of dynamics of flowering at population level was directed to register flowering magnitude of individuals per population. This was carried out by quick countings of the number of individuals flowering every two weeks in samples of populations studied. Registers were done between April and September 1995. The following magnitudes were considered for organising the information obtained:

1) Appearing of first flowers.
2) To 25% of the individuals flowering.
3) 25 to 50% of the individuals flowering, the rest still with closed buds.
4) 50% or more of the individuals flowering.
5) 25% to 50% of the individuals flowering, the rest already withered.
6) Less than 25% of the individuals flowering.
7) End of flowering (less than 10% of the individuals flowering).
8) Flowering complete.

Other part of the study included periodical visits every two to four weeks from April to November 1995. Detailed information on number of flowering buds, flowers in anthesis, immature and mature fruits per branch were registered for each individual during these visits.

A long stick with a mirror in the top was used as tool to ease observation of crowns of tall branches and counting. These data were used to define the following parameters according to Dafni (1992):

1. Flowering commencement, that is the date of the first flowering.
2. Rate of flowering, which is defined as the cumulative number or percentage of flowers in anthesis through time.
3. Peak of flowering, which is the date of maximum number of flowers per individual and flowering plants per population.
4. Flowering duration, which is the flowering duration of the sample in days.
5. Flowering termination, which is the last date of flowering.

Finally, general observations were recorded on reproductive season of *Stenocereus pruinosus* in Zapotitlán, Coxcatlán and Chinango, and on reproductive season of *S. treleasi* in the Central Valley of Oaxaca, near Oaxaca City. The purpose of recording this information was to confirm temporal possibilities of pollen flow between these species

3. RESULTS

CLONAL PROPAGATION

Vegetative propagation occurs in nature. In a first way, an old branch starts to die getting a gray colour first and then brownish. These branches progressively bend and finally fall down. The remaining living meristemes give rise to new plants which produces their own roots and grow independently from the rest of the older plant. The new individuals can be observed ordered in lines corresponding to the form of the branch that gave rise to them. In a second way, meristems from parts of roots exposed to the surface of soil give rise to photosinthetic stems. These stems produces their own roots but that are connected with the principal individual from whose roots they were produced and then may become independent Under cultivation, vegetative propagation is carried out by people through planting in vertical or horizontal position pieces of stems or young branches.

FLORAL BIOLOGY

Floral morphology

Flowers of *Stenocereus stellatus* are solitary at the areolas, typically appearing at the top of the plant forming a crown, but sometimes below of the top in rows along the ribs when vegetative growth occurs after commencement of flower differenciation. Britton and Rose (1920) and Bravo-Hollis (1978), described flowers being red or pink. However, in this study it was observed that tepals are bright red or pink in their external appearance but. when the flower is completely open their internal appearance so exposed is white or pale pink These authors also described flowers as narrowly campanulate or tubular, although in this study they were observed being rather funnelform. Floral tubes or cups, like in all Cactaceae, are complex structures formed by joining of the bases of stamens, the bases of the sepal-like and petal-like structures, and the upper part of the stem branch bearing the flower (Benson, 1982). At the base of the flowers the inferior part of the floral tube forms an outer coat of the ovary, bearing small scale-leaves subtending wool and bristly spines. This structure is called pericarpel by Bravo-Hollis (1978). The upper part of the floral tube is thick, fleshy, constituted by scale-leaves larger than those of the lower part. The stamens are numerous attached to the floral tube, with white filaments and cream anthers. The pistil is shorter than the perianth, with a stigma presenting 9 lobes (Figure 1). During anthesis, that occurs at night, flowers produce an unpleasant scent, fermented or cauliflower-like, very characteristic of flowers of other species of columnar cacti from the area that are pollinated by bats.

Details on dimensions of structural parts of the flowers are presented in Tables 1 and 2. Morphological characters of flowers were observed variating in contrasting environments and conditions of management by people. Table 3 summarises information from one-way Analyses of Variance per character. Table 4 indicates that the two sets of flowers analysed are significantly different, according to a multivariate Discriminant Analysis. Table 5 shows actual and predicted groups of flowers according to this analysis. It indicates that there are significant differences in all characters analysed and that in general, flowers from Chinango are bigger than flowers from Zapotitlán.

At the level of this information, size, colour and form of flowers; size of nectaries and number of anthers, suggesting relatively high yields of pollen and nectar; as well as odor of the scent produced by flowers during anthesis correspond to a syndrome of bat-pollinated flowers, according to Faegri & Van der Pijl (1979), Grant & Grant (1979) and Rouley (1980).

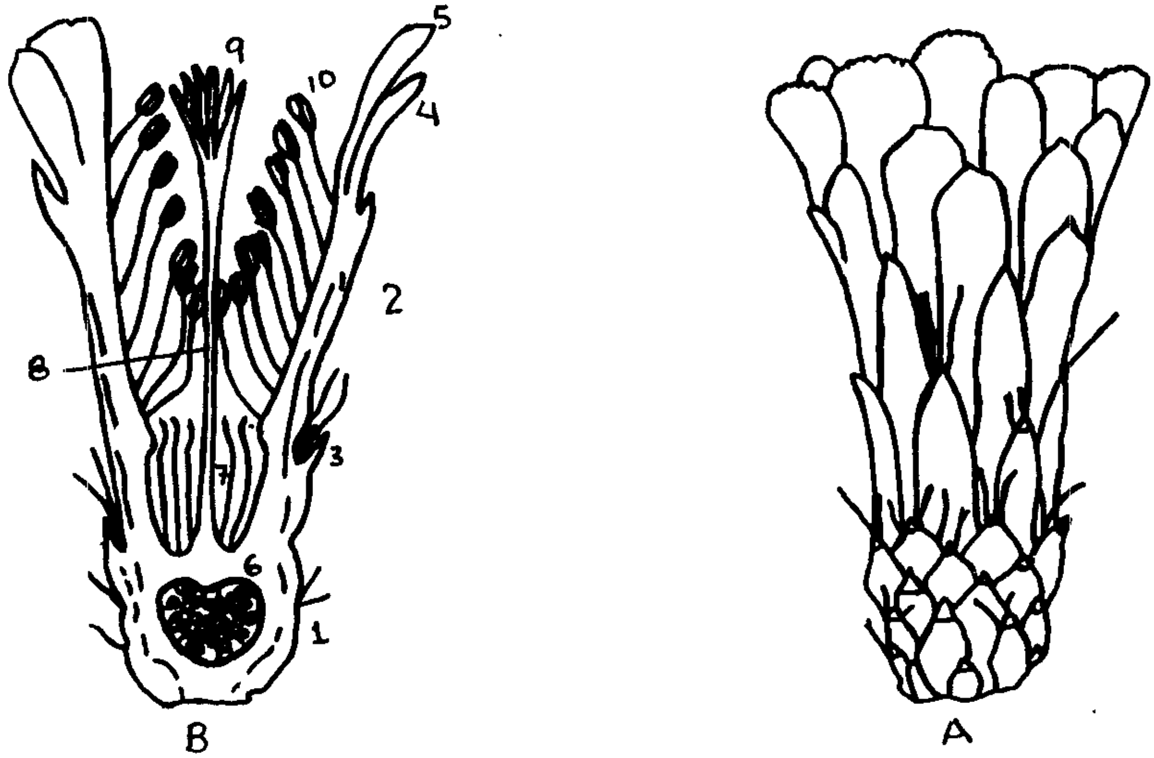

Figure 43. General scheme of a flower of *Stenocereus stellatus*. A) Exterior aspect, B) longitudinal section: 1) pericarpel; 2) floral tube; 3) scale-leaves; 4) exterior segments of the perianth; 5) interior segment of the perianth; 6) cavity of the ovary; 7) nectarial chamber, 8) style; 9) stigma lobes; 10) stamens. C) A flower in anthesis.

