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DISPERSIÓN BIÓTICA DE SEMILLAS Y CARACTERIZACIÓN DE FRUTOS DE *Bursera morelensis* EN EL VALLE DE TEHUACÁN, PUEBLA

TESIS

QUE PARA OBTENER EL GRADO ACADÉMICO DE

DOCTORA EN CIENCIAS BIOLÓGICAS

PRESENTA

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Sin otro particular, me es grato enviarle un cordial saludo.

Atentamente
"POR MI RAZA HABLARA EL ESPIRITU"
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CONTENIDO

RESUMEN

Los estudios realizados en esta tesis se enfocan a describir el fenómeno de la partenocarpia (producción de frutos sin semilla) y a analizar su papel en la depredación de semillas, así como a caracterizar el proceso de dispersión de *Bursera morelensis* en una zona semiárida del Valle de Tehuacán. El primer capítulo está orientado a la comprensión de los diferentes términos y teorías del proceso de la dispersión de semillas en los sistemas áridos y semiáridos y en el género *Bursera* (Burseraceae), así como del fenómeno de la partenocarpia y su función o valor adaptativo en plantas en donde dicho fenómeno se presenta de manera natural. Todo ello bajo la idea de que no hay en la actualidad un trabajo que relacione todos estos factores en un mismo sistema.

Los siguientes tres capítulos se enfocan a analizar la partenocarpia, su función y la dispersión de semillas. Las tres secciones representan artículos que están en proceso de impresión o revisión en revistas de arbitraje internacional, el primero aceptado en la revista Annals of Botany, el segundo sometido al Journal of Avian Biology y el tercero sometido al American Journal of Botany.

En el primero se presenta una descripción del sistema reproductivo de *Bursera morelensis*. Se proporcionan datos sobre la producción de estructuras reproductivas (flores, frutos, semillas) y el origen sexual de las semillas. También se muestra evidencia del fenómeno de la partenocarpia en esta especie, mediante un análisis anatómico e histológico de los frutos, y se muestra la relación entre la depredación de semillas por insectos y la partenocarpia. En el segundo se analiza la función de la partenocarpia en la interacción ave-planta. Por un lado se muestra la manera mediante la cual el efecto de coloración y densidad, los frutos partenocárpicos funcionan como un factor de atracción

para las aves que se alimentan de *B. morelensis* y por otro, se evalúa la depredación de semillas por aves granívoras y su relación con la producción de frutos partenocárpicos, mostrando evidencia de que la partenocarpia es una adaptación de la planta para disminuir la depredación. El tercer artículo comprende el análisis de la dispersión biótica de las semillas de *B. morelensis*, considerando varias fases del proceso tales como, remoción de frutos, tipo de fruto removido (con semilla o partenocárpico), efecto de la endozoocoria en la germinación (velocidad y porcentaje) y, la probabilidad de que las aves depositen las semillas en sitios favorables para la germinación y establecimiento. En este se muestra la importancia del mantenimiento de la interacción ave-planta para la conservación de ambos participantes.

En el quinto capítulo se presentan las conclusiones de las investigaciones realizadas. En general este trabajo es el primero que contribuye al conocimiento de la partenocarpia a un nivel anatómico e histológico y en donde se muestra el papel de este fenómeno y su importancia en las interacciones ave-planta e insecto-planta.

ABSTRACT

This thesis is focused in the description of parthenocarpy (production of fruits without seeds) and in the analysis of its function related to seed predation and dispersal of the endemic tree *Bursera morelensis* in a semi-arid zone of the Tehuacán Valley. The first chapter is oriented to understand different concepts and theories of the process of seed dispersal in arid and semi-arid systems and in the genus *Bursera* (Burseraceae), as well as the phenomenon of parthenocarpy and its function or adaptive value in plants.

The next three chapters are focused to analyze parthenocarpy, its function and seed dispersion. The three sections represent papers that are in press or revision in international indexed journals. The first one was published in the Annals of Botany, the second submitted to the Journal of Avian Biology and the third paper was submitted to the American Journal of Botany. In the first paper, a description of the reproductive system of *Bursera morelensis* is provided, including an assessment of the origin of the seeds (sexual or asexual), and an anatomical and histological analysis of the fruits documenting parthenocarpy and its relation with insect seed predation. In the second paper the function of parthenocarpy in the bird-plant´s interaction is analyzed. First the presence of parthenocarpic fruits acted as a way to increase attraction by means of a coloration and density effect. Second, seed predation by granivorous birds and their relation with the production of parthenocarpic fruits is evaluated, showing evidence that parthenocarpy is an adaptation to avoid predation. The third paper include the analysis of the biotic seed dispersal of *B. morelensis* considering several phases of the process such as, fruit removal, type of removed fruit (with seed or parthenocarpic), effect of

endozoochory in germination (speed and percentage) and, probability that the birds deposit the seeds in favorable sites for germination and establishment. The importance of maintaining the bird-plants interaction for the conservation of both participants is highlighted.

In the last chapter the main conclusions of the research are presented. This work is, as far as we know, the first one that contributes to the knowledge of parthenocarpy both at an anatomical and histological level and it the ecological perspective.

CAPITULO I. INTRODUCCIÓN

La dinámica poblacional de las plantas se encuentra moldeada por una gran cantidad de factores y procesos tanto bióticos como abióticos. Entre los abióticos podemos citar el clima, los nutrientes y la fragmentación del hábitat. Entre los bióticos debemos considerar la fenología, los sistemas reproductivos, la polinización, la dispersión de semillas, la dinámica del banco de semillas, la germinación, el establecimiento, la sobrevivencia, la competencia y la depredación (Schupp 1995, Schupp & Fuentes 1995, Godínez-Álvarez et al. 1999, Rey & Alcántara 2000, Bleher & Böhning-Gaese 2001, Traveset 2002, Traveset et al. 2003, Gulias et al. 2004). Varios autores concuerdan en que independientemente del ambiente de que hablemos, la dispersión de semillas, la germinación y el establecimiento, son los procesos más importantes en la dinámica poblacional, ademas de que se ha llegado a considerar a la dispersión como la fase inicial (Molinari 1993, Levin & Muller-Landau 2000, Dalling et al. 2001).

En los sistemas áridos y semiáridos como el del Valle de Tehuacán, Puebla, la precipitación suele ser muy baja e impredecible, los suelos presentan temperaturas muy altas y un bajo contenido de agua (Valiente-Banuet & Ezcurra 1991, van Rheede & van Rooyen 1999), en tales condiciones ambientales, se considera que el establecimiento es el principal mecanismo modelador de la estructura de las comunidades de plantas (Valiente-Banuet 1991) y la dispersión biótica de semillas adquiere un papel secundario, pero importante dependiendo de la especie de planta de que se hable (Steenbergh & Lowe 1969, Godínez-Álvarez et al. 1999, 2002, Nogales et al. 2005, Spiegel & Nathan 2007).

La contribución de cada agente dispersor de semillas es diferente, y dependerá del comportamiento de forrajeo, de los patrones de selección de frutos, del tiempo que el animal retiene las semillas en el tracto digestivo y del efecto que esto tiene sobre la germinación, particularmente, en los sitios en donde se depositan las semillas (Jordano 1992, Schupp 1993, Loiselle & Blake 1999). Para evaluar el efecto que un dispersor tiene en relación al éxito reproductivo de una especie de planta es necesario conocer su eficacia, es decir, la proporción de semillas que son dispersadas por una especie en particular (componente cuantitativo), y examinar si los sitios en donde se depositan las semillas son favorables para la germinación y el establecimiento (componente cualitativo; Schupp 1993). Así, en las últimas tres décadas se han realizado alrededor de 40 trabajos en los que se evalúa algún componente de la efectividad de la dispersión (cantidad y/o calidad) en ambientes áridos y semiáridos, 19 con aves y 22 con mamíferos, reptiles y hormigas (Tabla 1), de manera que se ha acumulado evidencia sobre la importancia que de la dispersión de semillas puede tener en estos ambientes.

La endozoocoria puede favorecer la germinación de las semillas así como el crecimiento de las plántulas. Las aves y murciélagos son dispersores efectivos ya que transportan las semillas a grandes distancias, lo que le permite a la planta: (1) reducir la competencia denso-dependiente entre juveniles o con adultos ya establecidos (Janzen 1970, Venable & Brown 1988), (2) colonizar nuevos sitios (Chambers & MacMahon 1994, García 1991; Granados 1994; Pakeman 2001), (3) incrementar la variabilidad genética local (Mandujano et al. 1997) y, (4) transportar las semillas a sitios seguros localizados por debajo de plantas nodrizas, en donde existen condiciones adecuadas para la germinación y sobrevivencia de las plántulas (Mandujano et al. 1996, Steenberg & Lowe 1977, Hutto et al. 1986, McAuliffe 1988, Olin et al. 1989, Valiente-Banuet & Ezcurra 1991, Valiente-Banuet & Verdú 2007).

En particular, para el género *Bursera*, característico de zonas áridas y semiáridas en México, no hay información que analice detalladamente las distintas etapas del proceso de dispersión. A pesar de que se han descrito más de 100 especies del género *Bursera* (Espinosa et al. 2006), apenas suman 19 los estudios que evalúan las tasas de visita y el consumo de frutos de *Bursera* por diferentes especies animales (Tabla 2). Los trabajos realizados indican que los dispersores son aves frugívoras y frugívoro-insectívoras. Los frutos de *Bursera* destacan como un recurso importante para las aves durante la migración (Scott & Martin 1984 Bates 1992, Greenberg et al. 1993, 1995) y durante los periodos de escasez de alimento (Bates 1992, Stevenson et al. 2005). Así mismo se ha visto que las aves son importantes para las especies de *Bursera* debido a que presentan altas tasas de remoción de semillas y favorecen el establecimiento de sus plántulas (Clark & Clark 1981, Scott & Martin 1984, Trainer & Will 1984, Hammond 1995, Ortiz-Pulido & Rico-Gray 2006).

Bursera morelensis es una especie endémica de México, caducifolia y "aparentemente" dioica (las flores femeninas presentan anteras). Esta especie se distribuye en el bosque tropical seco de los estados de Guerrero, Morelos, Puebla y Oaxaca; su fruto es trivalvado, oblicuamente ovoide de 5 a 8 mm de largo y de 4 a 6 mm de ancho, ligeramente apiculado y la semilla está recubierta por un pseudoarilo amarillo pálido (Rzedowski et al. 2004, 2005). Salvo por los trabajos de Becerra y colaboradores, quienes incluyen a *B. morelensis* en una serie de análisis sobre la interacción con escarabajos herbívoros, la historia natural de la especie es desconocida (Becerra 1994, 2003a, 2003b, 2003c, 2005, Becerra & Venable 1999a, 1999b, Becerra et al. 2001). Verdú & García-Fayos (1998) citan que ésta es una especie partenocárpica (produce frutos sin semilla) pero no describen los frutos ni muestran evidencia. En el mismo año, durante un trabajo con el sistema reproductivo de *B. medranoana,* Cortes (1998) menciona la existencia de frutos "vacíos" en *B. morelensis*, que pueden ser producto de un lento desarrollo del óvulo. Becerril (2004) describe la anatomía del fruto pero no menciona la partenocarpia.

Durante el periodo de fructificación de *B. morelensis* de junio 2005 a mayo 2006, en San Rafael Coxcatlán, Puebla, se observó que en los árboles había frutos que en lugar de semilla estaban llenos de tejido o tenían larvas de insectos, esto sugería que la especie es partenocárpica pero además fue una prueba de que no todos los frutos tenían una semilla que pudiera ser dispersada. Las características de los frutos presentan un síndrome de ornitocoria (van der Pijl 1972), sugiriendo que las semillas son dispersadas por aves, pero si la especie produce frutos sin semilla, surgen interrogantes: ¿Por qué y para qué desarrolla estos frutos? y particularmente, ¿Cuál es el papel de estos frutos en la dispersión de semillas?.

Las plantas partenocárpicas, han llamado la atención de muchos naturalistas e investigadores desde la época de la antigua Grecia, a partir de entonces el hombre ha utilizado desde la agricultura tradicional hasta la llamada tecnología "terminator", para obtener una gran cantidad de especies cuyos frutos carezcan de semillas (Varoquaux et al. 2000). Ciertamente, las ventajas económicas de este fenómeno le han llevado a ser muy estudiado, con el fin de describir sus causas y desarrollo (Gillaspy et al. 1993, Varoquaux et al. 2000), sin embargo su función (valor adaptativo) es casi desconocida.

Darwin (1876) decía que esta característica era una condición de infertilidad de las plantas. Sturtevat (1890) escribió *"los frutos sin semilla son un claro ejemplo de un acontecimiento natural que perjudica la continuidad y distribución de las especies"*. Esta idea prevaleció hasta el trabajo de Coetzee & Giliomee (1987) quienes mostraron que los insectos (coleópteros y lepidópteros) ovipositan indiscriminadamente tanto en los frutos con semilla de *Protea repens,* como en los partenocárpicos, permitiendo que muchas semillas escapen a la depredación. En 1991 Zangerl y colaboradores mostraron que las mariposas *Depressaria pastinacella* prefieren ovipositar en los frutos partenocárpicos de *Pastinaca sativa* debido a que estos contienen menos furanocomarinas (toxinas) que los frutos con semilla. Wright (1994) confirmó que la sobrevivencia de las semillas de varias especies de *Protea* está correlacionada con la variación en el "seed set".

Traveset (1993) y Verdú & García-Fayos (1998) expusieron que la presencia de frutos partenocárpicos disminuye la probabilidad de que las semillas de *Pistacia terebinthus* y *P. lentiscus* sean depredadas por avispas. Ziv & Bronstein (1996) también indicaron que los frutos partenocárpicos funcionan como una barrera física para que las polillas no puedan ovipositar libremente en los frutos que contienen semillas. En 1998 Fuentes & Schupp observaron que en *Juniperus osteosperma* la partenocarpia disminuye la depredación de semillas por parte de *Parus inornatus* que es un ave granívora. Verdú & García-Fayos (2001) obtuvieron un resultado similar en su trabajo con *P. lentiscus* y las aves granívoras, no obstante, en estos dos estudios las correlaciones se hicieron utilizando el número total de frutos comidos por las aves y el porcentaje de frutos partenocárpicos presentes en el árbol, asumiéndose que todo fruto depredado tenía una semilla.

A pesar de que los estudios sobre la función de la partenocarpia son pocos, se ha demostrado que hay una reducción en la depredación de semillas, sin embargo su impacto en la dispersión sigue siendo desconocido. La limitante ha sido que no se pueden distinguir los frutos partenocárpicos de los que tienen semilla sin cortarlos del árbol (Traveset 1993) y por tanto no se sabe a ciencia cierta si los dispersores remueven una semilla o un fruto vacío. Jordano (1990) describe que *Carduelis chloris* puede arrancar cinco frutos por minuto de las plantas de *Pistacia lentiscus*, pero sólo ingiere tres ya que descarta los frutos sin semilla. Este trabajo sugiere que hay un mecanismo de selección de los frutos por parte de las aves depredadoras de semillas. En 1996, Obeso menciona que en un ambiente competitivo en donde las hembras de *Ilex aquifolium* fructifican simultáneamente y producen cosechas elevadas, los frutos partenocárpicos podrían ayudar a atraer frugívoros que dispersen las semillas de los frutos viables, pero esta hipótesis no fue comprobada.

Acorde con los antecedentes expuestos, los objetivos principales de esta tesis fueron:

- Describir el sistema reproductivo de *B. morelensis*, comprobando si esta es una especie partenocárpica y caracterizando los frutos de modo que sea posible distinguir en el árbol los frutos con y sin semilla.
- Determinar la función ecológica de los frutos sin semilla, esto es, si la partenocarpia reduce la depredación de semillas por insectos y aves granívoras y

determinar si la partenocarpia es un factor que afecta el papel de los frugívoros en la dispersión de sus semillas.