TABLE 1. MEASURES OF MORPHOLOGICAL CHARACTERS OF FLOWERS FROM A WILD POPULATION FROM ZAPOTITLAN IN THE TEHUACAN VALLEY

Flower	Tube length	Corola diam.	Tube diam.	Nectary volume	Dist. corola/ nectary	Filament length	Anther size	Style length	Lobe length	Ovary volume
Z1	5.11	2.92	2.03	2.084	2.65	1.28	0.023	2.41	0.36	0.712
Z2	3.61	3.34	1.87	1.459	2.01	1.32	0.025	2.36	0.34	0.518
Z3	4.76	3.47	1.83	1.836	2 37	1.41	0.029	2.28	0.43	0.602
Z4	5.08	3.68	1.70	1.949	2.20	1.45	0.025	2.32	0.50	0.702
Z5	4.91	3.46	1.81	1.846	2.24	1.39	0.029	2.39	0.39	0.577
Z6	4.46	3.51	1.84	1.731	2.21	1.28	0.030	2.45	0.42	0.462
Z7	5.09	3.58	1.76	1.714	2.19	1.60	0.028	2.37	0.50	0.639
Z8	4.81	3.86	1.83	1.762	2.15	1.60	0.025	2.28	0.39	0.390
Z9	4.86	3.72	1.81	1.794	2.17	1.39	0.027	2.46	0.36	0.630
ZIO	4.78	3.45	1.82	1.852	2.01	1.48	0.030	2.50	0.48	0.577
Z11	4.85	3.48	1.82	1.635	1.97	1.53	0.026	2.38	0.35	0.647
Z12	4.96	3.32	1.80	1.942	2.16	1.47	0.030	2.24	0.42	0.627
Z13	4.82	3.88	1.73	1.963	2.22	1.39	0.026	2.61	0.41	0.713
Z14	4.23	3.45	1.64	1.682	2.13	1.40	0.024	2.70	0.38	0.857
Z15	3.99	3.31	1.65	1.715	1.96	1.41	0.025	2.42	0.36	0.904
Z16	4.75	3.79	1.82	1.744	2.07	1.50	0.024	2.37	0.37	0.815
Z17	4.46	3.81	1.78	1.752	2.20	1.38	0.029	2.41	0.40	0.550
Z18	4.80	3.80	1.76	1.734	2.29	1.60	0.023	2.30	0.39	0.823
Z19	4.13	3.44	1.60	1.678	2.15	1.26	0.023	2.31	0.42	0.613
Z20	4.24	3.54	1.85	1.857	2.47	1.38	0.026	2.36	0.31	0.979
Z21	4.32	3.48	1.76	1.794	2.32	1.41	0.023	2.32	0.36	1.130
Z22	3.96	3.42	1.68	1.522	1.90	1.56	0.025	2.41	0.34	0.762
Z23	4.21	3.81	1.73	1.928	2.51	1.60	0.024	2.37	0.40	0.919
Z24	4.02	3.78	1.70	1.635	2.09	1.40	0.022	2.42	0.51	1.127
Z25	3.92	3.38	1.63	1.539	1.89	1.37	0.028	2.60	0.39	0.889
Z26	3.86	3.18	1.56	1.466	1.91	1.50	0.031	2.47	0.43	0.620
Z27	4.21	3.67	1.72	1.734	2.16	1.45	0.027	2.57	0.46	0.776
Z28	4.01	2.45	1.99	1.731	2.17	1.20	0.030	2.22	0.34	0.443
Z29	4.06	3.36	1.49	1.800	1.88	1.47	0.024	2.37	0.40	0.373
130	4.33	3.13	1.68	1.867	2.81	1.27	0.027	2.90	0.47	1.745
Mean	4.453	3482	1.756	1.758	2.182	1.425	0.026	2.419	0.403	0.737
S.E.	0.066	0.049	0.027	0.094	0.034	0.016	0.000	0.021	0.008	0.041

TABLE 2. MEASURES OF MORPHOLOGICAL CHARACTERS OF FLOWERS FROM A CULTIVATED POPULATION FROM CHINANGO, IN LA MIXTECA BAJA REGION

Flower	Tube length	Corola diam.	Tube diam.	Nectary volume	Dist. corola/ nectary	Filament length	Anther size	Style length	Lob lenght	Ovary volume
CHI	5.26	3.26	2.11	2.018	2.47	1.46	0.033	2.59	0.41	0.958
CH2	4.97	2.97	1.92	1.878	2.40	1.49	0.028	2.42	0.47	0.804
CH3	5.42	3.48	2.25	2.237	2.61	1.57	0.034	2.63	0.41	1.055
CH4	5.31	3.48	2.21	3.106	2.56	1.60	0.035	2.60	0.45	1.313
CH5	5.66	3.62	2.39	2.934	2.72	1.56	0 038	2.58	0.49	1.102
CH6	5.28	3.69	2.15	2.590	2.70	1.63	0.034	2.69	0.46	1.215
CH7	6.16	3.89	2.86	4.265	3.12	1.57	0.047	2.70	0.51	1.206
CH8	5.65	3.92	2.28	3.399	2.85	1.67	0.036	2.66	0.48	1.468
CH9	5.46	3.88	2.20	3.473	2.63	1.65	0 042	2.56	0.53	1.368
CHl0	5.37	3.85	2.29	3.816	2.70	1.62	0 043	2.60	0.51	1.115
CH11	5.81	3.62	2.41	4.106	2.39	1.52	0 045	2.63	0.43	1.281
CH12	5.72	3.96	2.40	3.561	2.42	1.51	0.049	2.56	0.50	1.159
CH13	5.83	3.89	2.45	3.983	2.52	1.59	0 035	2.71	0.46	1.231
CHI4	5.76	3.68	2.46	3.827	2.60	1.60	0.042	2.87	0.43	1.224
CH15	4.98	3.91	2.02	3.357	2.58	1.49	0.039	2.76	0.50	1.291
CH16	5.74	3.83	2.35	3.398	2.71	1.60	0.032	2.66	0.49	1.320
CH17	5.89	3.52	2.46	4.056	2.63	1.53	0 029	2.70	0.54	1.106
CH18	5.66	3.91	2.38	3.898	2.70	1.55	0.033	2.73	0.55	1.210
CH19	5.81	3.61	2.42	3.798	2.59	1.61	0.039	2.69	0.50	1.380
CH20	5.72	3.88	2.31	3.933	2.62	1.57	0.045	2.65	0.47	1.541
CH21	5.93	3.82	2.45	4.200	2.65	1.49	0.045	2.74	0.53	1.206
CH22	5.68	3.59	2.42	3.875	2.65	1.51	0.033	2.71	0.52	1.293
CH23	5.76	3.80	2.36	4.232	2.73	1.61	0.032	2.76	0.50	1.594
CH24	5.94	3.89	2.51	4.688	2.75	1.60	0.042	2.70	0.52	1.093
CH25	5.95	3.72	2.48	4.707	2.80	1.49	0.047	2.72	0.48	1.161
CH26	5.67	3.91	2.36	3.714	2.60	1.53	0.038	2.71	0.50	1.368
CH27	5.45	3.82	2.15	3.730	2.57	1.60	0.033	2.69	0.49	1.451
CH28	5.73	3.87	2.43	4.345	2.58	1.59	0.038	2.72	0.49	1.206
CH29	5.68	3.90	2.37	4.181	2.73	1.61	0 035	2.71	0.53	1.346
CH30	5.75	3.85	2.41	3.880	2.71	1.52	0.039	2.73	0.51	1.262
Mean	5.633	3.734	2.342	3.640	2.643	1.565	0.038	2.67	0.489	1.244
S.E.	0.066	0.049	O027	0.094	0.034	0.016	0.000	0.021	0.008	0.041

TABLE 3. ONE-WAY ANALYSES OF VARIANCE FOR CHARACTERS OF FLOWERS FROM ZAPOTITLAN AND CHINANGO

Character	Source of variation	Sum of Squares	Mean Square	F-ratio	Sig. level
Tube length	Between groups	20.886000	20.886000	159.106	0.0000
	Within groups	7.613733	0.131271		
Corola diameter	Between groups	0.9500417	0.9500417	13.447	0.0005
	Within groups	4.0976567	0.0706493		
Tube diameter	Between groups	5.1450817	5.1450817	238.279	0.0000
	Within groups	1.2523767	0.0215927		
Nectary volume	Between groups	53.0912270	53.091227	199.911	0.0000
	Within groups	15.4032960	0.265574		
Dist. Corola! nectary	Between groups	3.1871500	3.1878150	93.404	0.0000
	Within groups	1.9795100	0.0341295		
Filament length	Between groups	0.2926017	0.2926017	39.998	0.0000
	Within groups	0.4242967	0.0073155		
Anthers size	Between groups	0.0020651	0.0020651	106.954	0.0000
	Within groups	0.0011199	0.0000193		
Style length	Between groups	0.9652017	0.9652017	71.092	0.0000
	Within groups	0.7874567	0.0135768		
Lobes length	Between groups	0.1109400	0.1109400	54.468	0.0000
	Within groups	0.1181333	0.0020368		
Ovary volume	Between groups	3.8537073	3.8537073	76.379	0.0000
	Within groups	2.9263843	0.0504549		