- Caracterizar el proceso de dispersión de semillas en *B. morelensis* haciendo énfasis en determinar el tipo de fruto que es removido por los agentes dispersores y determinar si este proceso tiene alguna importancia para la conservación de la planta.

Los resultados obtenidos se presentan en tres artículos sometidos a revistas de arbitraje internacional. El primero publicado en la revista Annals of Botany, el segundo fue sometido al Journal of Avian Biology y el tercero se encuentra en proceso de revisión por los coautores para ser enviado al American Journal of Botany.

En el primer artículo se describe la fenología y sistema reproductivo de *B. morelensis,* presentando evidencia de que la producción de frutos es el resultado de un proceso de absición escalonada de las estructuras reproductivas debido a una limitación por polen. De igual modo, se muestra el origen sexual de las semillas, y se comprueba la presencia de frutos partenocárpicos. Se describe por primera vez la partenocarpia a nivel anatómico y morfológico en una especie de *Bursera*, generando información que permite distinguir los frutos con semilla de los partenocárpicos en el árbol, y que puede ser utilizada en el estudio de la dispersión de semillas. Finalmente, se apoya la hipótesis que indica que la partenocarpia es una estrategia de defensa ante insectos depredadores de semillas y se presenta evidencia de que esta estrategia conlleva un ahorro energético para la planta.

En el segundo artículo se aborda la función de la partenocarpia en la interacción ave-planta. Por un lado se determinó la cantidad de frutos removidos y visitas realizadas por los frugívoros y el número y proporción de frutos partenocárpicos producidos. Los resultados mostraron que la partenocarpia es un factor que contribuye a aumentar la atractividad de la planta para los frugívoros mediante un efecto de coloración y densidad. En segundo lugar, se comprobó la hipótesis de que los frutos partenocárpicos reducen la depredación de semillas por aves granívoras. La posibilidad de diferenciar los frutos partenocárpicos de los que contienen semilla en el árbol, permitió relacionar la cantidad real de semillas que son depredadas con la cosecha total y partenocárpica producida por los árboles. A su vez, se presenta evidencia de que la partenocarpia es una adaptación de la planta para disminuir la probabilidad de depredación de semillas por aves granívoras.

En el tercer artículo se describe el proceso de dispersión de semillas tomando como base los componentes cuantitativo y cualitativo de la dispersión de acuerdo con lo descrito por Schupp (1993). Los resultados mostraron que cuatro especies de papamoscas (género *Myarchus*) son dispersores legítimos de *B. morelensis*, llevando una gran cantidad de semillas a los sitios en donde se distribuye la especie y con ello aumentando la probabilidad de que se lleve a cabo el establecimiento bajo plantas nodriza. Las altas tasas de remoción de frutos indican que *B. morelensis* es un elemento importante en la dieta de estos frugívoros migratorios. En conjunto los datos obtenidos permiten establecer la importancia de la conservación de la interacción dispersor-planta, misma que podría verse afectada por desfases en la fenología de la fructificación o la migración debido a factores como el cambio climático. En el último capítulo de esta tesis se hace una síntesis de los efectos que la partenocarpia tiene en el proceso de la dispersión y depredación de semillas, así como una serie de sugerencias de estudios que complementarían la información generada en este trabajo.

Tabla 1. Especies de plantas dispersadas por aves, mamíferos, reptiles y hormigas en ambientes áridos y semiáridos. Se proporciona la especie y la fuente.

Especies dispersadas por aves	
Acacia (23 especies)	Davidson & Morton (1984), Barnes (2001), Or & Ward (2003), Githiru et al. (2002)
Guaiacum sanctum	Wendelken & Martin (1987)
Pilosocereus maxonii, *Stenocereus eichlamii*	Wendelken & Martin (1988)
Cereus peruvianus	Silva (1988)
Lysiana exocarpi	Yan (1993)
Amyema preisii	Reid (1989), Yan (1993)
Lycium intrincatum, *Neochamaelea pulverulenta,* *Opuntia dillenii*	Valido & Nogales (1994)
Rubia fruticosa	Valido & Nogales (1994), Nogales et al. (2005)
Whitania aristata	Valido & Nogales (1994)
Phoradendron californicum	Larson (1996), Aukema (2004)
Neobuxbaumia tetetzo	Godínez-Álvarez et al. (1999, 2002)
Diferentes especies	Tebbich et al. (2004)
Opuntia puberula	Sortibrán et al. (2005)
Ochradenus baccatus	Spiegel & Nathan (2007)

Tabla 1. (Continuación).

Especies dispersadas por mamíferos, reptiles y hormigas	
Carnegiea gigantea	Steenbergh & Lowe (1977), Olin et al. (1989), Wolf & Martínez del Río (2000)
Camphoroamioideae	Davidson & Morton (1981)
Stenocereus griseus	Bosque (1984), Soriano et al. (1991, 1999, 2000), Sosa & Soriano (1993, 1996), Silvius (1995), Ruíz et al. (1997, 2000), Naranjo et al. (2003)
Chlorophora tinctoria, *Pilosocereus tillianus*	Soriano et al. (1991), Sosa & Soriano (1993, 1996)
Subpilocereus repandus	Soriano et al. (1991, 1999), Sosa & Soriano (1993, 1996), Naranjo et al. 2003)
Stenocereus gummosus	León de la Luz & Cadena (1991)
Opuntia streptacantha	Vargas-Mendoza & González-Espinosa (1992)
Festuca arundinacea	Knoch et al. (1993)
Melocactus violaceus	Côrtes et al. (1994), Vasconcellos-Neto et al. (2000)
Cáctaceas (3 spp.)	Fleming & Sosa (1994)
Prosopis flexuosa	Campos & Ojeda (1997)
Opuntia rastrera	Montiel & Montaña (2000)
Pilosocereus laniginosus	Soriano et al. (2000)
Cáctaceas (21 especies)	Rojas & Salinas (2002)

Tabla 2. Trabajos en los que se describe algún componente de la efectividad de la dispersión (cantidad y/o calidad) en diferentes especies del género *Bursera*.

Bursera	**Dispersor (es)**	**Referencia**
B. fagaroides	Aves (6 especies)	Ortiz-Pulido et al. (2000), Ortiz-Pulido & Rico-Gray (2000, 2006)
B. karsteniana	Aves (6 especies)	Poulin et al. (1994)
B. graveolens	Aves, iguanas, roedores	Clark & Clark (1981)
	Geospiza fortis, G. scandens, G. fuliginosa	Grant & Grant (1996)
B. inversa	*Lagothrix lagothricha*	Stevenson (2000)
	Ateles spp.	Stevenson et al. (2001)
	Aves (22 especies)	Stevenson et al. (2005)
B. microphylla	*Vireo vicinor*	Bates (1992)
B. simaruba	*Icterus galbula*	Timken (1970)
	Aves (39 especies)	Scott & Martin (1984)
	Aves (26 especies)	Trainer & Will (1984)
	Vireo griseus	Greenberg et al. (1993)
	Vireo pallens	Greenberg et al. (1995)
	Aves (8 especies)	Hammond (1995)
	Calocitta formosa	Ortiz-Pulido et al. (2000)
	Aves (27 especies)	Galindo-González et al. (2000)
	Aves (39 especies)	Graham (2002).

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CAPITULO II.

Parthenocarpy and seed predation by insects in *Bursera morelensis*

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Parthenocarpy and Seed Predation by Insects in Bursera morelensis

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† Background and Aims While parthenocarpy (meaning the production of fruits without seeds) may limit fecundity in many plants, its function is not clear; it has been proposed, however, that it might be associated with a strategy to avoid seed predation. Bursera morelensis is a dioecious endemic plant that produces fruits with and without seeds, and its fruits are parasitized by insects. Its reproductive system is not well described and no published evidence of parthenocarpy exists for the species. The purpose of this work was to describe the breeding system of B. morelensis and its relationship to seed predation by insects.
† Methods The breeding system was described using pollination experiments, verifying the presence of parthenocarpic fruits and apomictic seeds. Reproductive structures from flower buds to mature fruits were quantified. For fruits, an anatomical and histological characterization was made. The number of fruits in which seeds had been predated by insects was correlated with parthenocarpic fruit production.
† Key Results The major abortion of reproductive structures occurred during fruit set. The results discard the formation of apomictic seeds. Flowers that were not pollinated formed parthenocarpic fruits and these could be distinguished during early developmental stages. In parthenocarpic fruits in the first stages of development, an unusual spread of internal walls of the ovary occurred invading the locule and preventing ovule development. Unlike fruits with seeds, parthenocarpic fruits do not have calcium oxalate crystals in the ovary wall. Both fruit types can be separated in the field at fruit maturity by the presence of dehiscence, complete in seeded and partial in parthenocarpic fruits. Trees with more parthenocarpic fruits had more parasitized fruits.
† Conclusions This is the first time the anatomy of parthenocarpic fruits in Burseraceae has been described. Parthenocarpic fruits in B. morelensis might function as a deceit strategy for insect seed predators as they are unprotected both chemically and mechanically by the absence of calcium oxalate crystals.

Key words: Parthenocarpy, Bursera morelensis, predation, seeds, insects, breeding system, calcium oxalate crystals.

INTRODUCTION

Seed development is one of the key processes in angiosperm reproduction (Yadegari and Drews, 2004; Berger et al., 2006). The abortion of flowers, fruits and seeds is a physiological process in which plants can fit progeny levels according to resource availability avoiding predator-damaged seeds or genetically deficient ones (Janzen, 1971, 1977; Sorensen, 1982; Stephenson and Bertin, 1983; Evenari, 1984).

All species of the genus Bursera (Burseraceae) have seeds covered by a pseudoaril that has a colour contrasting with surrounding vegetation (Rzedowsky et al., 2004, 2005). These seeds possess all the features to be bird dispersed (Howe and Westley, 1988). Several studies have stressed the importance of seed dispersion of Bursera by birds (Scott and Martin, 1984; Trainer and Hill, 1984; Bates, 1992; Greenberg et al., 1993; 1995; Poulin et al., 1994; Grant and Grant, 1996; Ortiz-Pulido et al., 1999; Ortiz-Pulido and Rico-Gray, 2000; Graham, 2002; Stevenson et al., 2005) and other vertebrates (Clark and Clark, 1981; Evans, 1989; Stevenson, 2000; Stevenson et al., 2000). The genus has more than 100 species of trees and shrubs inhabiting tropical dry forests (Espinosa et al., 2006). Development of fruits and seeds in the genus are almost unknown except for Srivastava (1968) and Cortes (1998). Cortes (1998) described the production of apomictic seeds in Bursera medranoana, while Srivastava (1968) and Cortes (1998) reported that the development of ovules with respect to the ovary in B. delpechiana and B. medranoana suffered a delay giving the impression of a fruit without seed. The presence of parthenocarpic fruits has been reported for B. fagaroides and B. morelensis (Verdú and García-Fayos, 1998).

The production of parthenocarpic fruits has been regarded as a defensive strategy to lower predation probabilities of viable seeds (Zangerl et al., 1991; Traveset, 1993a, b; Ziv and Bronstein, 1996; Fuentes and Schupp, 1998; Verdú and García-Fayos, 1998, 2001). Insects lay eggs into fruits when ovules are still immature without knowing if the fruit will bear seeds. When fruits become mature only those larvae in fruits with seeds can survive (Scurlock et al., 1982; Coetzee and Giliomee, 1987; Jordano, 1989, 1990; Niwa and Overhulser, 1992; Mustart et al., 1995; Verdú and García-Fayos, 1998). Traveset (1993a) found a negative correlation between the number of parthenocarpic fruits in Pistacia terebinthus and the number of wasp-damaged seeds, suggesting that empty fruits can serve to lower predation risks. Ziv and Bronstein (1996) showed that moths avoid infertile seeds by flying away from trees where they find them thus reducing the impact on viable seeds.

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Zangerl et al. (1991) reported that butterfly larvae (*Depressaria pastinacella*) preferred the parthenocarpic fruits of *Pastinaca sativa* (Umbelliferae) due to the lower content of furanocoumarins (toxin) compared with seeded fruits.

The purpose of the present work was to determine the breeding system of *Bursera morelensis*, describing pollination and fruiting ecology, and following the maturation of seeds and fruits from the anatomic and histological perspective to determine the presence of parthenocarpic fruits or apomictic seeds in the plant, and its relationship with seed predation by insects.

MATERIALS AND METHODS

Study site

The study site was located near Barranca de Muchil in San Rafael Coxcatlán, in the southeast portion of the Tehuacan Valley, Puebla, México (18812′ and 18814′N; 97807′ and 97809′W), at 1000 m a.s.l. and has a dry climate with summer rains (Fernández, 1999). Mean annual temperature is 25 8C and mean annual rainfall 394·6 mm, with a dry season from November to May and a rainy season from June to October (Valiente, 1991). It is an alluvial fan where the predominant vegetation is tropical deciduous forest with 57 species of angiosperms reported (Fernández, 1999). It has a high soil diversity (Medina, 2000) resulting in the formation of different vegetal associations: the 'Fouquerial' dominated by *Fouqueria formosa* Kunt, the 'Cuajiotal' dominated by *Bursera morelensis* Ramírez, the 'Chiotilal' dominated by *Escontria chiotilla* (Weber) Rose and 'Cardonal' dominated by *Pachycereus weberi* (Coulter) Buxb. (Ríos-Casanova et al., 2004).

Species studied

Bursera morelensis is a dioecious tree endemic to Mexico. Male flowers are produced in paniculated or inflorescent racemes while female flowers can be solitary, in pairs or in short paniculates. Female flowers have non-functional anthers. Fruits are trivalvated ovoid (5–8 mm long; 4–6 mm wide). Seeds are covered by a yellow pseudoaril (Rzedowski et al., 2005). The tree was used to produce matches and now is used locally for live-fences (Reyes et al., 2004). It also has medicinal properties (Jolad, 1977). It is distributed in the tropical dry forests of the Mexican states of Guerrero, Morelos, Puebla and Oaxaca (Reyes et al., 2004; Becerra, 2005).

Breeding system

Phenology was described by monthly visits to the study area from May 2005 to May 2007. Forty individuals were observed and flowers, fruits and leaf production was followed.

The breeding system was determined using six trees, where three branches were randomly chosen for each treatment; in each branch ten inflorescences were chosen for each pollination treatment (10 inflorescences × 3 branches × 3 treatments × 6 trees). The total number of inflorescences used was 540 and total flowers was 5930. The experiment was carried out in May 2006 and was followed until January 2007, and was done separately from the phenological observations. The number of fruits formed after pollination, number of full-grown fruits, and fruits with and without seed was registered in each treatment. All fruits produced in the experiment were collected and dissected. Three pollination treatments were applied.

(1) Open pollination (control treatment: n = 2013 flowers). Inflorescences were marked and the number of flowers available counted. Flowers were exposed to biotic pollinators and abiotic factors. When they were dry, they were covered with mosquito mesh to avoid fruit loss.
(2) Manual pollination (n = 1992 flowers). Flower buds were enclosed before anthesis. Flowers were hand-pollinated using pollen from 12 male trees. Each female flower received pollen from three different male trees. Flowers were enclosed after pollination and fruit production was monitored.
(3) Pollination exclusion (n = 1925 flowers). Flower buds were enclosed with fine mosquito mesh and flowers left open were enclosed for the duration of their lives. Fruit production was followed.

Fruit development

Of the fruits formed in May 2005 and May 2006, 50 fruits were collected from 14 randomly chosen plants of *Bursera morelensis* in April 2006 and in April 2007, respectively, 11 months after flowering when they reached full size and maturity. Fruits collected in this part were independent of those of the pollination experiment. Total dimensions (width and length in millimetres), weight (dry and fresh in grams), colour and presence of odour (Berlanga, 1991; Martínez, 1996) were measured. External features were measured using an electronic caliper with a resolution of 0·01 mm. Fresh weight was measured using an analytical balance while the dry weight was obtained using a dryer to 70 8C until the sample reached a constant weight. Fruit type was noted (with or without seed).