TABLE 4. DISCRIMINANT ANALYSIS FOR CHARACTERS OF FLOWERS FROM ZAPOTTTLAN AND CHINANGO CULTIVATED

Discriminant Function	Eigenvalue	Relative Percentage	Canonical Correlation	
1	8.8119536	100.0	0.94767	
Functions Derived	Wilks Lambda	Chi-Square	DF	Sig. Level
0	0.1019165	121.03087	10	0.00000

TABLE 5. CLASSIFICATION OF FLOWERS FROM ZAPOTITLÁN AND CHINANGO ACCORDING TO DISCRIMINANT ANALYSIS

Actual group	Predicted group 1		Predicted group 2		Total	
	Count	%	Count	%	Count	%
1	30	100	0	0	30	100
2	1	3.33	29	96.67	30	100

Events occurring during anthesis

During anthesis, three whorls of tepals were observed opening at different times as described below. Activity of anthesis started to be evident around 19:00 hours when the most external whorl of tepals began to separate. One hour later the middle whorl started also to open and around 21:00 hours the most internal whorl did the same. Around 22:00 hours flowers were completely open but stamens were grouped inclined towards the centre of the flower, lobes of stigma were closed together and flaccide, enclosed by stamens. One hour later (around 23:00) stamens got vertical posture and pollen started to be liberated. By this time, lobes of stigma started to open and to get turgency slowly, but they were completely open until two or three hours later (around 1:00 and 2:00). Flowers were open through the night and started to close around 6:00 when stamens and lobes of stigma incline towards the centre of the flower again and also whorls of tepals started to contract. Around 7:00 the internal whorl was completely closed and one hour later the whole flower was completely closed.

Table 6 shows amounts of nectar produced by flowers at different hours through anthesis in the wild population of Zapotitlán and the cultivated population of Chinango. These results can be appeciated in a graphic mode in the plot of figure 2. It can be observed that the peack of production coincides with the time when lobes of stigma are completely open and turgent.

These observations indicate that anthesis is predominately nocturnal, nocturnal visitors having chance to visit flowers during 7 hours while diurnal visitor only 2 hours. All visitors have chance to get both pollen and nectar, although amounts of these products are particularly abundant during the night. This information suggests that pollination most probably occurs from 1:00 to 4:00 when maximum turgency of stigma lobes coincides with the peak of production of nectar.

TABLE 6. PRODUCTION OF NECTAR DURING ANTTESIS IN FLOWERS FROM ZAPOTITLAN AND CHINANGO.

Amount of nectar (ml)					
Hour	Zapotitlán	Chinango	Hour	Zapotitlán	Chinango
	0.04	0.12		1.82	2.27
22:00	0.14	0.19	3:00	1.76	2.15
	0.10	0.16		1.96	1,86
Mean	0.093		Mean	1.847	
S.E.	0.029		S.E.	0.059	
	0.83	0.95		2.00	2.11
23:00	0.87	0.88	4:00	0.90	1.36
	0.79	0.92		1.45	1.85
Mean	0.830		Mean	1.450	
S.E.	0.023		S.E.	0.318	
	1.40	1.85		0.76	0.83
24:00	1.62	1.73	5:00	0.81	0.89
	1.56	1.65		0.59	0.72
Mean	1.527		Mean	0.720	
S.E.	0.066		S.E	0.067	
	2.05	2.20		0.60	0.71
1:00	2.21	2.45	6:00	0.50	0.63
	2.16	2.56		0.46	0.53
Mean	2.140		Mean	0 520	
S:E:	0.047		S.E	0 042	
	2.80	3.21			
2:00	2.50	2.98			
	2.60	3.37			
Mean	2.63				
S.E.	0.088				

Breeding systems

Tables 7, 8 and 9 show the results of experiments on breeding systems carried out in the wild populations of Zapotitlán and Coxcatlán in the Tehuacán Valley and the cultivated population of Chinango in La Mixteca Baja respectively. Table 10 shows numbers of flowering buds tested for automatic and manual self-pollination in the remaining six populations. And finally, Table 11 summarizes information from all experiments carried out, including total numbers of flowering buds tested in the different treatments.

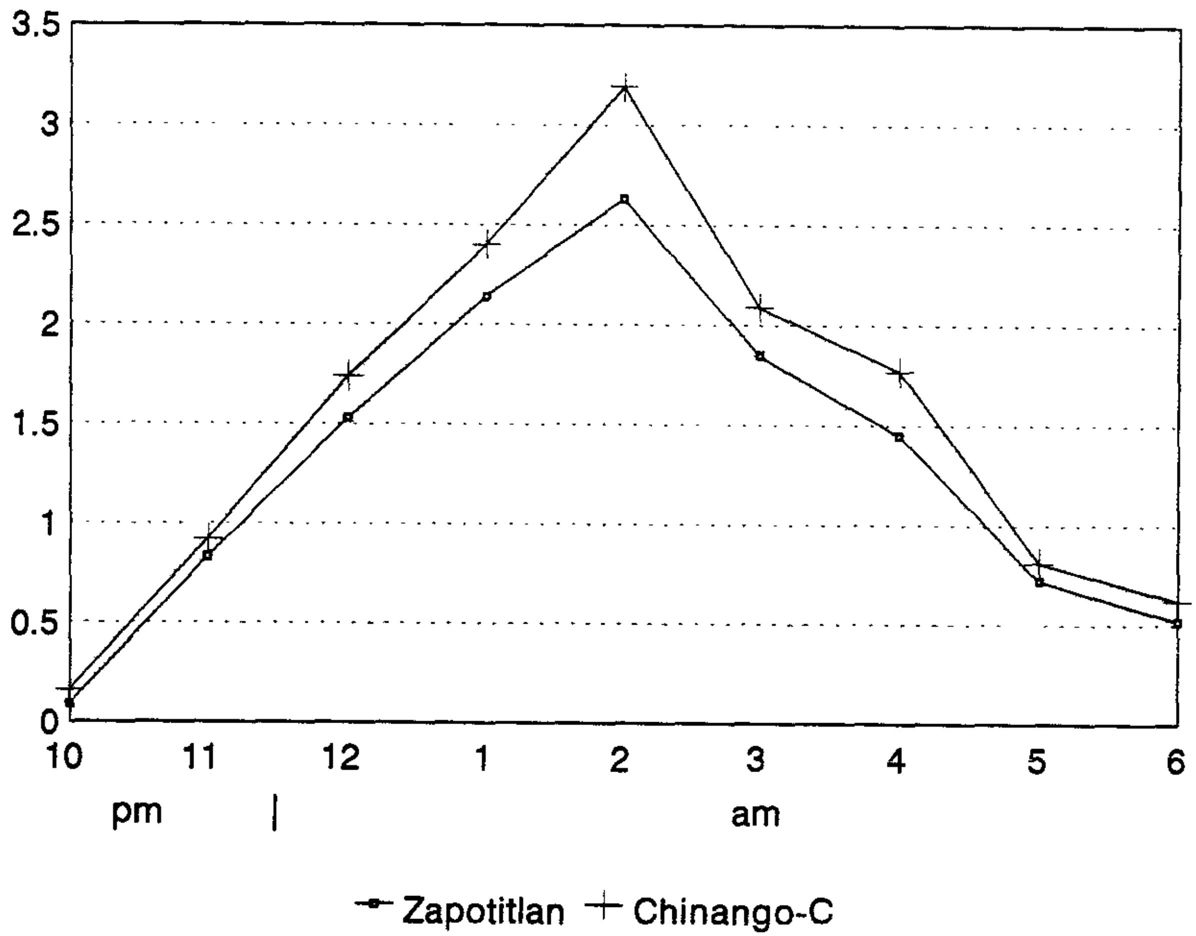

Figure 2. Production of nectar during anthesis in Zapotitlán and Chinango-C populations of *Stenocereus stellatus*

Results from these experiments indicate that self-fertilization did not occur in all flowers tested while some, although relatively low, production of fruits and seeds was obtained from manual cross pollination. Results also indicate clearly that successful pollination was achieved by nocturnal visitors while no pollination resulted from diurnal visitors.

TABLE 7. NUMBER OF FRUITS AND SEEDS PRODUCED IN DIFFERENT BREEDING TREATMENTS IN THE POPULATION OF ZAPOTITLÁN (JULY 1, 1995)

Treatment	Flowering buds	Aborted fruits	%	Successful fruits	%	Number of seeds Mean	S.E.
Automatic self-pollination	37	37	100	0	0	0	0
Manual self-pollination	10	10	100	0	0	0	0
Manual cross-pollination	10	4	40	6	60	290.33	47.78
Nocturnal pollination	10	2	20	8	80	951.25	24.09
Diurnal pollination	10	10	100	10	100	0	0
Natural pollination	20	5	25	15	75	933.60	35.07

TABLE 8. NUMBER OF FRUITS AND SEEDS PRODUCED IN DIFFERENT BREEDING TREATMENTS IN THE POPULATION OF COXCATLÁN (JULY 27, 1995)

Treatment	Flowering buds	Aborted fruits	%	Successful fruits	%	Number of seeds Mean	S.E.
Automatic self-pollination	20	20	100	0	0	0	0
Manual self-pollination	10	10	100	0	0	0	0
Manual cross pollination	10	5	50	5	50		
Nocturnal pollination	10	3	30	7	70	703.17	32.89
Diurnal pollination	10	10	100	0	0	0	0
Natural pollination	20	7	35	13	65	750.13	15.23

TABLE 9, NUMBER OF FRUITS AND SEEDS PRODUCED IN DIFFERENT BREEDING TREATMENTS IN THE CULTIVATED POPULATION OF CHINANGO (AUGUST 7, 1995)

Treatment	Flowering buds	Aborted fruits	%	Successful fruits	%	Number of seeds	
						Mean	S.E.
Automatic self-pollination	35	35	100	0	0	0	0
Manual self-pollination	20	20	100	0	0	0	0
Manual cross pollination	10	4	40	6	60		
Nocturnal pollination	20	5	25	15	75		
Diurnal pollination	15	15	100	0	0	0	0
Natural pollination	30	8	26.7	22	73.3		

TABLE 10. NUMBER OF FLOWERING BUDS PER POPULATION TESTED FOR SEF-POLLINATION. IN ALL CASES PERCENTAGE OF FRUITS ABORTED WAS 100%

Population	Date	Automatic self-pollination	Manual self-pollination
Chinango-W	August 6	22	10
San Juan Raya	July 23	12	8
San Lorenzo	July 25	20	10
Metzontla-M	July 29	15	10
Chinango-M	August 5	16	10
Metzontla-C	July 30	30	10

TABLE 11. TOTAL NUMBER OF FLOWERING BUDS AND ABORTED AND SUCCESSFUL FRUITS INCLUDED IN EXPERIMENTS ON BREEDING SYSTEM

Treatment	Flowering buds	Aborted fruits	%	Successful fruits	%
Automatic self-pollination	207	207	100	0	0
Manual self-pollination	98	98	100	0	0
Manual cross pollination	30	13	43.33	17	56.67
Nocturnal pollination	40	10	25	30	75
Diurnal pollination	35	35	100	0	0
Natural pollination	70	20	28.57	50	71.43

Flower visitors and seed dispersors

Table 12 shows a list of species of bats, birds and hawkmoths captured in mistnets as well as insects captured during their visits to flowers. Bats *Leptonycteris curasoae, Choeronycteris mexicana* and *Artibeus jamaicensis* presented pulp and seeds as the main component of faeces during fruit season. Birds *Melanerpes hypopolius* (Picidae), *Carpodacus mexicanus* (Fringillidae), *Zenaida asiatica* (Columbidae), *Mimus polyglotos* (Mimidae) and *Phainopepla nitens* (Ptilogonatidae) were observed consuming fruits of *S. stellatus.* Excretes were collected and tested for germination by Godínez and Valiente-Banuet. In preliminary experiments, seeds from digestive tracts of birds resulted to present especially high percentage of germination (Godínez and Valiente-Banuet, personal communication).

PHENOLOGY

Flowering buds and fruit growth

Tables 13 and 14 show data on the development of flowers and fruits respectively from the wild population from Zapotitlán while Tables 15 and 16 show the same information for flowers and fruits from the cultivated population from Chinango. Figures 3 and 4 are plots of mean values of information for development of flowers and fruits respectively in the two populations. This information shows generally that development of flowers and fruits from Chinango is slower than in Zapotitlán.

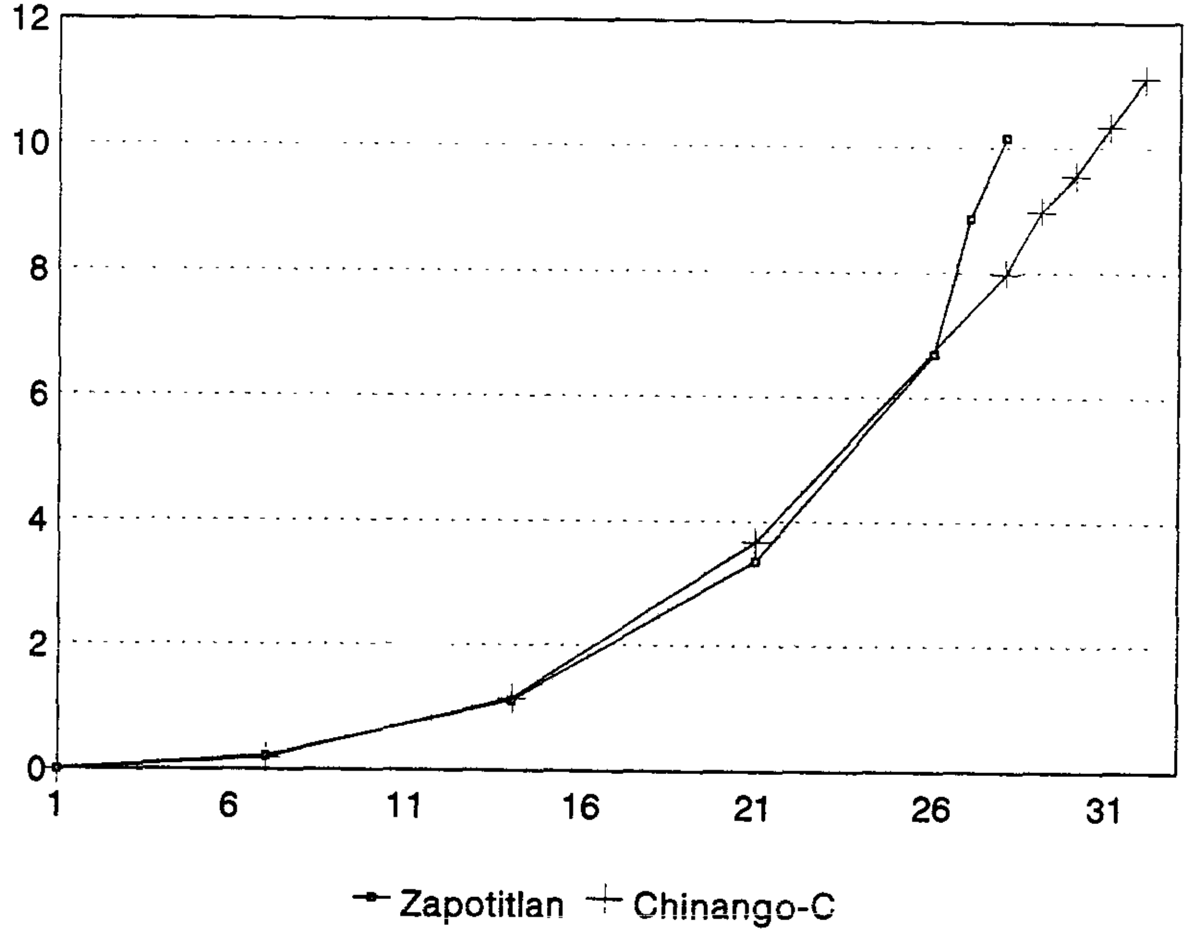

Figure 3. Development of flowering buds until anthesis in Zapotitlán and Chinango-C populations of *Stenocereus stellatus*