Monthly collections of different stages of fruit formation were carried out to follow fruit development using anatomical techniques (López et al., 2005). Fifty fruits each month were collected between June 2006 and February 2007 from three randomly chosen trees. Fruits were collected and fixed in FAA (formol : acetic acid : 96 % ethanol : water, 1 : 0·5 : 5 : 3·5) and transported to the laboratory where they were embedded in paraffin and stained with safranin–fast green. Also collected were flowers which were embedded in LR-White and stained with toluidine blue. Fruits were dissected to describe all developmental stages. Fruits were classified according to their characteristics. Parts of the fruits were dried to critical point, coated with gold and observed under the scanning electron microscope (SEM).

Insect seed predation

The proportion of damaged seeds was determined, collecting 50 fruits from 23 randomly chosen trees.

Fruits were dissected and classified as fruits with or without seeds and damaged or undamaged. Insect-damaged fruits were those containing eggs or larvae inside or those presenting a hole by which the insect abandoned the fruit after hatching. The proportion of damaged and empty fruits was calculated and a correlation between variables was carried out.

To identify parasitic insects, 70 fruits were collected, isolated inside plastic bags and placed in total darkness until fruit maturation and the insects hatched. The insects were collected and preserved in 70 % alcohol for further identification by a specialist. To determine the timing of infection, 50 fruits were collected monthly from three randomly chosen trees and dissected to search for eggs or larvae. Fruits were collected in April 2007 when the fruits produced in May 2006 were maturing.

Data analysis

To analyse the breeding system, an ANOVA with arcsine square root-transformed data was used. Fruit size variation among fruit types was analysed using a one-way ANOVA. Correlations were carried out to test the relationship between crop size, number of parasitized fruits and parthenocarpic fruits. All analyses were done using SPSS (SPSS, 2003) and XLSTAT (Addinsoft, 2007).

RESULTS

Phenology and breeding system

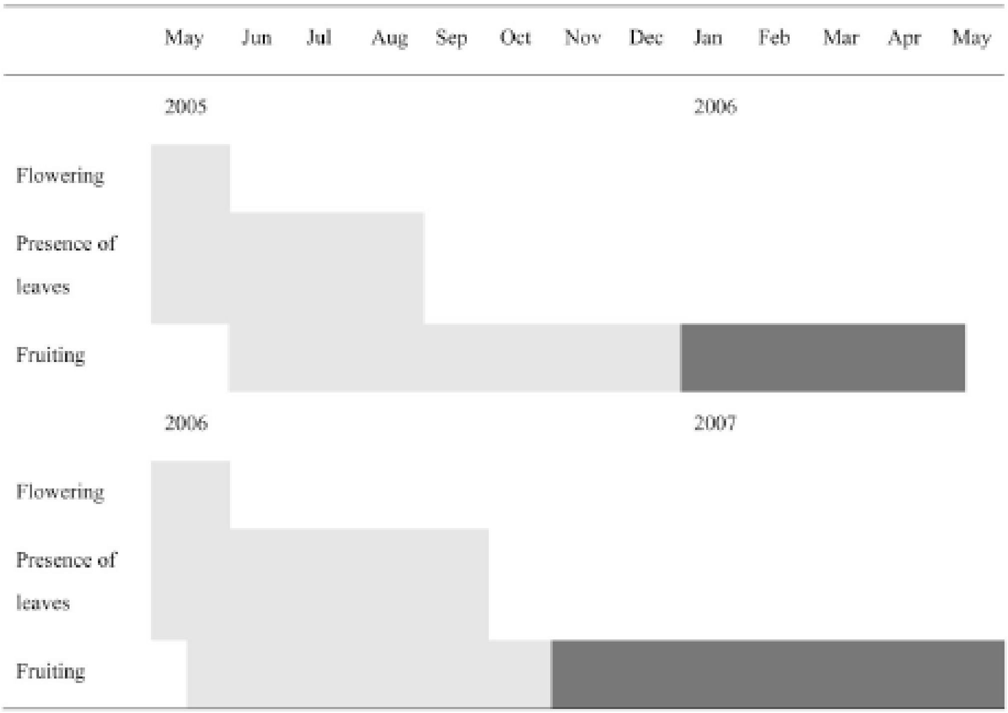
Flowering in B. morelensis was synchronic and occurred in the two observed years 1 week following the first rains (third week of May 2005 and second week of May 2006). Male buds formed earlier than female buds and anthesis followed the same pattern. Male flowers lasted between 5 d and 7 d while female flowers lasted between 3 d and 4 d. Pollination was completed by bees (*Apis mellifera*).

Anthers were present in the female flowers of B. morelensis but they were not developed and did not produce pollen.

Flowering lasted 2 weeks and after that immature fruits could be seen in trees. Immature fruits were green and reached their full size (7–8 mm) in 1 week. Maturation time was between 7 and 8 months with a maximum of 11 months (Table 1). Fruits became red when maturing.

Pollination experiments showed that there were two important times of fruit loss, the first from flower to fruit

TABLE 1. Phenology of Bursera morelensis for the 2 years of observations (May 2005 to May 2007) in the Tehuacan Valley, México. Light shading indicates the presence of flowers, leaves and immature fruits; dark shading indicates the presence of mature fruits



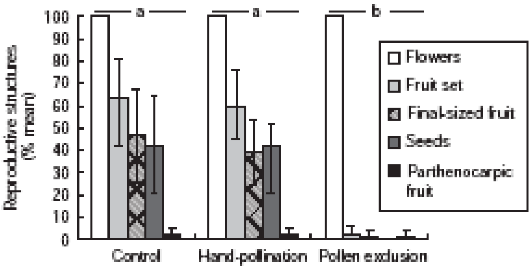


FIG. 1. Percentage mean of reproductive structures (+ s.d.) produced for Bursera morelensis in pollination experiment: flowers, fruit set, full-grown fruits, seeded and parthenocarpic fruits produced. Control and hand-pollination treatments (a) were different from pollen exclusion (b) for percentage fruit set ($F_{2,5}$ · 846·76, P , 0·001), final-sized fruits ($F_{2,5}$ · 649·8, P , 0·001), seeds ($F_{2,5}$ · 682·2, P , 0·001) and parthenocarpic fruits ($F_{2,5}$ · 14·5, P , 0·001).

(fruit set) and the second between fruit set and maturation (Fig. 1). In the open pollination treatments, 63·59 + 17·31 % of the flowers formed fruits (n · 2013 flowers) and 46·62 + 21·18 % of these reached full size. Most of those fruits had seeds (42·47 + 21·47 %) while the others had no seeds but presented two different types of tissues inside (2·23 + 2·77 %). Hand-pollinated treatments resulted in 59·34 + 16·97 % of fruit set (n · 1992 flowers) and 38·91 + 14·60% of full-sized fruits formed. Almost all these fruits formed seeds with only 2·73 + 1·89 % being seedless. In pollen-exclusion treatments only 2·26 + 4·01 % of fruit set (n · 1925 flowers), and of these only 1·54 + 2·99 % grew to full size and none contained seeds. The plant is self-incompatible and no pollen limitation is occurring (Fig. 1).

Fruit development

Overall, four different fruit types in Bursera morelensis were found (Fig. 2 and Table 2; n · 700 fruits). Fruit size was not different either in the total length or width, nor for fresh or dry weight (P . 0·05).

Type 1 fruit was red in colour and had three lines of dehiscence. Fruit opened completely separating three valves through these lines. The pseudoarile was orange surrounding the seed coat completely. The seed coat was formed completely, and the seed itself was trigonous measuring 5·7 + 0·7 mm in length and 5 + 0·3 mm in width. Seed colour was grey dotted with black.

FIG. 2. Fruit types of Bursera morelensis observed in the field: type I (a), type II (b), types III or IV (c). The photographs were taken from the same tree during the maturity stage in the Tehuacan Valley, México.

Type II fruits were also red, with the three dehiscence lines but, when ripening, dehiscence was incomplete in 100 % of cases. From a total of 280 type II fruits, only 191 were opened by one valve (68·2 %), 78 opened by two valves (27·85 %) and 11 (3·92 %) presented dehiscence in at least one valve but this was never complete. In the areas without dehiscence, the pseudoarile was not formed; in the areas with dehiscence the pseudoarile was orange. When some part of the seed with pseudoarile became exposed the exocarp dehydrated and the pseudoarile became brown. Seed measurements were 5·4 + 0·6 mm in length and 4·8 + 0·5 mm in width. Seeds were white dotted with black spots. The seed coat was not completely formed and presented two types of tissue: one hard and white with the other soft and translucent. The only way to separate fruits of type I and II in the tree was by observing valve dehiscence.

Fruit types III and IV were similar. They were green to red depending on maturation stage. Fruit tissues were not differentiated and no dehiscence formed. Type III presented one to two ovules and type IV presented a tissue instead of ovules in the locules.

Inside type III fruits three locules, each bearing two ovules, were found. When the fruit was growing (approx. 4–5 mm in diameter) only one locule persisted with one of the two ovules being aborted and the other developing into a seed. Usually, there was one seed per fruit. The ovary walls were well defined (Fig. 3). Inside type IV fruits all the locules were occupied by tissue with obliterated locules, ovary walls were diffuse, and ovules had either degenerated or were absent (Fig. 3). Type IV fruits represented parthenocarpic fruits and could be differentiated under a microscope from the first month after blooming.

In type III fruits, ovary layers showed a different arrangement than type IV fruit (Fig. 4). The tissue found filling the locule in type IV fruits was formed by cells from endocarp and mesocarp (Becerril, 2004) that grew into the locule squashing the ovule (Fig. 4).

In the seeded fruits (type III) the mesocarp and endocarp were formed by cells with relatively thick walls and calcium oxalate crystals. In the parthenocarpic fruits, cells were larger with thin walls and calcium oxalate crystals were absent (n · 21 fruits randomly chosen) (Fig. 5).

Type III fruit had small ovules that remained small for 5–8 months, after which they reached full size when they dehisced and were ready for seed dispersal. Type III fruits were classified as such when immature; however, upon reaching full size they became type I (Figs 3 and 6). Similarly, type IV fruit represented the immature phases of type II.

The outermost layer that protected the seed was a tissue derived from the endocarp. In the seeded fruits it was a continuous layer that protected the seed, but in the parthenocarpic fruits the layer was incomplete.

Insect seed predation

Of the fruits examined, 79·15 + 2·79 % (range 43·6–98·2 %) presented seeds, 17·6 + 2·2 % (range 1·75–45·45 %)

TABLE 2. Morphological characteristics of fruit types monitored in 14 trees of Bursera morelensis in the Tehuacan Valley

	Type I	Type II	Type III	Type IV
Colour	Red	Red	Green to red	Green to red
Smell	Resin	Resin	Resin	Resin
Length (mm)	7·54 + 0·44	7·45 + 0·36	7·33 + 0·58	7·34 + 0·53
Wide (mm)	6·27 + 0·26	6·27 + 0·28	6·41 + 0·12	6·42 + 0·14
Fresh weight (g)	0·49 + 0·02	0·48 + 0·05	0·48 + 0·04	0·48 + 0·02
Dry weight (g)	0·18 + 0·05	0·17 + 0·06	0·18 + 0·02	0·18 + 0·04
Pseudoaril	Complete, orange	Incomplete, orange	Not differentiated	Not differentiated
Seed	Complete, grey with black spots	Incomplete, white with black spots	Ovule or embryo	Indefinite tissue
Dehiscence	Complete	Incomplete	None	None

The values presented are mean + s.e. (n • 700 fruits).

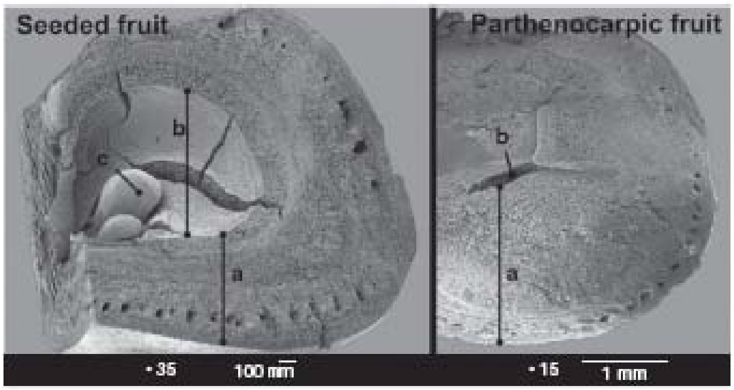


FIG. 3. Type III (seeded fruit) and IV (parthenocarpic fruit) fruits of Bursera morelensis. a, Ovary wall; b, locule; c, ovule. Both fruits are at less than 2 weeks of development. The photograph on the right shows the tissue that is filling the locules. Photographs were taken using a scanning microscope JEOL, model JSM-5310LV.

were parthenocarpic and 3·05 + 0·89 % (range 0–18 %) were parthenocarpic and parasitized by flies of the family Cecidomyiidae (Diptera) and wasps of the superfamily Chalcidoidea (Himenoptera; n • 1150 fruits, 23 trees, 50 fruits per tree). Insects began laying eggs on fruits in the seventh month of fruit development. Dissected fruits for the observation of fruit development showed also that insects visit the fruits in the seven month of development. It was not possible to determine hatching time. Only one larva per fruit was recorded and only in parthenocarpic fruits. Parasitized fruits could be easily recognized because the puncture that the insect made to insert eggs in fruits was full of resin forming a white scar. Of the 280 parthenocarpic fruits dissected 62 were parasitized, while of the 870 fruits with seeds examined none was parasitized. A negative and significant correlation between the percentage of damaged fruits and the percentage of parthenocarpic fruits in a tree was found (r^2 • 2 0·71, d.f. • 22, P , 0·05; Fig. 7).

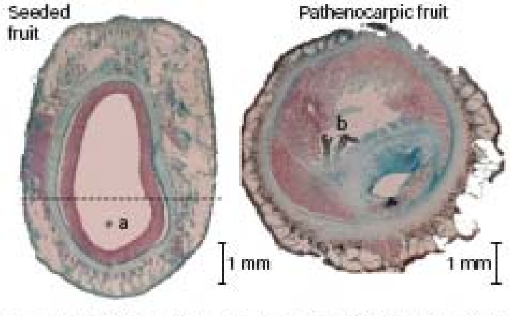


FIG. 4. Longitudinal section of a seeded fruit and transverse section of a parthenocarpic fruit of Bursera morelensis stained with safranin-fast green. a, Dormant ovule; b, aborted ovules. The dashed line in the seeded fruit represents the level at which the transvere section of the parthenocarpic fruit was taken. Scale bar • 1 mm. Micrographs were taken under an optic microscope (Olympus Provis AX70).

DISCUSSION

Breeding system

Flowering of B. morelensis occurred after the first summer rains in May. Flowering synchrony can be a strategy to avoid competition for pollinators (Frankie et al., 1974). This phenological pattern has been reported for several species of the tropical dry forests such as Plumeria rubra and Guazuma ulmifolia (Borchert et al., 2004). The delay of female flower maturation related to male flowers is a frequent pattern between dioecious trees (Lloyd and

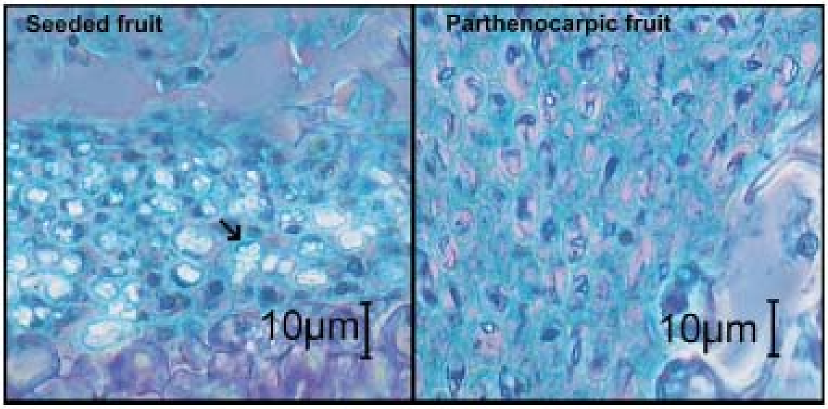


FIG. 5. Mesocarp of a seeded fruit and a parthenocarpic fruit. Calcium oxalate crystals, indicated by an arrow on the left, are absent on the right. Scale bar = 10 mm. Micrographs were taken with phase contrast under an optic microscope (Olympus Provis AX70).