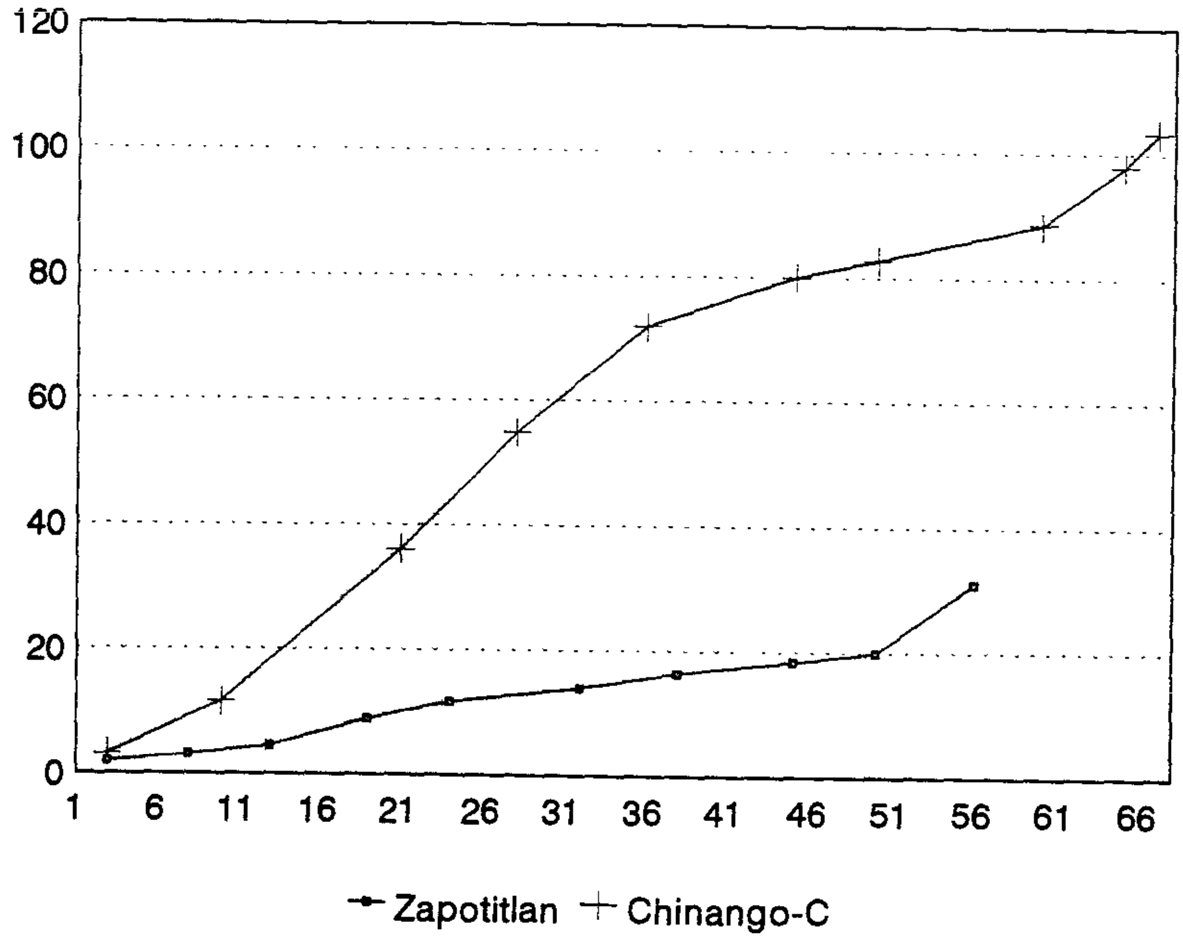

Figure 47. Development of fruits from anthesis to fruit maturation in Zapotitlán and Chinango-C populations of *Stenocereus stellatus*.

TABLE 12. ANIMAL SPECIES VISITORS OF FLOWERS OF *STENOCEREUS S'TELLATUS*

Group	Species	Habit
Insects	*Apis mellifera Hymenopthera* (Apidae)	Diurnal
	Mellipona sp. Hymenopthera (Apidae)	Diurnal
	Trigona sp. Hymenopthera (Apidae)	Diurnal
	Musca domestica Diptera	Diurnal
	Bombus spp. Hymenopthera (Apidae)	Diurnal
	Hawkmoth sp. I	Nocturnal
	Hawkmoth sp.2	Nocturnal
	Carpohylus sp. *1*	Diurnal-Nocturnal
	Carpohylus sp. 2	Diurnal-Nocturnal
Birds	*Amazilia violiceps* (Trochilidae)	Diurnal
	Cynanthus latirostris (Trochilidae)	Diurnal
	Melanerpes hypopolius	Diurnal
Bats	*Leptonycteris curasoae* (Glossophaginae)	Nocturnal
	Leptonycteris nivalis (Glossophaginae)	Nocturnal
	Choeronycteris mexicana (Glossophaginae)	Nocturnal
	Artibeus jamaicensis (Stemodermatinae)	Nocturnal

Dynamics of flowering and fruit production in populations

Tables 17 and 18 summarise information on dynamics of blooming among populations and Table 49 summarises general information of temporality of production of flowers and fruits. Figure 5 illustrates dynamics of production of buds, flowers and fruits through time for the nine populations. Information shows that flowering occured within a period of at least 91 days, with few flowers blooming per individual every night (see Table 18). Information also reveals that date of flowering commencement and termination may differ in more than one month between populations. However, except in San Juan Raya, peak of blooming season in all populations occurred between the first and third week of July. All populations overlapped their flowering periods in at least 75 days.

Although no detailed countings were carried out, *Stenocereus pruinosus* was observed starting production of flowering buds in late December and early January in populations from Coxcatlán, Zapotitlán and Chinango, sympatric to *S. stellatus.* Blooming period was observed from early February to mid may, with the flowering peak between the third week of March and the second week of April. Mature fruits are available from mid May to late June. From late March to mid May, therefore, exchange of pollen between *S. stellatus* and *S. pruinosus* is possible. This is possible also because *S. pruinosus* presents nocturnal anthesis and is

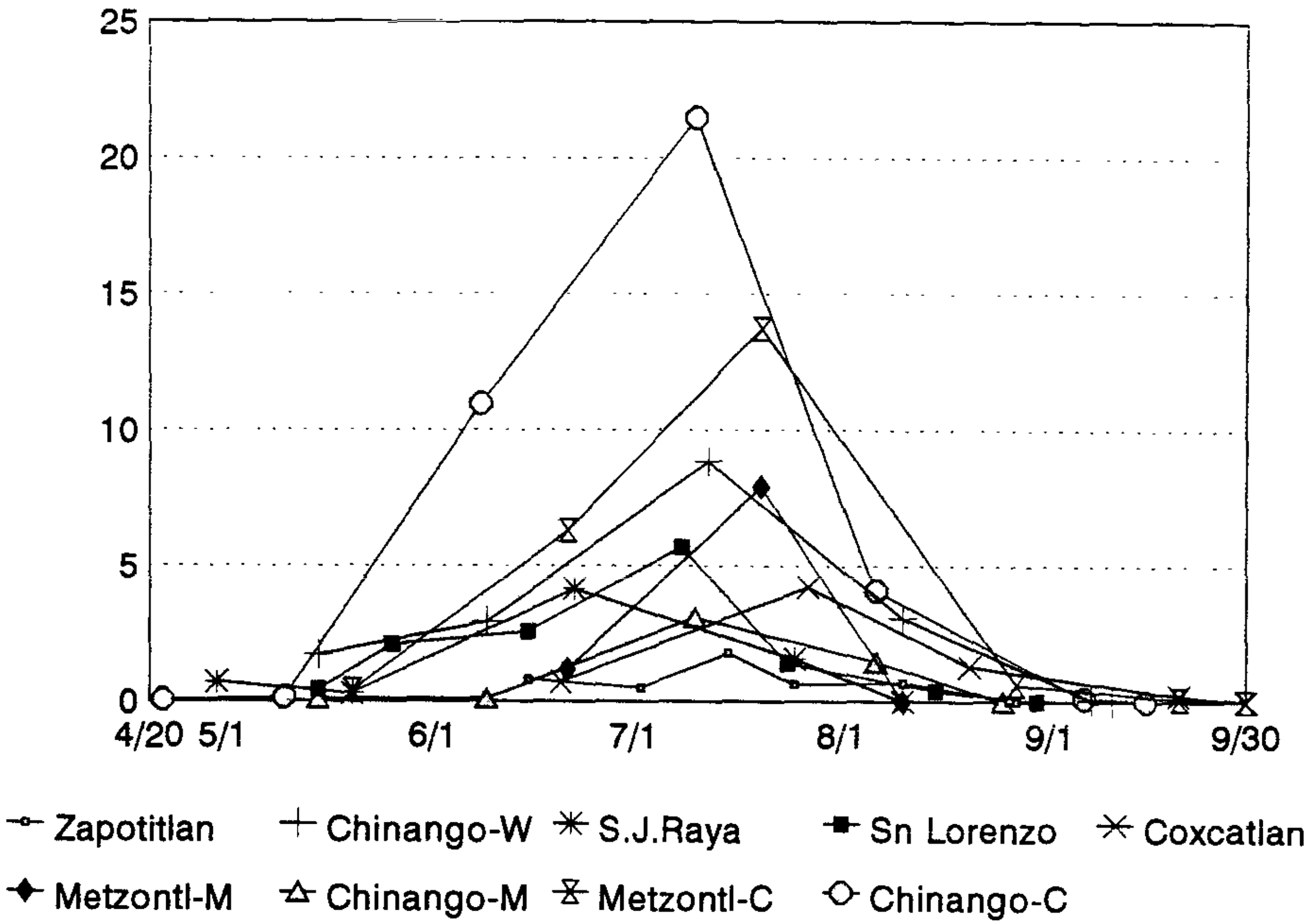

Figure 5. Dynamics of blooming among populations studied of *Stenocereus stellatus*.

pollinated by the same species of bats as *S. stellatus* (Valiente-Banuet, personal communication).