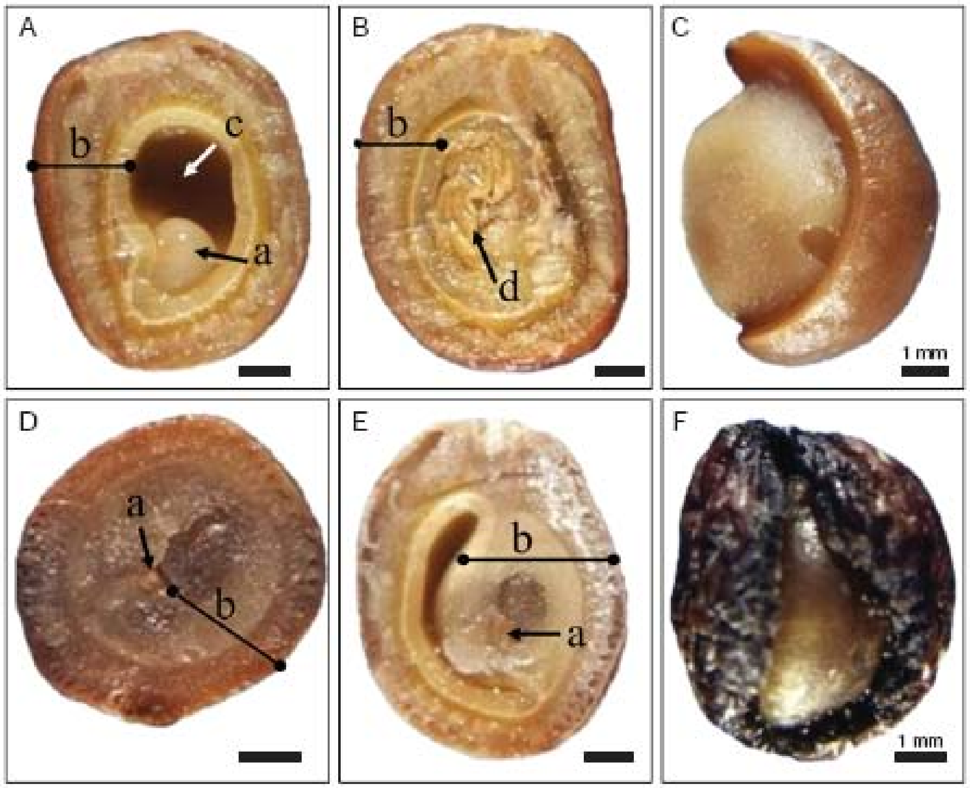


FIG. 6. Developmental stages of seeded (A–C) and parthenocarpic (D–F) fruits of Bursera morelensis. From left to right upper line, growing ovule (A), embryo in development (B), seed without a valve (C). In the lower line, fruit full of tissue with a developing ovule (D), fruit full of tissue squashing ovule (E), parthenocarpic fruit as can be seen in trees (F). a, Ovule; b, ovary wall; c, locule; d, embryo. Scale bar = 1 mm; Macrographs were taken with a stereoscopic microscope (Zeiss).

Webb, 1977; Obeso, 1996), and has been related to the higher energetic costs of female related to male plants (Lovett-Doust and Lovett-Doust, 1988).

Fruit set reported here for B. morelensis was similar to values reported by Jordano (1988) in the three pollination treatments and slightly lower that those reported by Verdú

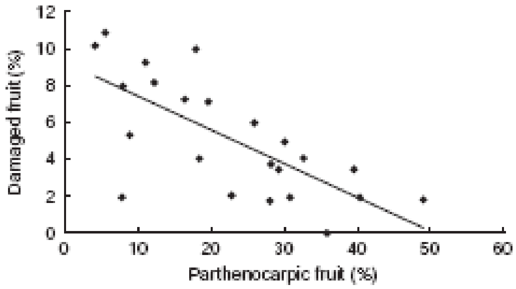


FIG. 7. Linear regression and correlation between percentage of parasitized fruits by insects and parthenocarpic fruits, in collected and dissected fruits of 23 trees of Bursera morelensis during April 2007, in the Tehuacan Valley Mexico (y · 20·1826x · 9·2655, R^2 · 0·71, d.f. · 22, P , 0·05).

and García-Fayos (1998) for P. lentiscus. Fruit production is limited by pollen availability as shown by the high abortion rate of enclosed flowers as stated by other authors (Jordano, 1988; Verdú and García-Fayos, 1998; Bañuelos and Obeso, 2005). Pollination can be affected by the number of pollinators available, number of visits and distance between trees of different sex in dioecious species (Pascarella, 1996; Bañuelos and Obeso, 2003; de Jong et al., 2005). Abortion can also be a consequence of environmental scarcity of resources, seeds being genetically deficient or seed predation and damage (Janzen, 1971, 1977; Stephenson, 1981; Aker, 1982; Ehrlén, 1991; Bañuelos and Obeso, 2005).

Seeds produced by B. morelensis clearly had a sexual origin. This if often related to the maintenance of high variability in the population that can ensure adaptation in the long term (Muller, 1964; Michod and Levin, 1988; Kondrashov, 1994; Hurst and Peck, 1996; Doncaster et al., 2000; Maynard-Smith and Szathmáry, 2001; Rice and Chippindale, 2001).

Fruit description and development

Parthenocarpic fruits in B. morelensis can be recognized and separated from seeded fruits in trees when maturation has finished because of the incomplete dehiscence of the valves; however, during the long period in which fruit are immature, these two types cannot be distinguished as is the case in many other angiosperms (Jordano, 1988; Traveset, 1993b; Fuentes, 1995).

There are many reports of plants producing parthenocarpic fruits but most of them involve an induced phenomena to produce seedless fruits for commercial purposes (Varoquaux et al., 2000; Ampomah-Dwamena et al., 2002; Zohary, 2004). In species where parthenocarpy is believed to exist naturally, there are no complete anatomical descriptions of fruit development. In P. lentiscus, parthenocarpic fruits presented only remnants of the funicule without any trace of embryos (Jordano, 1988), and in P. terebinthus the fruits presented remnants of both funicule and ovules (Traveset, 1993a). In B. morelensis traces of funicule and ovule were observed but a huge spread of probably mesocarp and endocarp was also found. This suggests that different factors (environmental, genetic, physiological) may promote the production of parthenocarpic fruits in the different species studied (Gillaspy et al., 1993).

Parthenocarpy can originate by several factors both internal and external. Sources of external factors include scarcity of resources (Bertin, 1995; Jang and Sheen, 1997; Sato et al., 2001), thermal stress (Sato et al., 2001, 2002; Higashiyama et al., 2003; Young et al., 2004), hydric stress (Gay et al., 1987) and damages in the reproductive organs (Galil and Eisikowitch, 1971; Solomon, 1980). Internal causes include changes in hormone concentration (Nitsch, 1950; Gillaspy et al., 1993; Azcon-Bieto and Talon, 2000; Fos et al., 2003), polyploidy and errors in gene expression (Mazzucato et al., 1998, 2003; Varoquaux et al., 2000; Ampomah-Dwamena et al., 2002; Carmi et al., 2003; Zohari, 2004).

Parthenocarpy and insect seed predation

Seed predation registered for Bursera morelensis (3·05 + 0·89 %) was lower than that registered in other parthenocarpic species such as Olea europaea (18 % + 8·8 %; Jordano, 1987), Pastinaca sativa (14·4 %; Zangerl et al., 1991), Pistacia lentiscus (0·4–2·9 %; Jordano, 1989; Verdú and García-Fayos, 1998) and P. terebinthus (9 %; Traveset, 1993a). This could probably be related to the presence of resins that characterize Bursera and decrease survivorship and growth rates in some larvae (Becerra, 1994). It is probable that insects have evolved some mechanism enabling them to parasitize Bursera fruits, with smaller survivorship and growth rates, such as that described for beetles feeding on leaves of Bursera (Becerra and Venable, 1990; Becerra, 1994; Evans et al., 2000). According to Traveset (1993a), it is possible that insects can differentiate between fruits with and without ovules while inserting the ovipositor. If this is true, the growth of soft tissue inside parthenocarpic fruits of B. morelensis might serve to deceive parasitizing insects.

The pollination experiment showed that 2 % of the fruits produced were parthenocarpic and without parasites, nevertheless when the number of parasitized fruits was determined it was found that approx. 20 % of the fruits were parthenocarpic and 3 % had insects. In the pollination experiment, fruits were protected by the bags preventing the entrance of insects, while in the other experiment the fruits developed without protection. The presence of parasites and the increase in the number of parthenocarpic fruits could suggest that insects could be one of the factors that promote the formation of parthenocarpic fruits as indicated by Galil and Eisikowitch (1971) and Solomon (1980), although further studies are necessary to investigate it.

Parthenocarpy has been proposed to be related to seed predation in Pastinaca sativa (Zangerl et al., 1991). The hardness of the fruit wall depends on the internal layer of mesocarp, which is full of crystals of calcium oxalate, and the lignified endocarp. In parthenocarpic fruit when the mesocarp spreads and the cell became more elonged, the endocarp gets fragmented forming unprotected sites.

The presence of crystals has been regarded as a defence against seed predation (Franceschi and Horner, 1980; Sunell and Healey, 1985; Perera et al., 1990; Ward et al., 1997; Webb, 1999; Molano-Flores, 2001; Ruiz et al., 2002). The production of calcium oxalate crystals is a specialized process analogous to bone formation in animals (Webb, 1999). These crystals are produced as a way of metabolizing harmful elements such as oxalic acid (Franceschi and Horner, 1980; Carvalhão, 1997), and serve to store calcium, minimizing the amount of calcium in circulation but maintaining calcium available for tissue formation (Franceschi and Horner, 1980; Tilton and Hornet, 1980; Volk et al., 2002). Crystals provide reinforcement, giving additional strength to the tissues (Franceschi and Horner, 1980; Fink, 1991; Webb, 1999), and minimize predation (Molano-Flores, 2001). Chemically they are considered as irritating compounds that reduce palatability and for some insects are toxic (Smith, 1989). Absence of insects in the fruits with crystals of calcium oxalate of B. morelensis suggests that the plant can produce fruits armed mechanically and chemically to ensure seed development as well as unprotected seedless fruits as a deceit low-cost strategy to reduce the probability of seed predation as suggested by Lee et al. (1991), and enhance an attraction unit for seed dispersers (Traveset, 1993a; Fuentes, 1995; Fuentes and Schupp, 1998; Verdú and García-Fayos, 1998). Nevertheless more studies are needed to assess the effect of the presence of calcium oxalate crystals on parasitization and survival rates of insects (Smith, 1989; Zangerl et al., 1991; Molano-Flores, 2001).

Parthenocarpy was reported previously for B. morelensis and B. fagaroides by Verdú and García Fayos (1998), and during the present work this type of fruit was observed in B. aptera, B. schlechtendalii and B. submoniliformis. Recently, Bonfil et al. (2007) reported parthenocarpy in B. grandifolia, B. bipinnata, B. lancifolia, B. copallifera, B. glabrifolia and B. bicolor. This suggests that parthenocarpy is a widespread phenomenon in the genus Bursera but more studies are needed to demonstrate this. This adds weight to the proposal of Verdú and García-Fayos (1998) that parthenocarpy was present in a common ancestor of the families Anacardiaceae and Burseraceae, and this character was positively selected for some reason and remains today. Although the original function of parthenocarpy is still unknown, presently it is proposed that parthenocarpic fruits can enhance attraction to seed dispersers and lower the individual probability of a seeded fruit being parasitized (Zangerl et al., 1991; Traveset, 1993a, b; Fuentes, 1995; Ziv and Bronstein, 1996; Fuentes and Schupp, 1998; Verdú and García-Fayos, 1998; M. F. Ramos-Ordoñez, unpubl. res.).

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CAPITULO III.

Parthenocarpy and seed dispersal of *Bursera morelensis*

Parthenocarpy and seed dispersal of *Bursera morelensis*

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ABSTRACT

Red cuajiote (*Bursera morelensis*) is an endemic tree species of Mexico that produces fruits whit and without seed (parthenocarpy). In this work we examined whether parthenocarpy is a factor that increases the number of bird visits to trees and determined if it is a strategy to diminish the predation of seeds by granivorous birds. In a population of the Tehuacan Valley, Mexico, we made field observations to determine the relation between the number of bird visits and total parthenocarpic fruits produced. We determined the number of bird-predated fruits and correlated this with the number and proportion of parthenocarpic fruits in the trees. We found that in trees with a greater quantity of parthenocarpic fruits birds made more visits; we then suggested that parthenocarpic fruits can act like a signal of attraction by means of a density and coloration effect. Also, we found that in trees with greater proportions of parthenocarpic fruits predation by granivorous birds is smaller, thus providing evidence that parthenocarpy it has an adaptative values. This is the first study of a *Bursera* specie where the real amount of bird-predated fruits with seeds was quantified.

Key Words: Parthenocarpy, Attraction, Seed predation, Birds, *Bursera morelensis*.

INTRODUCTION

The production of fruits without seeds among flowering plants can be triggered by several factors that promote ovary development and restricted ovule maturation (Gillaspy et al. 1993, Varoquaux et al. 2000). This process may be caused by pollen scarcity, damaged flower organs, environmental abnormalities, hormone disequilibrium, polyploidy and mistakes in gene expressions (Solomon 1980, Gay et al. 1987, Jordano 1988, Gillaspy et al. 1993, Varoquaux et al. 2000, Sato et al. 2001, 2002, Young et al. 2004). The ecological function of parthenocarpy is little known, with most research related to the production of seedless commercial fruits (Varoquaux et al. 2000).

One hypothesis is that parthenocarpy it can act as an adaptative trait that diminish the individual probability of fruits predated by birds and insects in the tree. Coetzee & Giliomee (1987) and Traveset (1993) showed that insects lay eggs indistinctly in fruits with or without seeds allowing higher survival probabilities for seeded fruits. Zangerl et al. (1991) reported that lepidoterans preferred seedless fruits of *Pastinaca sativa* as these fruits contained less toxic materials than seeded ones. Ramos-Ordoñez et al. (2008) found that Cecidomids and Calcioideae only used parthenocarpic fruits of *Bursera morelensis* and suggested that this might be due to the absence of calcium oxalate crystals making seeded fruits more toxic and harder to penetrate.

Jordano (1990) described that *Carduelis chloris* can, on average, take five fruits per minute of *Pistacia lentiscus*, but only ingested three while discarding seedless fruits. Obeso (1996) studied *Ilex aquifolium* that had asynchronic fruiting period and produced very high numbers of fruits with parthenocarpic fruits likely a way to increase attractiveness to frugivorous birds. Fuentes & Schupp (1998) showed that trees of *Juniperus osteosperma* that had more parthenocarpic fruits had less predated seeds and suggested that *Parus inornatus* foraged selectively in trees with more fruits. Verdú & García-Fayos (2001) stated that seed predation by birds was reduced as the number of parthenocarpic fruits increased in *Pistacia lentiscus*. However, in all studies seedless fruits could not be assessed in trees and the reductions in seed predation probabilities were calculated as a correlation with total fruit crop.

Bursera morelensis produces parthenocarpic fruits that remain in trees for a long period until dispersion. In this case three different fruit types can be distinguished in trees according to dehiscence: mature seeded fruits, mature parthenocarpic fruits and immature fruits (Ramos-Ordoñez et al. 2008). The purpose of this work was to evaluate if: (1) parthenocarpy can be considered as a factor that increases the attraction unit and so the number of frugivorous birds visits as suggested by Obeso (1996), and to (2) determine if parthenocarpy reduces seed predation by birds as proposed by Fuentes & Schupp (1998) and Verdú & García-Fayos (2001).

METHODS

Study Site

The study site was located in the Muchil Ravine in San Rafael Coxcatlán, in the southeastern portion of the Tehuacan Valley, Puebla, México (18° 12’ and 18° 14’ N; 97° 07’ and 97° 09’ W). Mean altitude is 1000 m a.s.l. Mean annual temperature is 25°C and annual precipitation 395 mm. Rains occur between June and October. It is an alluvial fan covered by tropical deciduous forest (Fernández 1999). Soils on site are very heterogeneous and determine four different vegetation zones (Medina 2000): i) first one dominated by *Fouqueria formosa* Kunt denominated Fouquieral, ii) Cuajiotal dominated by *Bursera morelensis* Ramírez, iii) Chiotillal dominated by *Escontria chiotilla* (Weber) Rose and iv) Cardonal dominated by the columnar cacti *Pachycereus weberi* (Coulter) Buxb (Medina 2000, Ríos-Casanova et al. 2004).

Studied species

Bursera morelensis is a dioecious endemic tree that reaches between 3 and 10 m tall, and produces an aromatic resin. Locally it is known as copalillo, cuajiote rojo, palo mulato, palo colorado or xixiote (Rzedowski et al. 2004). It is a representative species of the tropical dry forests of Guerrero, Morelos, Puebla and Oaxaca where along with other burseras forms forests known locally as “Cuajiotales” (Reyes et al. 2004, Becerra 2005). Their fruits are trivalvated. Flowering in the Tehuacan Valley occurs after the first rains (May). Two weeks later immature fruits are completely formed and when fully grown change from green to red while maturing. Fruits measure 7.42 ± 0.47 cm mean long by 6.34 ± 0.8 cm mean wide and weigh 0.48 ± 0.03 g. They have a complete orange pseudoarile. In parthenocarpic fruits orange pseudoarile is not complete. Seeds are gray dotted with black while in parthenocarpic fruits seed coat are not completely formed and remain white. Fruit maturation is asynchronic and occurs during the dry season (between November and May). During this season fruits in trees can be separated into seeded fruit (presenting complete dehiscence), parthenocarpic fruits (with incomplete dehiscence) and immature (unripe) fruits (Ramos-Ordoñez et al. 2008).

Produced crop

To estimate total fruit crop we used 23 female trees of 40 individuals selected at random in the cuajiotal and fouquerial. In each tree we selected four branches (of similar diameter) at random and counted the number of fruits on each branch. Mean fruits per branch times the number of branches equalled total crop per tree. This procedure was repeated monthly from May 2006 to May 2007. To estimate size of trees and their ability to produce fruits, we measured the diameter at breast height of each individual (Bullock and Solis-Magallanes 1990, Chapman et al. 1994).

To estimate the parthenocarpic crop we collected at random 50 fruits from each of the 23 trees (n= 1150 fruits) during January 2007 when most of the seeds were developing. Fruit were dissected and the proportion of parthenocarpic, seeded and insect-infested fruits was calculated. The total crop and parthenocarpic crop were correlated during the observation period.

Parthenocarpy as attraction unit for bird dispersers

To determine the relation between total crop and bird visitation and seed removal we did focal observations from December 2006 to February 2007. We used the 23 female trees in which the crop size was calculated. In three randomly chosen trees we observed bird visitations during peak periods of bird activity according to Foster (1990): from 07:00 to 13:00 h and from 16:00 to 18:00 h. We did not observe on windy or rainy days. We registered bird species, the number of visits, and the number of fruits consumed during each visit. One or two observers made observations and total observation time was 92 hours (4 hours/tree in 23 trees). To explore if number of visits was related with total crop and parthenocarpic crop sizes in each tree using lineal regression analysis and the Pearson coefficient (r) with a significance level of 0.05. Statistical analysis was done using SPSS version 12 (SPSS 2003) and XLSTAT version 2007.8.04 (Addinsoft 2007).

Seed predation

Field procedures

Of the 23 trees in which the size crop was calculated we selected 12 trees at random, in order to know the type fruit removed by birds, we counted and marked in the branches the number of fruits with seed and parthenocarpic, in at least an 80% of the tree (according to observed dehiscence; Ramos-Ordoñez et al. 2008), fruits were counted before observations. Focal observations were done from 07:00 to 13:00 h, from March to May 2007 for a total of 156 hours (13 hours/tree for 12 trees). We registered bird species, number of visits, number of fruits ingested and type of consumed fruit (with seed or parthenocarpic). During observations, a person registered the activity of the bird and a second observer confirmed the type of removed fruit once the bird went away of the tree.

A bird was considered as granivorous when in a captive field experiment done in the area, seeds that were ingested were found destroyed in excretions (Ramos-Ordoñez in prep.). We calculated number of fruits removed by each species and number of fruits with a predated seed. We compared predation among species using a Kruskal-Wallis test with significance level corrected by Bonferroni. We correlated number of seeded fruits with total crop as well as parthenocarpic fruits. To evaluate seed predation and its relation with parthenocarpy we correlated the number of seeded predated fruits and parthenocarpic fruits removed with parthenocarpic crop size. To determine if individual predation probability is reduced by having parthenocarpic fruits we divided seeded crop by total crop, results were correlated with parthenocarpic crop per individual. All correlations were analyzed using lineal regressions, calculating Pearson Coefficient (r) with a significance level of 0.05.

Field Captivity Experiment

To determine if the different bird species preferred one fruit type (parthenocarpic vs. seeded) we conducted a field experiment from March to May 2007. We captured 11 granivorous birds using 10 nets (12m x 2.6m, 9m x 2.6m and 6m x 2.6m) in sites around *B. morelensis* trees for a total of 28 days (14 d in March, 11 d in April and 3 d in May). Nets were opened for 10 hours per day resulting in a total of 2220 net hours and 218.4 m^2. Captured birds were placed in individual cages (*Zenaida asiatica*, n = 3; *Aimophila mystacalis*, n = 1; *Pheucticus chrysopeplus*, n = 3; *Passerina versicolor*, n = 1; *Carpodacus mexicanus*, n = 3). We offered mature seeded fruits, parthenocarpic fruits, and immature fruits in different proportions resembling measured proportions in trees: (a) 33%:33%:33% (n =30), (b) 40%:40%:20% (n =25), (c) 40%:20%:40% (n =25), (d) 20%:40%:40% (n =25) and, (e) 0%:50%:50% (n =20). Experiments were done during mornings and lasted one hour. We registered fruit type selected by different birds, and whether it was ingested or rejected. After trials birds were fed using commercial food (Trill) and soft fruit. For each bird we did three trials. With the data obtained we measured the number of seeded fruits consumed and correlated with different proportions offered.

RESULTS

Fruit Production

Trees produced a mean of 8743 ± 6057 (mean values and standard deviation are presented) fruits between December 2006 and February 2007 (range 654 - 23484, n = 23 trees). Bigger trees produced higher fruit numbers ($r = 0.612$, df = 22, $P = 0.002$, Table 1). Fruits dissected showed that all trees produced parthenocarpic fruits with percentage between 11.76% and 52.73% of the total crop (Table 1). Mean parthenocarpic crop was 2876 ± 2457 fruits (range 249 – 10932). The number of parthenocarpic fruits increased as total crop increased ($r = 0.91$, df = 22, $P < 0.0001$), but no correlation was found when we compared the proportion of parthenocarpic fruits to total fruit crop ($r = -0.012$, df = 22, $P > 0.95$, Fig. 1).

Attraction unit and visitation rates

We registered 15 bird species visiting the *B. morelensis* trees, but only 13 fed on fruits, with 66.6% of them being migrants. In Table 1 we present the total fruit crop, fruits removed (n = 503) and number of bird visits (n = 643) for each of the 23 observed trees. In trees with bigger crops more fruits were removed ($r = 0.796$, df = 22, $P < 0.0001$, Fig. 2). The number of visits was not related with total crop size ($r = 0.343$, df = 22, $P > 0.05$,

Fig. 2). Not all of the bird visits resulted in fruit consumption. Trees were also used as resting or preening sites. All bird species, both dispersers and seed predators, first visited a large number of fruits on different branches and then consumed them. All bird species consumed mature and parthenocarpic fruits.

The number of fruits removed by birds increased with the number of parthenocarpic fruits (r = 0.708, df = 22, P = 0.00015, Fig. 3). Visitation rate also increased as the number of parthenocarpic fruits increased (r = 0.634, df = 22, P = 0.001, Fig 3).

Seed Predation

Field tests

Mean number of fruits per observed tree was 10976 ± 3693 (range 4992 – 19441 fruits, n = 12). Mean number of parthenocarpic fruits per tree was 3428 ± 1585 fruits (range 587 – 5828 fruits, n = 12). We registered 13 bird species feeding on *B. morelensis* that removed 559 fruits in 356 visits. Frugivorous birds removed more fruits (427 fruits), with only 8.89% being parthenocarpic (38 fruits) and almost all of them were rejected and dropped (23 fruits). Granivorous birds removed 132 fruits (23.61%) of all, 67.42% (89 fruits) containing seed and were predated, the rest were parthenocarpic (43 fruits). Seed predators selected a mean of 35.68 ± 14.31 parthenocarpic fruits, but not all of them were consumed (Table 2). *Passerina versicolor* selected a small amount of seedless fruits (18.18%) consuming all of them; *Pheucticus chrysopeplus* selected 55.56% of parthenocarpic fruits but rejected 20% of them, while *Zenaida asiatica* selected 32.43% of parthenocarpic fruits and rejected 83.33%. Bird species that consumed more seeds were *Carpodacus mexicanus* (33.7%), *Z. asiatica* (28.1%) and *Aimophila mystacalis*

(19.1%). Small species consumed more seeded fruits that larger ones (H = 3.984, df =1, P = 0.05).

Number seeded fruits removed by granivorous birds (seed predation), was lower in trees with a higher proportion of parthenocarpic fruits (r = -0.699, df = 12, P = 0.008, Fig. 4). Also seed predation was lower as the number of parthenocarpic fruits increased but the relation was not significant (r = -0.345, df = 12, P = 0.249). Seed predation was not correlated with crop size (r = 0.122, df = 12, $P > 0.05$, Fig. 5). Individual probability of predation decreased as the number of parthenocarpic fruits increased (r = -0.795, df = 12, P = 0.05, Fig. 6).

Captivity experiments

Granivorous birds consumed mature seeded and parthenocarpic fruits and rejected immature fruits (Table 3). They preferred fruits with seeds to parthenocarpic ones. When proportion of seeded/parthenocarpic was equal or higher for parthenocarpic birds consumed both fruit types in equal amounts. As the proportion of parthenocarpic fruits increased less seeds were predated (r = -0.777, P = 0.001, df = 14, Fig. 7).

DISCUSSION

Number of removed fruits in trees of *B. morelensis* was positively related with total fruit crop size as predicted by other works (Snow 1971, McKey 1975, Howe and Estabrook 1977). Moreover, we documented that bird visitation rates increased as parthenocarpic crop size increased as predicted by Obeso (1996).

Parthenocarpic fruits increased fruit crop size and this increased bird visitation. This can be related to an increment in the attraction unit due to a greater display of color due to density as stated by others (Wilson and Melampy 1983, Wilson and Hoppes 1986, Willson et al. 1990, Facelli 1993, Fuentes 1995). Both parthenocarpic and seeded mature fruits have an orange pseudoarile that contrast with background coloration (Ramos-Ordoñez et al. 2008). Parthenocarpic fruits dehisce partially and contribute to attraction exposing pseudoarile by a density of color increment effect (van der Pijl 1982).

Birds inspected fruits on branches before removing them but also manipulated removed fruits rejecting and ingesting different amounts of fruit types. Jordano (1990) described this behavior in *Carduelis chloris* which manipulated fruits detecting seeds and rejected parthenocarpic ones.

Frugivorous birds apparently were more selective than the granivorous birds, choosing more fruits with seeds. Most of them were migrants that needed a lot of lipids to cover their energetic needs (Janzen 1977, Bates 1992, Greemberg et al. 1995, McCarty et al. 2002, Ramos-Ordoñez en prep.). Pseudoariles are known as structures that contain high amounts of lipids (Foster and McDiarmind 1983). Seeded fruits in *B. morelensis* showed a complete dehiscence exposing all the pseudoarile probably increasing attractiveness to frugivorous birds.

Verdú & García-Fayos (2001) proposed that birds facing a plant with a high proportion of parthenocarpic fruits can fly away and search for another plant with more seeded fruits but the cost of this can be high if i) the density of female plants is low and ii) the proportion of parthenocarpic fruits present in trees in the population is similar among them. In our study, of the 40 trees chosen 23 were female. The proportion of parthenocarpic fruits in 23 trees varied between 11 and 52%, but was independent of the total crop size as shown in Fig. 1, making the decision of flying away and searching for another tree a non-profitable choice as stated by Verdú and Garcia-Fayos (2001).

Parthenocarpy decreases seed predation as proposed by Fuentes and Schupp (1998) and Verdú and García-Fayos (2001). This is the first attempt to evaluate the number of parthenocarpic and seeded fruits removed in relation to fruit crop size. According to Janzen (1971a, 1971b), to consider parthenocarpy as an adaptation to avoid seed predation two conditions must be met: i) first, it must occur early in the ontogenesis of fruit development to minimize the cost for the plant and ii) the number of predated seeds must not be correlated with fruit crop size. Both aspects are met in the case of *B. morelensis*. The development of parthenocarpic fruits begins during the first days after pollination and they lack calcium oxalate crystals which are present in the seeded fruits thus being less costly (Ramos-Ordoñez et al. 2008). Besides, as it was shown in Fig. 5, the number of seeds predated was not correlated with total fruit crop size. This reinforces the idea of the ecological function of parthenocarpy as a mechanism to decrease seed predation probability as was reported for *Pistacia lentiscus*, a plant from the Anacardiaceae family, closely related to Burseraceae (Verdú and García-Fayos (2001).

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Tables

Table 1. Total crop size, diameter at breast height (DBH), percentage of parthenocarpic fruit, parthenocarpy crop size, number of removed fruits and number of bird visits registered in the 23 female trees observed in the Tehuacan Valley. Data were sorted ascending according to total fruit crop size. Observation effort was 92 hours (4 h/tree).

Tree id	DBH (cm)	Crop size	Parthenocarpic crop size (% total crop)	Number of removed fruits	No. of visits
9	169	654	249 (38)	0	36
1	35	1027	542 (52.73)	0	26
15	88.5	1752	553 (31.58)	1	34
2	43	2358	854 (36.21)	0	26
3	44	2620	939 (35.85)	9	29
5	50.5	3552	1052 (29.63)	2	6
4	45.5	3744	1270 (33.93)	13	31
6	54.5	4320	1549 (35.85)	19	33
14	87.9	4992	587 (11.76)	11	7
7	64	8060	2183 (27.08)	37	18
13	84	8151	2223 (27.27)	41	11
19	110.3	8280	2855 (34.62)	21	44
8	65.5	8418	2020 (24)	2	6
22	169	9768	3712 (38)	36	23
12	81.5	10892	4357 (40)	44	46

20	138.8	11264	2988 (26.53)	32	14
21	149.4	12420	5493 (44.23)	18	47
18	108.6	13320	4117 (30.91)	61	16
10	75	13413	2635 (19.64)	7	7
11	76.3	14280	5829 (40.82)	33	57
17	106	14880	3644 (24.49)	53	27
23	205	19441	5555 (28.57)	65	21
16	94.5	23484	10932 (46.55)	54	78

Table 2. Granivorous bird species detected consuming fruits of *Bursera morelensis*, and types of fruits consumed. Data were sorted by the number of fruits removed.