Stenocereus treleasi was observed starting production of flowering buds at late May in the Central Valley of Oaxaca, near Oaxaca City. Blooming period was observed between late June to August, with the flowering peak in July. Mature fruits are available from late August to early October. Phenology is similar to that of *S. stellatus.* However, except for some populations observed between Huajuapan de León and Oaxaca Cities, these two species rarely were observed occurring sympatric.

4. DISCUSSION

Information from this study reveals that *Stenocereus stellatus* in all populations studied presented a clear out-breeding system of sexual reproduction. Self-fertilisation failed in all cases for both automatic and manual self-pollination. This seems to indicate that individuals were incompatible to their own pollen. Self-incompatibility in *Stenocereus stellatus* would not be an isolated case among columnar cacti. Actually, all species of nocturnal-anthesis columnar cacti that have been studied in detail, including 10 species from the Tehuacán Valley and Balsas river Basin, have been reported in the literature as self-incompatible (Alcorn *et al.*, 1959; Alcorn *et al.*, 1962; Fleming et al., 1993; McGregor et al., 1959, 1962; Soriano et al. 1991; Valiente-Banuet *et al.* 1995 a, 1995 b and submitted).

Nevertheless, according to authors such as Proctor, Yeo & Lack (1996), the balance between self- and cross-pollination is especially flexible in plants. Thus, self-pollination often appears spontaneously in normal self-incompatible plants. For instance, these authors mention cases among apples, pears, plums, cherries and other species that as *S. stellatus* are also perennial plants, self-incompatibles and vegetatively propagated. In these plants, self-incompatibility may change somewhat from year to year. The degree of self-pollination, according to these authors, seems to be affected by pollination interactions and in the highly seasonal communities of the world where flowering is restricted by seasonality, this may be the most likely feature to respond (Proctor, Yeo & Lack, 1996). More evidence is therefore still recquired to conclude that self-incompatibility is a rule as breeding system of this plant species. It would be useful, for instance, to explore genetic diversity in samples of seeds as well as to investigate more precisely at which level self-fertilisation is stopped (stigma, style or ovule). It would be also necessary to repeat experiments, such as carried out in this study, at different moments of flowering season and in different years.

TABLE 14 GROWTH OF FRUITS FROM POLLINATION OF FLOWERS TO MATURATION IN THE WILD POPULATION OF ZAPOTITLAN (SIZE OF FRUITS IN CM^3)

Fruit	Days									
	3	8	13	19	24	32	38	45	50	56
1	2.12	3.96	5.41	11.10	13.02	15.20	16.45	18.21	19.26	30.12*
8	2.69	4.11	5.67	11.61	13.58	15.5	17.20	20.32	21.60	32.11*
10	2.27	+								
12	1.72	2.54	+							
13	1.81	+								
16	1.87	3.21	4.60	10.01	13.20	15.09	16.60	18.10	20.1	30.95*
18	2.03	3.48	4.27	9.27	12.76	15.20	19.84	19.90	20.80	32.06*
19	1.89	2.19	+							
20	1.75	2.95	4.01	6.85	9.78	11.80	+			
21	1.83	3.02	4.28	6.59	9.36	11.60	12.57	+		
22	2.02	3.31	4.56	9.87	12.90	15.31	18.63	18.70	19.50	31.29*
23	1.81	2.84	3.87	6.73	9.57	12.70	13.90	15.51	18.60	30 07*
Mean										
S E.										

+ Fruits death *
Fruits mature

Information on breeding systems also revealed that there were not differences between 'wild and cultivated individuals. Flexibility of breeding systems in plants has pennited human beings to favour self-pollination over cross-pollination sometimes in the history of plant domestication. One of the advantages for atificial selection of in breeding systems, is to ease fixation of desirable characters in progenies. In the case of *Stenocereus stellatus,* selection on this character is unnecessary because vegetative propagation permits fixation of desirable characters easily. Rather, out-breeding system seems to be an important advantage to generate new variation. Mother advantage of in-breeding systems is to reduce dependence on pollinators agents and sources of fertile pollen that characterise outbreeding plants. This could be especially important in plants vegetatively propagated, as is the case of *S. stellatus.* However, dynamic pollinator agents such as bats as well as technological measures such as cultivation of several variants of xoconochtli in home gardens may have contributed to solve possible problems in this direction and to do unnecessary selection against out-breeding systems.

TABLE 13. GROWTH OF FLOWERING BUDS UNTIL ANTHESIS IN THE WILD POPULATION FROM ZAPOTITLAN (SIZE IN CM^3)

Flowering Buds	Days 1	7	14	21	26	27	28
1	0	0.23	1.17	3.47	9.80*		
2	0	0.20	+				
3	0	0.17	+				
4	0	0.17	+				
5	0	0.23	+				
6	0	0.25	+				
7	0	0.23	1.06	+			
8	0	0.23	1.15	3.40	6.29	9.93*	
9	0	0.21	1.18	3.46	5.57	8.25	10.31*
10	0	0.20	1.07	3.40	6.02	9.85*	
11	0	0.18	1.02	3.25	5.46	7.97	9.98*
12	0	0.21	1.15	3.26	5.35	7.92	10.08*
13	0	0.22	1.16	3.30	5.46	8.02	10.28*
14	0	+					
15	0	+					
16	0	0.18	1.02	3.25	5.58	8.17	10.12*
17	0	0.24	+				
18	0	0.22	1.08	3.30	6.12	9.70*	
19	0	0.20	1.14	3.26	5.74	8.20	10.18*
20	0	0.19	1.06	3.29	6.15	9.78*	
21	0	0.26	1.17	3.43	6.08	9.75*	
22	0	0.27	1.20	3.50	10.27 *		
23	0	0.28	1.22	3.51	9.87*		
24	0	+					
25	0	+					
Mean	0	0.218	1.123	3.363	6.697	8.867	10.158
S.E.	0	0.007	0.017	0 026	0.483	0.272	0.051

+ Flowering buds death
* Flowering buds in anthesis

TABLE 15. GROWTH OF FLOWERING BUDS UNTIL ANTHESIS IN THE CULTIVATED POPULATION FROM CHINANGO (SIZE IN CM^3)

Flowering	Days								
buds	1	7	14	21	28	29	30	31	32
1	0	0.18	1.20	3.71	6.71	7.81	8.57	9.19	11.16*
2	0	0.17	1.16	3.68	7.81	8.60	9.14	11.20*	
3	0	0.17	1.10	3.70	7.56	8.87	10.65*		
4	0	0.19	1.16	3.74	6.96	7.71	8.61	9.27	11.38*
5	0	0.22	1.12	+					
6	0	0.19	1.11	3.69	6.45	7.42	8.28	9.06	10.80*
7	0	0.18	1.18	3.52	7.90	8.81	10.71*		
8	0	0.21	1.15	+					
9	0	0.20	1.15	3.73	6.70	7.50	8.43	9.12	11.08*
10	0	0.16	1.16	3.66	10.81*				
11	0	0.21	1.08	3.58	7.96	8.91	10.68*		
12	0	0.19	1.10	3.65	8.90	11.21*			
13	0	0.18	1.15	3.70	+				
14	0	0.18	1.20	3.76	7.98	9.02	11.12*		
15	0	0.22	1.21	3.80	8.21	10.80*			
16	0	0.21	1.21	3.79	8.02	10.65*			
17	0	0.19	1.12	3.60	7.12	7.89	9.27	11.20*	
18	0	0.16	1.09	3.57	7.68	8.92	9.36	11.36*	
19	0	0.17	1.11	+					
20	0	0.16	1.08	3.49	7.35	8.51	9.19	10.72*	
21	0	0.19	1.15	3.67	7.67	8.78	9.18	10.65*	
22	0	0.21	1.19	3.70	10.76*				
23	0	0.20	1.19	3.68	8.11	9.01	10.59*		
24	0	0.20	1.18	3.65	7.87	8.71	9.41	11.57*	
25	0	0.21	1.20	3.72	9.12	11.32*			
Mean	0	0.190	1.150	3.672	7.983	8.971	9.546	10.334	11.105
S.E.	0	0.004	0.009	0.017	0.244	0.275	0.246	0.331	0.120