Species	Removed fruits	% seeded fruits	% parthenocarpic fruits	% parthenocarpic fruits rejected	Number of visits
Carpodacus mexicanus	44	68.18	31.82	42.86	21
Zenaida asiatica	37	67.57	32.43	83.33	23
Aimophila mystacalis	23	73.91	26.09	16.67	22
Passerina versicolor	11	81.82	18.18	0	19
Pheucticus chrysopeplus	9	44.44	55.56	20	14
Columbina passerina	8	50	50	25	18

Table 3. Number of fruits with seeds, parthenocarpic and immature fruits of *B. morelensis* consumed by five granivorous birds in captive conditions.

Proportion of offered fruits	Consumed Fruits		
seeded : parthenocarpic : immature	seeded	parthenocarpic	immature
00% : 50% : 50%	0	42	0
20% : 40% : 40%	67	60	0
33% : 33% : 33%	131	62	0
40% : 40% : 20%	135	71	0
40% : 20% : 40%	136	15	0

Figures

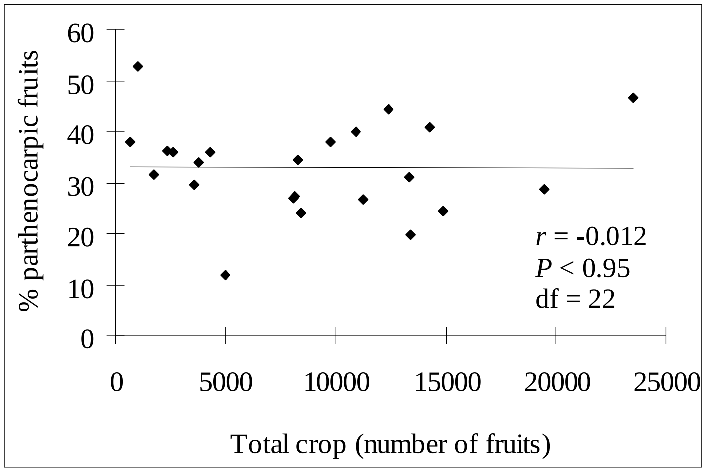

Fig. 1. Regression analysis and Pearson's correlation (r) between the proportion of parthenocarpic fruits with respect to total crop in 23 trees of *B. morelensis* in the Tehuacán Valley.

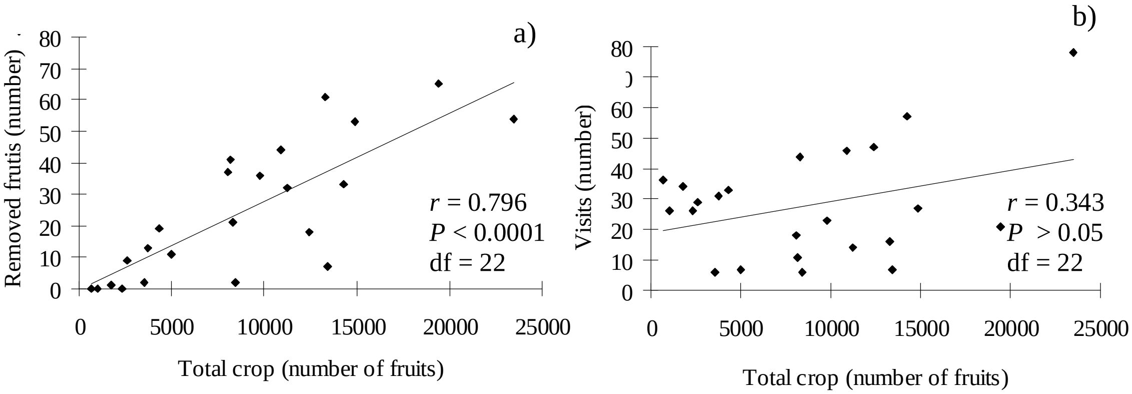

Fig. 2. Regression analysis and Pearson's correlation (r) between the number of removed fruits (a) and visits realized (b) with respect to total crop in 23 trees of *B. morelensis* in the Tehuacán Valley.

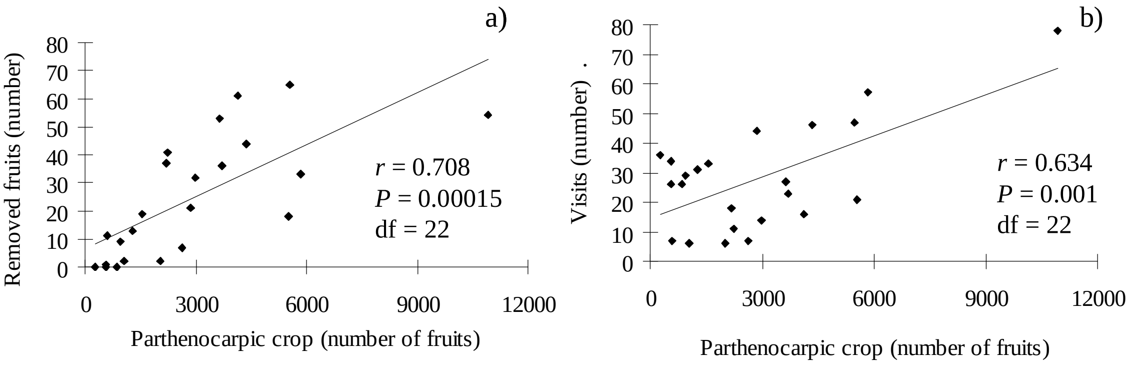

Fig. 3. Regression analysis and Pearson’s correlation (r) between the number of removed fruits (a) and visits realized (b) with respect to parthenocarpic crop in 23 trees of *B. morelensis* in the Tehuacán Valley.

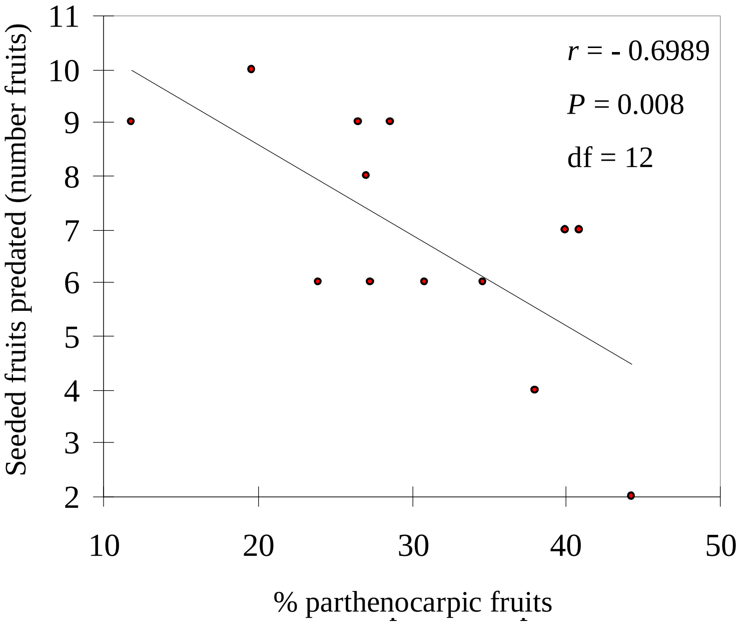

Fig. 4. Regression analysis and Pearson’s correlation (r) between the number of seeded fruits removed by granivorous birds and the proportion of parthenocarpic fruits in 13 trees of *B. morelensis* in the Tehuacán Valley.

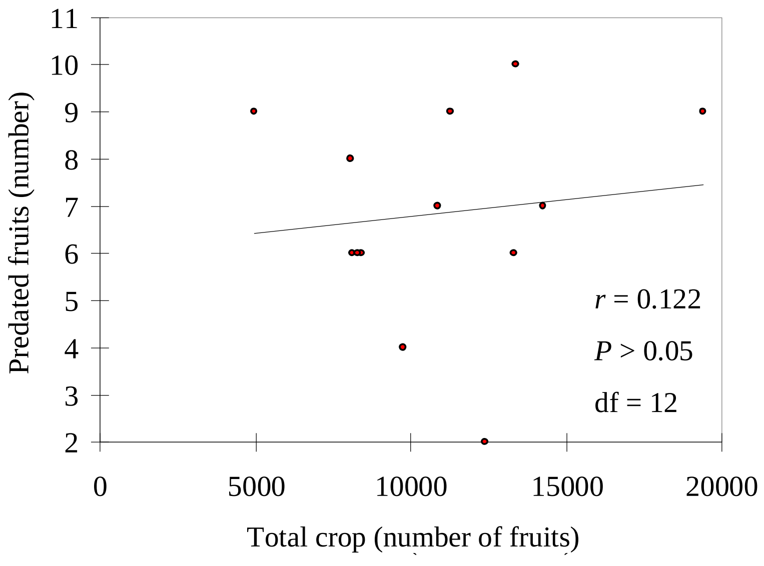

Fig. 5. Regression analysis and Pearson´s correlation (r) between the number of seeded fruits removed by granivorous birds and the total crop size in 13 trees of *B. morelensis* in the Tehuacán Valley.

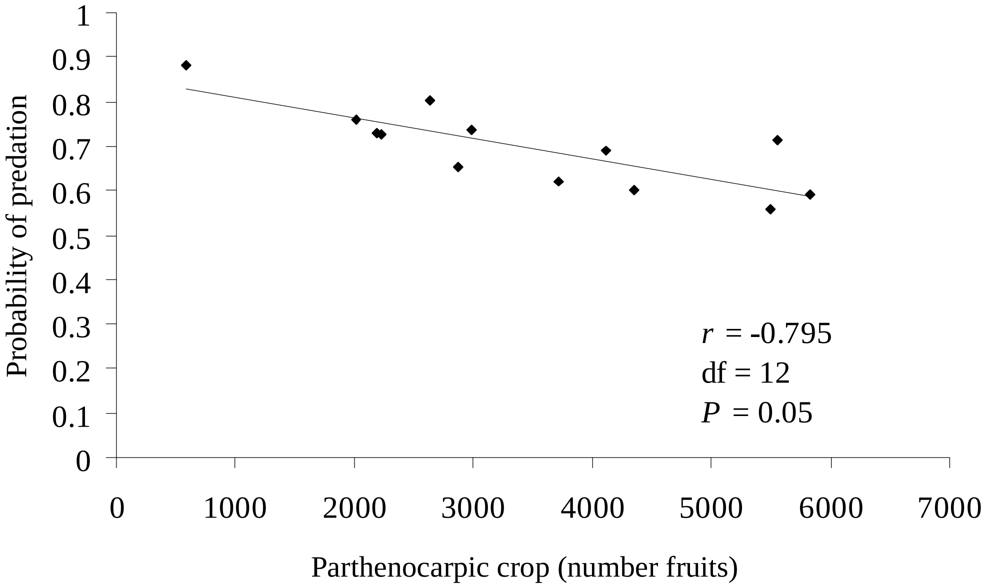

Fig. 6. Regression analysis and Pearson´s correlation (r) between the probability of seed predation and the parthenocarpic crop produced by 13 trees of *B. morelensis* in the Tehuacán Valley.

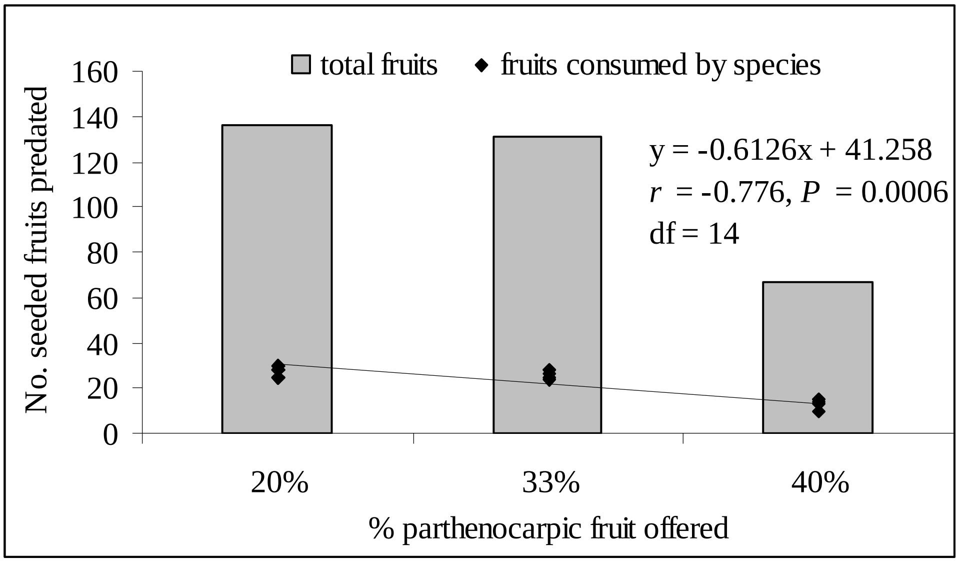

Fig. 7. Number of seeded fruits predated by granivorous birds feed in conditions of captivity with respect to the percentage of parthenocarpic fruits offered. For regression and Pearson's correlation we used the number of fruits eaten by each species of bird, the bars represent the total number of fruits eaten by five species.

CAPITULO IV.

Avian frugivores and seed dispersal of *Bursera morelensis* (Burseraceae)

AVIAN FRUGIVORES AND SEED DISPERSAL OF *BURSERA MORELENSIS* (BURSERACEAE)[1]

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We evaluated the seed dispersal process by frugivorous birds that feed on *Bursera morelensis* an endemic species of Mexico that produces seeded and parthenocarpic fruits. We measured the abundance of dispersers, the amount of dispersed seeds and the quality of the dispersion (effect of endozoochory and sites of greater recruitment of seedlings). We registered 13 species of birds feeding, from which six were seed predators. The resident birds and the local migratories presented small rates of seed removal and visitation compared with the long distance migratory species. The more effective species were four flycatchers (genus *Myiarchus*) that took a large amount of seeds to the types of vegetation with greater seed recruitment and deposited them under nurse trees and shrubs. Most of the resident species were not as effective dispersers as migratory birds, and visited a wider array of available fruiting trees. Factors that can uncouple the temporal and spatial occurrence of migrant dispersers and fruits, as global climate change, can have important effects in both bird and plant survival and conservation.

Key Words: *Bursera morelensis*; frugivorous birds; parthenocarpy; seed dispersal.

For those species in which seedling establishment depends on facilitative interactions and suitable soil properties in heterogeneous landscapes such as alluvial fans, seed dispersal is a key process responsible for their successful establishment (Steenbergh and Lowe, 1969; Valiente-Banuet and Ezcurra, 1991; Godínez-Álvarez et al., 1999, 2002; Nogales et al., 2005; Spiegel and Nathan, 2007). In these environments, soils are highly variable depending on age of deposition of alluvium leading to a differential distribution of species (McAuliffe, 1988). Different studies have shown that, depending on deposit age, soils exert a considerable effect on hydric properties and availability for plants leading to vegetation mosaic characterized by differences in species composition and therefore in suitability differences in species recruitment over the landscape. Consequently, seed dispersal effectiveness of frugivores depends on the quantity of seeds removed (quantity component), the foraging behavior pre and post ingestion (i.e. if they move seeds under specific soil patches and under the shade of nurse plants), and differential effects on seeds after passing through their digestive system (quality component) (Jordano, 1992; Schupp, 1993; Loiselle and Blake, 1999; Godínez-Álvarez et al., 2002).

The genus *Bursera,* is a tropical group of plants distributed only in America whit its center of diversity in the Balsas River Basin and the Tehuacán Valley (Rzedowski et al., 2004). In the Tehuacán-Cuicatlán Valley, these species only recruit beneath the canopy of perennial plants (Valiente-Banuet and Verdú, 2007) and have a differential distribution on four different alluvial deposits in the Muchil alluvial fan located in southern part of the valley.

The purpose of this work was to describe seed dispersal by frugivorous birds in *Bursera morelensis*, a Mexican endemic and parthenocarpic tree, examining some phases of the process, as the amount of removed seeds and visits realized by frugivores, the effect of seed passage through digestive tract on the percentage and velocity of seed germination, and probability of seed deposition in favorable sites for establishment, considering that in arid lands, seed dispersion and plant establishment have been recognized as keystone processes for plant conservation (Valiente-Banuet et al., 1991a; 1991b; 2006; Godinez-Alvarez et al., 2002).

MATHERIALS AND METHODS

***Study area* —** Study area was located at Barranca de Muchil in San Rafael Coxcatlán, in the southwestern part of the Tehuacan Valley Puebla, México (18° 12’ & 18° 14’ N; 97° 07’ & 97° 09’ W). Mean altitude was 1000 m a.s.l. Climate is dry with summer rains (Fernández, 1999). Mean annual temperature is 25°C and mean annual rainfall 394.6 mm, with a long dry season lasting from November till May and a rainy season from June to October. It is an alluvial fan where vegetation is a tropical dry forest where 57 species of flowering plants are described (Fernández, 1999). It has a high heterogeneity on soil types (Medina, 2000), that generates four surfaces with different vegetation associations: the “Fouquerial” dominated by *Fouqueria formosa* Kunt, the “Cuajiotal” dominated by *Bursera morelensis* Ramírez, the “Chiotillal” dominated by *Escontria chiotilla* (Weber) Rose and the so called “Cardonal” dominated by *Pachycereus weberi* (Coulter) Buxb. (Medina, 2000; Ríos-Casanova et al., 2004).

Studied species — *Bursera morelensis* is a dioecious endemic tree that reaches between 3 and 10 m height, with abundant aromatic resins. It is a representative species of the tropical dry forests of the states of Guerrero, Morelos, Puebla and Oaxaca where alone with other *Bursera* species form the so called “Cuajiotales” where those trees form the dominant elements of the forests (Reyes et al., 2004; Becerra, 2005). Flowering occurs with the first rains of the season between May and June. Fruits are trivalvated. The ovule in this species remains without changes for between 5 and 8 months after pollination, then the embryo develops (Ramos-Ordoñez et al., 2008).

Fruit crop size was 8743 ± 6057 (range 654 - 23484, n = 23 trees; measured from May 2006 to May 2007, Ramos-Ordoñez et al., 2008). Between 9 and 52% of the crop was parthenocarpic, 3.05±0.89 % (range 0 – 18 %) of this fruits were parasited by wasps (Hymenoptera: Chalcidoidea) and flies (Diptera: Cecidomiidae) (Ramos-Ordoñez et al., 2008). Unripe fruits were green, both seeded and parthenocarpic. Mature fruits were red and measured 7.42 ± 0.47 cm long by 6.34 ± 0.8 cm wide, with a fresh weight of 0.48 ± 0.03 gr. Seeded fruits had a complete orange pseudoarile while parthenocarpic fruit presented an incomplete pseudoarile. Seeds in seeded fruits were gray dotted with black while in the parthenocarpic fruits seed did not developed and remained whitish. Fruit maturation was asyncronic during dry season (November to May). During maturation fruits can be separated in trees as mature seeded (with complete dehiscence), mature parthenocarpic (with incomplete dehiscence) and immature (without dehiscence) (Ramos-Ordoñez et al., 2008).

Seed dispersal — The quantity component of effectiveness was calculated using the abundance of species, the visitation frequency and the mean number of fruits removed per visitation. The quality component only was estimated as the percentage of seeds germinating after passing through the bird digestive system and the frequency of flights to the different vegetation types in the area. In the same way, a survey was conducted to determine the nurse plants and sites where successful establishment of *Bursera morelensis* occurred. Effectiviveness was calculated as the product of the quantity and quality components using the following components:

E = (bird abundance * visitation frequency * mean number of fruits removed by visit) (% germination * frequency of flight to specific vegetation types * importance of the birds in the site of establishment)

Quantity Component—

1. Bird abundance — To calculate bird abundance we used 10 mist nets (12m x 2.6m, 9m x 2.6m & 6m x 2.6m) located among *Bursera morelensis* from December 2006 until April 2007 for a total of 37 net days (4 d December, 3 d January, 5 d February, 14 March and 11 d April) and 3160 h/net (Fleming et al., 1972; Amín, 1996). Relative abundance was calculated as the number of individuals captured by net hour.

2. Visitation rates and fruit removal rates — To obtain visitation frequency and fruits removed per visit we conducted observations using binoculars to 12 randomly chosen trees bearing mature fruits (in cuajiotal and chiotillal), from March to May 2007. Observations were done during the mornings (0700-1400) and afternoons (1600-1900) using one hour observation periods totaling 156 observation hours (13 hours/tree). We registered the species of frugivores visiting studied trees, and for each frugivore species number of individuals per visit, total visitation time, number of visits, number of ingested fruits, type of the ingested fruit (with seed or parthenocarpic) total manipulation time (in seconds counted from initial touch of the fruit until ingestion), way of ingesting the fruit (if swallow fruits whole or mashing the fruit with the bill), type of plant to where they fly (tree, shrub or cacti) and vegetation type. Frugivore species were identified using field guides (Peterson and Chalif 1989; Howell and Webb 1995).

In order to quantify the number of seeded vs. parthenocarpic fruits removed we marked 80% of the fruit crop of individual trees distinguishing fruit types by observing dehiscence (full dehiscence mature seeded fruit, incomplete dehiscence mature parthenocarpic fruit). During observations we used an additional observer to verify the type of fruit removed by inspecting the previously marked fruits. Using only seeded fruits consumed we calculated the visitation time, the number of removed fruits per visit and per individual, the number of fruits removed by minute and the time of manipulation. All values are presented as mean and standard error.

Additionally we used the abundance-based coverage estimator (ACE), proponed by Collwell (2006) to estimate the total number of visitor species.

Quality Component —

1. Seed germination — To determine the proportion and the velocity of seed germination after passing through the bird digestive system, we used seeds excreted by the different captured birds. All captured birds were placed in individual cloth sacs for 30 min to collect their feces (*Zenaida asiatica* n=3, *Melanerpes hypopolius* n=7, *Myiarchus nuttingi* n=2, *M. tuberculifer* n =1, *M. tyrannulus* n=1, *Aimophila mystacalis* n=1, *Pheucticus* *chrysopeplus* n=3, *P. versicolor* n=1, *Icterus pustulatus* n=2, *Carpodacus mexicanus* n=3). Then birds were placed in individual cages (2 x 1 x 1 m and 60 x 40 x 30 cm) where were feed using mature fruits of *B. morelensis*. Birds were kept in cages for at most two days. During the experimental procedure we measured total time of seeds passing through the bird digestive system, measured since seeds were ingested until they were defecated or regurgitated.

We also searched for feces of non-flying animals in the study area to search for *B. morelensis* seeds. Feces were identified using Aranda (2000) field guide.

Seeds obtained from feces or from fruits were tested for viability using a flotation test (López et al., 2005) to determine the proportion of viable seeds. Seeds were washed using sodium hypochlorite (10%) and imbibed (Andrés-Hernández and Espinosa-Organista, 2002; López et al., 2005). Then seeds were sown in Petri dishes with filtered paper (Whatman No. 1; Whatman, Chifton, New Jersey, USA) moistened with distilled water following the treatments:

a) Control 1: seeds obtained from trees with the pseudoarile attached
b) Control 2: seeds obtained from trees without the pseudoarile
c) Seeds that passed through the digestive system of the different visitor species.

Number of seeds per dish was variable, depending on defecated seeds availability, but a maximum of 15 seeds per dish was used. Germination experiments were done in the field placing individual dishes under nurse trees (*Acacia* spp. and *Mimosa* spp.), covered with a protection metallic mesh cage and surrounded by a commercial poison for ants (Furidon) to avoid predation. Viable seeds that did not germinate were tested using Tetrazolium (Rivas, 1993; López et al., 2005).

Cages were revised daily registering number of germinated seeds. The criterion to consider a seed germinated was radicle emergence (Rivas, 1993). We evaluated by means of one-way ANOVA if there were significant differences in the percentage of germination of the seeds that passed through gut of the birds and the controls, the normality of the data was verified with Kolmogorov-Smirnov test. We calculated the average rate of germination (ARG) for each group using formula ARG = (N1T1+N2T2+…+NnTn) / (N1+N2+…+Nn). Where N1 is the number of seeds germinated in the day 1 or T1, N2 is the number of germinated seeds in the time interval T1 and T2. We compared the rates of germination by means of a one-way ANOVA using data transformed to arcsin square root. We used models of logistic regression to construct the curves of germination of seeds obtained in each group. All analyses were done using Simfit version 5.7.2 (Bardsley, 2007).

2. Frequency of flight to specific vegetation types— We evaluate the frequency of visitation to each vegetation type using a contingency table. The null hypothesis considered an equal number of visits to each vegetation unit. Standardized residuals were used to test for preferential use of vegetation units where recruitment was better. We analyzed the residuals of the test to determine that species go most frequently to each type of vegetation after feeding. A similar analysis was done with visitation after ingesting fruits of *B. morelensis* of trees, shrubs and columnar cacti to determine the probability with which the birds deposit the seeds under nurse plants.

3. Importance of the birds in the site of establishment — To determine favorable recruitment sites for seedlings of *B. morelensis* we registered the presence of young plants in the four vegetation associations recognized for the study (Medina, 2000). We used 12 plots of 15 x 10 m (3 plots per each vegetation unit) where all the non reproductive plants of *B. morelensis* were recorded.

We analyzed the importance of the birds at each site using the residual analysis. We established an importance rank (IR) to determine that species make more flights to the sites of greater recruitment, so that to the species that flown most frequently to the site of greater recruitment of seedlings we assigned value 1, and so on.

RESULTS

Quantity Component — We registered only13 bird species feeding on the fruits of *B. morelensis,* being 61.5% long distance migrants (birds that migrate from North America to Center and South America, Table 1). *Melanerpes hypopolius* and *Myiarchus nuttingi* were the species with the highest relative abundance followed by *Myiarchus tyrannulus* and *Passerina versicolor* (Table 1). Visitation frequency and number of fruits removed are shown in Table 2. Four species of the genus *Myiarchus* were responsible for the 50.56% of the total visits (n= 356) consuming 72.17% of the fruits removed (n= 478). Visitation rates were higher for *M. nuttingi* (0.315 visits/h), than for *M. cinerascens* (0.199 visits/h), *M. tyrannulus* (0.193 visits/h) and *M. tuberculifer* (0.185 visits/h). The longer visits were done by *Zenaida asiatica* (6.76 ± 2.05 min) and *Carpodacus mexicanus* (4.42 ± 1.19 min).

Many of the birds visited trees individually except for *Pheucticus chrysopeplus* and *Icterus pustulatus* that visited in pairs and Z. *asiatica* that visited in groups of two to three individuals. From the total removed fruits (n = 559), 85.5% (478 fruits) were seeded fruits being the rest parthenocarpic. Most of the seeded fruits were removed by *M. nuttingi* (34.72%), followed by M. *tuberculifer* (13.59%) and *M. tyrannulus* (12.13%). The species that removed more fruits per visit was *M. tyrannulus* (2.91 ± 0.63), followed by *M. nuttingi* and *M. tuberculifer* (2.41 ± 0.29 and 2.06 ± 0.31 fruits per visit respectively). According to ACE predictions, we detected 93% of all predicted visitors (Fig.1).

Quality Component —

1. Seed germination — Seeds ingested by P. *versicolor, C. mexicanus, A. mystacalis, Z. asiatica* and *P. chrysopeplus* were partially or completely destroyed. In the feces of *C. passerina* we did not found seeds or seed parts. All of the above species were considered as seed predators herein.

Average passing time of seeds through birds guts were 47.64 ± 10.84 minutes (mean and standard deviation; range 11-121 minutes, n = 22 birds). The presence of a pseudoaril around the seeds had a severe effect on seed germination. Seeds covered by the pseudoaril did not germinate in the 30 days observed (n=80), compared with uncovered seeds that germinated in full (n=80). The percentage of seeds that germinated after passing through the bird's gut was different significantly form the covered seeds (control 1) ($F_{5,\,18}$ = 3.8, P = 0.01). The percentage of germination of defecated seeds obtained for flycatchers *M. nuttingi* (17.5%), *M. tuberculifer* (17.5%), *M. tyrannulus* (15%) and the oriole *I. pustulatus* (22.5%), were the highest. The seeds defecated by the woodpecker *M. hypopolius* had the lower germination percentage (12.6%), but no species differed from manually uncovered seeds (control 2, 13.8%), ($F_{5,\,18}$ = 71.21, P = 0.622). For all species the estimated average germination rates varied from 1.0 to 3.6 germinated seeds per day, not differing from manually uncovered seeds ($F_{3, 20} = 51.7$, $P = 0.675$). Germination happened quickly in the first five days (Fig. 2).

2. Frequency of flight to specific vegetation types — After ingesting the fruits, birds used vegetation units in different ways ($X^2 = 48.4$, df = 12, $P < 0.001$), being the more visited unit the fouquerial (31.3%), followed by the chiotillal (24.17%), the cuajiotal (22.54%) and lesser in the cardonal (19.2%) (Fig. 3). *M. nuttingi* made more flights than expected to the four types, fouquerial (11.54%), cuajiotal (9.34%), chiotillal (6.59%) and cardonal (4.95%). *M. cinerascens* used more than expected the fouquerial (9.34%), chiotillal (7.69%) and cuajiotal (4.94%). *M. tuberculifer* used the fouquerial and chiotillal as expected (4.94% and 4.39% respectively) but made less flights to the cuajiotal and cardonal (3.29% and 2.19%). *I. pustulatus* used like expected the cardonal (4.39%) and *M. tyrannulus* used less than expected all the vegetation units (1.09% to 3.84%). Finally, *M. hypopolius* used only the cardonal and chiotillal (1.64% and 1.1% respectively). Birds used mostly trees (51.1%) and shrubs (45.6%) as perching sites after consuming fruits of *B. morelensis*. Only 3.29% used columnar cacti as perching sites (only *M. hypopolius* and *I. pustulatus*).

3. Importance of the birds in the site of establishment — In 1800 m^2 surveyed we found only 8 individuals of *B. morelensis* seedlings and young plants with a mean height of 22.3 ± 17.5 cm, a very low density (0.044 ind/m^2). All seedlings were associated with shrubs or small trees, none were found in the open space or beneath columnar cacti. The vegetation unit that was more important for *B. morelensis* recruitment was the cuajiotal

(0.011 individuos/m^2) followed by the chiotillal (0.004 individuos/m^2), fouquerial (0.002 individuos/m^2) and at the end the cardonal where no recruitments were found.

In agreement with the frequency of flight and results of recruitment, the more important species was *M. nuttingi* (IR = 1), followed by *M. cinerascens* (IR = 0.8), *M. tuberculifer* (IR = 0.6), *I. pustulatus* (IR = 0.4), *M. tyrannulus* (IR = 0.2) and *M. hypopolius* (IR = 0.1).

4. Effectiveness index — We were able to calculate effectiveness of 12 from the 13 species registered as visitors of *B. morelensis* (Table 3). The most effective species was *M. nuttingi*, followed by *M. tuberculifer*, *M. tyrannulus* and *I. pustulatus*. The effectiveness of six species was zero because seeds were destroyed by gut passage. Finally the effectivity of *P. scalaris* (0.00019) was doubtful because of scarcity of defecated seeds and preference of columnar cacti as perching sites.

DISCUSSION

In spite of the more than 100 species of the genus *Bursera* described (Espinosa et al., 2006) and their widespread uses by humans (Reyes et al., 2004) this is the first attempt to describe seed dispersal for the genus. *B. morelensis* is a dioecious parthenocarpic plant (Ramos-Ordoñez et al., 2008) where fruit consumers removed few parthenocarpic fruits. Except for *I. pustulatus* and *M. hypopolius*, up to 90% of the fruit consumed were seeded fruits and of the few parthenocarpic fruits that were selected between 64 and 100% were rejected after manipulation.