+ Flowering buds death
* Flowering buds in anthesis

TABLE 16. GROWTH OF FRUITS FROM POLLINATION TO MATURATION IN THE CUT. CIVATED POPULATION FROM CHINANGO (SIZE IN CM^3)

Fruits	Days									
	3	10	21	28	36	45	50	60	65	67
1	3.21	11.51	32.31	51.28	75.21	83.81	86.10	89.21	96.36	98.76*
2	4.36	12.37	38.27	58.37	81.31	84.12	88.50	91.26	99.57	110.86*
3	3.81	11.72	36.12	45.26	63.12	75.45	79.25	81.32	92.37*	
4	3.10	10.96	34.15	42.12	59.62	72.18	81.43	86.13	91.17	96.27*
6	2.87	+								
7	2.96	11.01	+							
9	3.65	12.21	40.17	61.36	83.18	85.07	87.41	90.39	98.16	101.35*
10	3.01	11.17	35.13	44.62	61.17	72.36	74.71	79.87*		
11	3.21	11.67	33.91	55.43	75.17	76.59	78.26	80.12	87.98*	
12	2.91	10.85	27.86	47.91	70.15	75.47	77.01	86.52*		
14	2.78	+								
15	3.02	12.98	40.12	55.19	67.39	80.16	82.56	93.37*		
16	2.69	9.31	24.15	+						
17	3.56	12.31	41.12	63.52	85.16	86.46	88.01	92.36	101.25	105.27*
18	3.72	12.87	43.24	65.18	87.14	90.02	91.13	95.86	102.61	107.35*
20	3.75	12.91	41.17	63.21	72.15	85.66	87.12	94.61	103.81*	
21	3.22	12.22	37.61	60.10	69.29	81.16	83.47	91.18	98.36*	
22	2.71	+								
23	2.68	10.51	36.16	51.25	58.71	63.12	65.52	76.25*		
24	3.49	13.23	44.18	65.13	72.14	91.42	94.36	100.22	106.36*	
25	2.96	10.91	28.21	48.01	71.12	76.51	79.58	89.36*		
Mean	3.22	11.71	36.11	54.87	72.00	79.97	82.78	88.63	98.00	103.31
S.E;	0.100	0.242	1.361	1.957	2.230	1.863	1.776	1.636	1.704	3.176

+ **Fruits death**

* **Fruits mature**

TABLE 18. GENERAL INFORMATION ON DYNAMICS OF BLOOMING IN POPULATIONS.

Population	Flowering commencement (date)	Flowering peak (date)	Flowering termination (date)	Flowering duration (days)	Flowering rate (flowers/ day/sample)	Mean number of flowers per individual at flowering peak
Zapotitlán	June 3	July 15	Sept. 2	91		1.78
Chinango-W	May 2	July 12	Sept. 9	99		8.86
S.J.Raya	Apr. 22	June 22	Aug 19	119		4.14
San Lorenzo	May 8	July 8	Sept. 8	93		5.70
Coxcatlán	June 14	July 27	Sept. 27	105		4.21
Metzontla-M	May 24	July 20	Aug. 29	97		7.92
Chinango-M	May 15	July 10	Sept. 5	113		3.09
Metzontla-C	May 16	July 20	Sept. 30	137		13.73
Chinango-C	Apr. 21	July 10	Sept. 19	151		21.48

In summary, *Stenocereus stellatus* presents two general strategies of reproduction. Vegetative propagation, conservative in terms of variation, maybe as part of a natural strategy that permits successful phenotypes to extend in particular environments. And out-breeding sexual reproduction, appartently obligatory, very dynamic in terms of generation of variation, maybe as part of a natural strategy to generate phenotypic variation available to survive in inhospitable, unpredictable and diverse environments characteristic of the area studied. As described in the chapter on ethnobotanical studies, people make use of these two reproductive strategies to manage variation of xoconochtli. The most common form of management is by vegetative propagation, that permits to increase numbers of desirable phenotypes and to increase variation by introduction of new phenotypes from the wild and from other home gardens. The other is tolerance of seedlings in home gardens, that permits mainly to increase phenotypic variation generated by sexual means. This last is not as common as vegetative propagation, but certainly occurs, and it seems to be crucial to explain origin of variation that occurs exclusively in home gardens.

TABLE 19. GENERAL INFORMATION ON PRODUCTION OF FLOWERS AND FRUITS THROUGH REPRODUCTIVE SEASON

(NUMBERS WITHIN PARENTHESIS ARE WEEKS FOR A GIVEN MONTH).

Population	Flower differentiation	Blooming period	Fruit maturation	Mature fruits availability	Total duration of season
Zapotitlán	May (2)-Sep (1)	Jun (1)-Sep (1)	Jun (1)-Sep (4)	Aug (4)-Oct (1)	May (2)-Oct (I)
Number of day's	113	91	115	39	145
China :go-W	Apr (1)-Sep(2)	May(1)-Sep (2)	May (1)-Oct (1)	Jul (2)-Oct (2)	Apr (1)-Oct (2)
Number of day's	152	99	155	87	188
S.J. Raya	Mar (4)-Aug (3)	Apr (3)-Aug (3)	Apr (3)-Sep (3)	Jun (4)-Sep (4)	Mar (4)-Sep (4)
Number of days	144	119	151	63	186
San Lorenzo	Mar (4)-Sep (2)	May (2)-Sep (2)	May (2)-Oct (3)	Jul (4)-Nov (1)	Mar (4)-Nov (1)
Number of days	165	93	172	97	222
Coxcatlán	May (4)-Sep (4)	Jun (2)-Sep (4)	Jun (2)-Oct (3)	Sep (3)-Nov (1)	May (4)-Nov (1)
Number of days	128	105	128	47	168
Metzontla-M	May (l)-Aug (4)	May (4)-Aug (4)	May (4)-Oct (3)	Aug(4)-Oct (4)	May (1)-Oct (4)
Number of days	120	97	144	61	182
Chinango-M	Apr (3)-Sep (1)	May (3)-Sep (1)	May (3)-Oct (1)	Aug (1)-Oct (3)	Apr (2)-Oct (3)
Number of day's	141	113	145	72	179
Metzontla-C	Apr (3)-Sep (4)	May (3)-Sep (4)	May (3)-Oct (4)	Aug (3)-Nov (2)	Apr (3)-Nov (2)
Number of days	166	137	167	90	210
Chinango-C	Mar (4)-Sep (3)	Apr (3)-Sep (3)	Apr (3)-Oct (4)	Jul (2)-Nov (3)	Mar (4)-Nov (3)
Number of days	178	151	192	133	240

Information on floral morphology, events during anthesis and experiments on breeding systems seem indicate that bats are the most probable pollinators of this plant species. Capture of bats among flower visitors and observation of pollen in their bodies seem to corroborate such information. Certainly, bats could not to be the exclusive pollinators of *Stenocereus stellatus.* Most plant species are capable of being pollinated by a range of visitors, even if they are specialised and pollinated most efficiently by one or a small related group of visitors (Proctor, Yeo & Lack, 1996). In this study, hawkmoths were observed taking nectar from outside flowers of S. *stellatus,* apparently without any contact with the stigma or withers. This contrasts with foraging pattern of bats which get into the flowers becoming covered from head to shoulders with pollen and necessarily touching the stigma surface when look for access to nectar. These two patterns of nectar foraging might explain differences in amounts of pollen in bodies of bats and hawkmoths. All this, together with bat pollinating syndrome presented by flowers suggests that bats rather than hawkmoths are the effective pollinators of xoconochtli, but some participation of hawkmoths cannot be discarded. Also, although experiments indicated that diurnal pollinators were uneffective to pollinate flowers of this plant, their participation cannot be absolutely discarded.

However, the principal role of bats in pollination seems to be evident in S. *stellatus.* Bat species that participate in pollination of this plant *(Leptonycteris curasoae, L. nivalis* and *Choeronycteris mexicana)* are the three species of Northamerican specialised nectarivorous bats (Fleming *et al.* 1993). Some features of their relationship with *S. stellatus* and other columnar cacti of the area are illustrative of the extent of such specialisation. Valiente-Banuet *et al.* (1995 a) observed that in different nights from April to June in the Tehuacán Valley, *L. curasoae* and C. *mexicana* presented two peaks of nocturnal activity. One occurring between 19:00 and 23:00 hours and the other between 1:00 and 5:00 hours. In general, information from the present study, obtained from July to September corresponds with this information. It is interesting to compare this information with events during anthesis because during the first peak of bat activity liberation of pollen takes place and during the second peak the maximum production of nectar and turgency of stigma occur. This suggests that during the first peak bats are taking part of the nectar from the flowers and at the same time their pollen. In this way, during the second peak of activity, new vistis to flowers are carried out by bats with their bodies full of pollen from different flowers. This could imply that some flowers function as donnors of pollen and others as receptors. But this possibility seems not to be the most probable because Fleming *et al.* (1993) observed that when L. *corasoae* visits cardon *Pachycereus pringlei* flowers, bats may visit repeatedly the same flowers through the night. This is entirely possible because, as revealed by our phenological studies, few flowers are available fix the visitors every night. A flower visited during the first peak of bats activity continues producing nectar in apparently enough amount to attract visitors during the second peak of activity, especially because of the intermediate period of inactivity of bats.

Results of experiments on breeding systems indicating exclusive nocturnal pollination and information on floral biology indicating clear features of specialisation of flowers for interaction with bats, suggest that *S. stellatus* might depend strongly on bats for pollination. This observation is similar to that by Valiente-Banuet *et al.* (1995 a and 1995 b) in other 10 species of nocturnal anthesis columnar cacti of the Tehuacán Valley. An also it is similar to the pattern observed by Soriano *et al.* (1991) and Sosa and Soriano (1993) in 3 species of nocturnal anthesis columnar cacti from Venezuela. In these studies referred, columnar cacti were observed depending strongly on bats for pollination. This pattern contrasts with that presented by columnar cacti from Northern Mexico and Southern U.S.A. with partially nocturnal and partially diurnal anthesis which are pollinated by bats but also by bees and hummingbirds (Alcorn *et al.* 1959; Alcorn *et al.,* 1961; McGregor *et al.* 1959; McGregor *et al.* 1962; Fleming, 1993).

Authors such as Davis (1969); Cockrum (1991) and Fleming *et al.* (1993) have suggested that nectarivorous bats from tropics and subtropics of Mexico migrate into the Sonoran and parts of the Chihuahuan deserts in Northern Mexico and Southern U.S.A. during the spring and summer and return south in the fall. However, sampling of nectarivorous bats from July to September in this study, constitutes an evidence that nectarivorous bats are occurring in the Tehuacán Valley and Balsas river basin during the summer continuing their presence during spring, from April to June, as reported by Valiente-Banuet *et* al (1995 a). During summer time, not only *Stenocereus stellatus* but also other plant species such as near 16 *Agave* spp. which bloom from July to November (Gentry, 1982; Valiente-Banuet *et al.,* 1995 a) depend on bats for pollination. This confirm that at least some populations of nectarivorous bats are resident in the area, as discussed by Valiente-Banuet *et al.* (1995 a)

Participation of bats in pollination and seed dispersion of *Stenocereus stellatus* makes sexual reproduction of this plant species very dynamic in terms of generation of variation. Thus, although bats seem to restrict nocturnal activity to areas near caves where they roost (Flattery, et al. 1993) they potentially have the opportunity to move far away and to move with them pollen from different areas. Seed dispersion agents also may permit movement of seeds to new areas. This may contributes to explain why although particular populations do not present very high morphological or genotypic variation, this turns to be considerable when several population in a given area are considered, as observed by Parker & Hamrick (1993) in *Lophocereus schotli.*

Information on phenology indicates that development of flowers and fruits is more slow in Chimango cultivated population than in Zapotitlán. This could only be correlated to size of flowers and fruits which is higher in Chinango and it helps to explain why reproductive period in Chinango is longer than in Zapotitlán. Particular differences in starting and duration of the whole period of sexual reproduction among populations could also be related to differences in humidity. Among local people, it seems to be a concense that commencement, and duration of the rainy season and levels of precipitation directly influence commencement and duration of reproductive season as well as fruit yields. Although no precise information is available, certainly rainy season started early in San Juan Raya and late in Coxcatlán. More studies would be necessary to confirm these observations. However, influence of humidity in sexual reproduction of columnar cacti seems to be important as revealed by Pimienta-Barrios *et al.* with *Stenocereus queretaroensis.* This species starts flowering differenciation in January and ends fruit production in June (a dry season-reproduction). Authors experimantally tested that water supply before flowering differenciation resulted in an antagonic effect reducing significantly number of flowers per plant and delaying anthesis. In contrary, an agonic effect of water supply could be expected in species with rainy season-reproduction like *S. stellatus.* These authors also observed that water supply during anthesis increased amounts of seeds per fruit.

Two general features of phenology of *Stenocereus stellatus* seem to be relevant in relation to generation of variation and reproductive isolation. The first is the asynchronous pattern of production of flowers and fruits characterised by long blooming seasons and few flowers blooming per plant every night. This pattern has been discussed in relation to protection of reproductive structures against environmental adversities (Stephenson, 1981). But, according to Sosa & Soriano (1992), this pattern of production of flowers, also observed in other columnar cacti, constitues a mechanism that favours transference of pollen from one individual to other because flower visitors are forced to visit flowers from different individuals. The second feature is that blooming season overlaps in all populations studied for more than 75 days per year. This indicates that no temporal barriers are operating for reproductive isolation between populations. This aspect is very important to discusse what mechanisms of reproductive isolation are operating to explain divergence as presented in former chapters.

According to information from this study, not only no temporal barriers exist to avoid pollen flow between wild and cultivated populations but also participation of bats as pollinators permits to consider unlikely geographic isolation. In Chinango, for instance, no more than 200 linear metres separate wild and managed *in situ* populations and no more than 1000 linear metres separate wild and cultivated populations. While in Metzontla no more than 500 linear metres separate *in situ* managed and cultivated populations. All these distances within the range of movement of bats in one night. Geographic barrier could be more important between wild populations which are separated from each other fro 20 to 80 kilometres.

But if no apparent temporal and geographic barriers are operating between wild managed *in situ* and cultivated populations of a particular area, which factors then are causing the morphological divergence discussed before? One factor, as discussed, is artificial selection through which people spare and enhance desirable phenotypes within areas strongly influenced by them. This explains why only part of the variation existing in wild populations is present in home gardens and populations managed *in situ.* But although all variation existing in wild populations can be observed in home gardens, not all variation observed in home gardens occur in wild populations. This is, for instance, the case of variants with the biggest fruits with pulp colour different than red. Not only pollen but also seeds may travel from home gardens via bats and birds to wild populations. But the absence of these variants in wild populations suggests that different processes could be occurring. One of them is that seeds directly from these variants from home gardens fail to germinate or survival of seedlings or young plants is failing under wild conditions. The other is that hybrid seeds or plants derived from cultivated and wild individuals may possess lower fitness than seeds or plants arising within wild populations (Wallace effect, as discussed by Grant, 1981). All these hypotheses can be tested experimantally.

Origin of the home garden exclusive variants is uncertain for the moment. More detailed morphologic and genetic studies with these materials have to be carried out to put that in clear. They seem to have originated in home gardens and their arising can be explained by the dynamic reassortment of alleles permited by their out-breeding sexual reproduction. Interspecific hybridisation seems to be another probable source of variation. Although more detailed studies have to be carried out to confirm interspecific hybridisation and the status of interspecific hybrids of variants such as "xoconochtli aventurero", phenological information confirms that there are not temporal barriers and apparently geographic barriers either for interspecific hybridisation in the wild. Furthermore, participation of bats in pollination of these three species at the same time may cause interspecific hybridisation occurring commonly. Ethnobotanical and morphological information from this study suggests that such possible hybrids have been produced sometime and they have survived because of their maintenance by people in home gardens. Establishment of "xoconocthli aventurero" seem not to be successful neither in wild nor in managed *in situ* populations, where they were not observed