The quantity of seeds dispersed was affected by several factors such as migratory status, diet, reproductive season and abundance. Resident and local migrants showed the lower visitation and removal rates. Migrants as *M. nuttingi* and *M. cinerascens* removed the highest quantity of fruit using short foraging times. *B. morelensis* represented an important part of the winter diet of those species as it has been reported for other birds foraging on *Bursera* (Bates, 1992; Greemberg et al., 1995). In this genus, the pseudoaril has high lipid content (Foster and McDiarmind, 1983), and fruits are available during winter when migrant birds have high energetic demands (Janzen, 1977; Bairlein, 1990; Bairlein and Gwinner, 1994; Parrish, 1997; McCarty et al., 2002).

The presence of other fruiting plants in the vicinity was another possible cause of the lower visitation rates of the residents. Several species were observed fruiting simultaneously with our study plant and some birds as *M. hypopolius* and *P. scalaris* concentrated their activities on those plants such as the columnar cactus *Pachycereus weberi* being less common on *B. morelensis*. In the feces of captured *M. hypopolius* a lot of seeds of *Bursera aptera* were found. The interactions between plant phenologies in a neighborhood is an important factor that can trigger visitation and removal rates, the inclusion of other elements in the bird’s diet can also be another cause of low visitation rates (Moermond and Denslow, 1985; Howe, 1986; Foster, 1990; Sargent, 1990; Jordano, 1992; García et al., 2001; Saracco et al., 2005). In addition, breeding activities in resident species can diminish visitation rates due mainly to changes in bird´s diet, including more insects as a source of proteins for chicks (Koutsos et al., 2001). We could document courtship behavior in *P. chrysopeplus* and the presence of chicks of *P. scalaris* in the areaat the same time our study was done.

Visitation time can affect the quality of the dispersal effectiveness. Birds that spend longer periods in the plant where they feed, generally leave seeds under the shade of parent plant increasing therefore the probability that they are depredated by a density effect (Wheelwright, 1991). In this study, passing time through the bird's gut varied between 11 and 120 minutes with a mean of 47.64 ± 10.84. The visits did not exceeded 10 min and, in general, birds did not defecate or regurgitated in these periods, suggesting that seeds were transported in the digestive tract to sites far away from the parent tree. In this study we observed that the removal of the pseudoarile was necessary for seeds to germinate, supporting the presence of substances in the pulp that can inhibit germination and the need of this elimination by the pass through the gut of dispersers (Cipollini and Levey, 1997; Yagihashi et al., 1999; Figueroa and Castro, 2002). The similarity between the average rates of germination of the nude seeds and defecated, suggest that seed coat does not need scarification to germinate (Barnea et al., 1990). In many plants, seeds in intact fruits may lose their viability during pulp decomposition by attack of fungal or bacterial pathogens and seed predators (Webb and Willson, 1985; Willson and Whelan, 1990). The rapid germination of *B. morelensis* seeds may contribute to seed survival as an strategy for temporal escape from seed predators (Janzen, 1971; Curran and Webb, 2000).

The probability os a seed to be deposited in a particular site varied depending of disperser species. The woodpecker *M. hypopolius* used as perching sites columnar cacti located in the chiotillal and cardonal, species were we did not find young plants of *B. morelensis*. This suggests that besides presenting a low quantity, the quality of the dispersion of this species was also low (Godínez-Alvarez, et al., 2002). The four flycatchers, used trees and shrubs after feeding, under which the facilitation is a key process, mainly in arid and semiarid environments (McAuliffe, 1988; Valiente, 1991; Aguiar et al., 1992; Vetaas, 1992; Callaway, 1995; Franco-Pizaña et al., 1996; Pugnaire et al., 1996; Valiente-Banuet et al., 2006; Valiente-Banuet and Verdú, 2007). The flycatchers *M. nuttingi* and *M. cinerascens* presented the highest effectiveness because the frequency of visits, removal rates and the seed deposition probability under nurse plants.

Although we observed high rates of seed removal and high abundance of the dispersers in cuajiotal and chiotillal, the recruitment of *B. morelensis* was very low (eight young plants in 1800m^2). Fernández (1999), says that *B. morelensis* is an abundant species only in one of the four levels of the alluvial fan of the Barranca de Muchil, and mentions that this situation is not attributable to processes of dispersion of the species, but that is associated to abiotic elements as soil type. In this study, *B. morelensis* was found recruiting under the shade of nurse plants in three of the four vegetation units in the area. The presence of seedlings in the cuajiotal, chiotillal and fouquerial could be attributed to the activity of the dispersers birds, however the low recruitment in the three levels can be more related to the soil type where seeds germinate. A combined action of particular edaphic conditions and vegetation association may limit plant development, possibly affecting their ability of permanence in the site (Silva, 1996; Fernández, 1999). It is necessary to make field experiments to determine nurse plants and their effect upon seed recruitment and establishment in the four vegetation associations to determine better the dispersal effectiveness for all the birds using this plant (Schupp 1993).

Factors affecting the timing of migration and fruiting can have important effects on bird and plant conservation. Global climate change can cause changes in plant phenology that can uncouple important interactions such as pollination and seed dispersal causing declines and extintion of colonization of new sites (McCarty, 2001; Primack and Miao, 2002; Crick, 2004). Migration timing can also be affected and changes have already being described (Cotton, 2003; Jenni and Kery, 2003).

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TABLES

Table 1. Relative abundance (number of individuals · hour^{-1} · net^{-1}) and migratory status of the birds that ingested fruits of *B. morelensis* in the Tehuacán Valley. Status: R (resident), M (migrant), ML (local migrant) according to Arizmendi & Espinosa de los Monteros (1996).

Family	Species	Status	Relative Abundance
Columbidae	*Zenaida asiatica*	R	0.02
	Columbina passerina	R	0.018
Picidae	*Melanerpes hypopolius*	R	0.0349
	Picoides scalaris	R	0.0146
Tyrannidae	*Myiarchus tuberculifer*	ML	0.0141
	Myiarchus cinerascens	M	0.0147
	Myiarchus nuttingi	M	0.0348
	Myiarchus tyrannulus	ML	0.0237
Emberizidae	*Aimophila mystacalis*	M	0.0148
Cardinalidae	*Pheucticus chrysopeplus*	M	0.0132
	Passerina versicolor	M	0.0207
Icteridae	*Icterus pustulatus*	ML	0.018
Fringillidae	*Carpodacus mexicanus*	R	0.0171

Table 2. Visitation schedules of the birds that consumed fruits of *B. morelensis* in the Tehuacán Valley. Values shown are mean and standard errors.

Species	No. of visits	Visitation Frequency	Visitation time (min)	Individuals per visit	No. of fruits consumed by species	Fruits consumed per visit
M. nuttingi	68	0.315	1.64 ± 0.19	1.00 ± 0.00	166	2.41 ± 0.29
M. cinerascens	51	0.199	1.78 ± 0.20	0.98 ± 0.06	56	1.22 ± 0.29
M. tuberculifer	35	0.185	2.01 ± 0.25	0.84 ± 0.07	65	2.06 ± 0.31
I. pustulatus	34	0.177	2.46 ± 0.44	1.04 ± 0.14	23	0.75 ± 0.28
M. tyrannulus	26	0.193	2.88 ± 0.51	1.00 ± 0.00	58	2.91 ± 0.63
Z. asiatica	23	0.109	6.76 ± 2.05	1.34 ± 0.24	25	1.7 ± 0.54
A. mystacalis	22	0.096	1.47 ± 0.40	0.81 ± 0.11	17	0.85 ± 0.09
C. mexicanus	21	0.073	4.42 ± 1.19	2.53 ± 0.35	30	1.72 ± 0.45
P. versicolor	19	0.071	2.19 ± 0.40	0.5 ± 0.13	9	0.57 ± 0.15
C. passerina	18	0.071	1.37 ± 0.34	0.76 ± 0.09	4	0.25 ± 0.11
P. chrysopeplus	14	0.083	1.69 ± 0.26	1.26 ± 0.16	4	0.18 ± 0.11
M. hypopolius	13	0.035	1.05 ± 0.50	0.88 ± 0.31	4	0.23 ± 0.1
P. scalaris	12	0.025	3.71 ± 0.96	1.00 ± 0.00	17	1.42 ± 0.23

Table 3. Dispersal effectiveness of the 13 bird species that visited *Bursera morelensis* in the Tehuacan Valley, Mexico. Relative abundance, visitation frequency, removed fruits per visit, germination percentage, frequency of flight, importance of the birds in the site of establishment (IR) and effectiveness index.

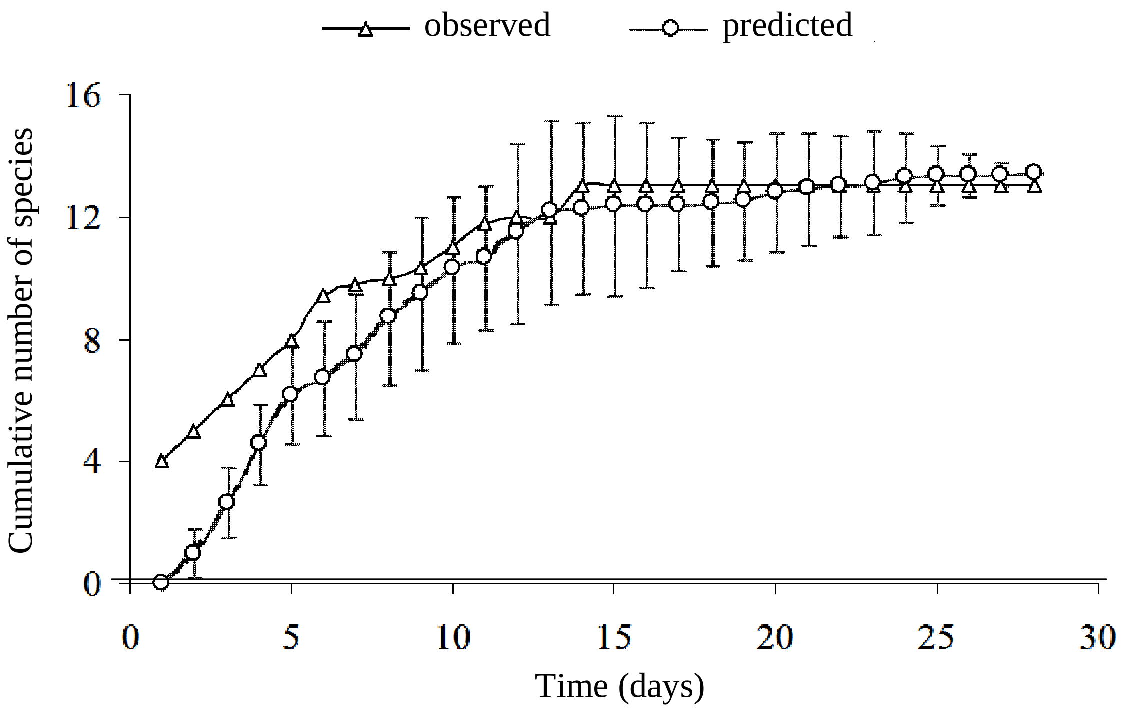
Species	Relative abundance (individuals · hour^{-1} · net^{-1})	Mean visitation frequency (visits/hour)	Mean removed fruits per visit	Germination Percentage	Frequency of flight	IR	Effectiveness
M. nuttingi	0.0348	0.315	2.41	15	21.77	1	8.627
M. tuberculifer	0.0141	0.185	2.06	17.5	9.96	0.6	0.562
M. cinerascens	0.0147	0.199	1.22	11.1	17.34	0.8	0.55
M. tyrannulus	0.0237	0.193	2.91	15	6.64	0.2	0.265
I. pustulatus	0.018	0.177	0.75	22.5	9.59	0.4	0.206
M. hypopolius	0.0349	0.035	0.23	8.33	1.85	0.1	4.3×10^{-4}
P. scalaris	0.0146	0.025	1.42		0.37		1.9×10^{-4}
P. versicolor	0.0207	0.071	0.57	0	4.06	0	0
Z. asiatica	0.02	0.109	1.7	0	5.54	0	0
C. passerina	0.018	0.071	0.25	0	3.69	0	0
C. mexicanus	0.0171	0.073	1.72	0	8.86	0	0
A. mystacalis	0.0148	0.096	0.85	0	8.12	0	0
P. chrysopeplus	0.0132	0.083	0.18	0	2.21	0	0

FIGURE LEGENDS

Figure 1. Predicted and observed species of fruit consumers of *Bursera morelensis* in the Tehuacán Valley according to the Abundance-based Coverage Estimator (ACE, Colwell 2006). Error bars represent standard deviation.

Figure 2. Germination of *Bursera morelensis* seeds after gut passage for different species of birds and control 2 (uncovered seeds). MEHY (*Melanerpes hypopolius*), MYTY (*Myiarchus tyrannulus*), MYNU (*Myiarchus nuttingi*), MYTU (*Myiarchus tuberculifer*), ICPU (*Icterus pustulatus*).

Figure 3. Residuals of a contingency table including bird species and vegetation units visited alter ingestion of *Bursera morelensis* fruits. Bars depict residual frequencies and their significance, indicating preference (positive residuals) or avoidance (negative residuals) by each bird species. * $P < 0.05$; ** $P < 0.01$. ICPU (*Icterus pustulatus*), MYCI (*Myiarchus cinerascens*), MYNU (*Myiarchus nuttingi*), MYTU (*Myiarchus tuberculifer*), MYTY (*Myiarchus tyrannulus*), MEHY (*Melanerpes hypopolius*).


observed
predicted
Cumulative number of species
16
12
8
4
0
0
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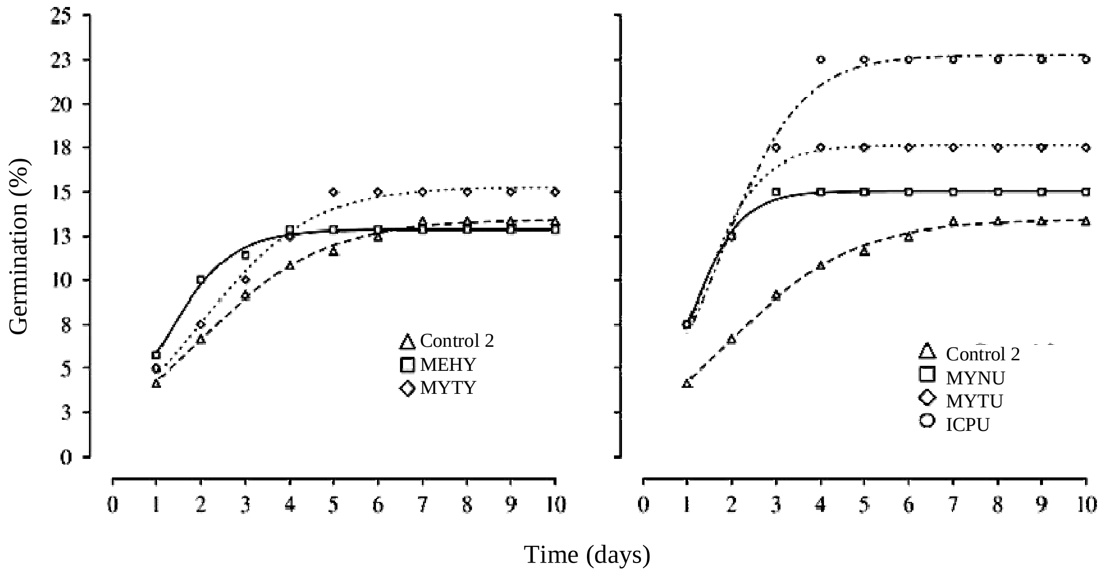
20
25
30
Time (days)


Germination (%)
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Control 2
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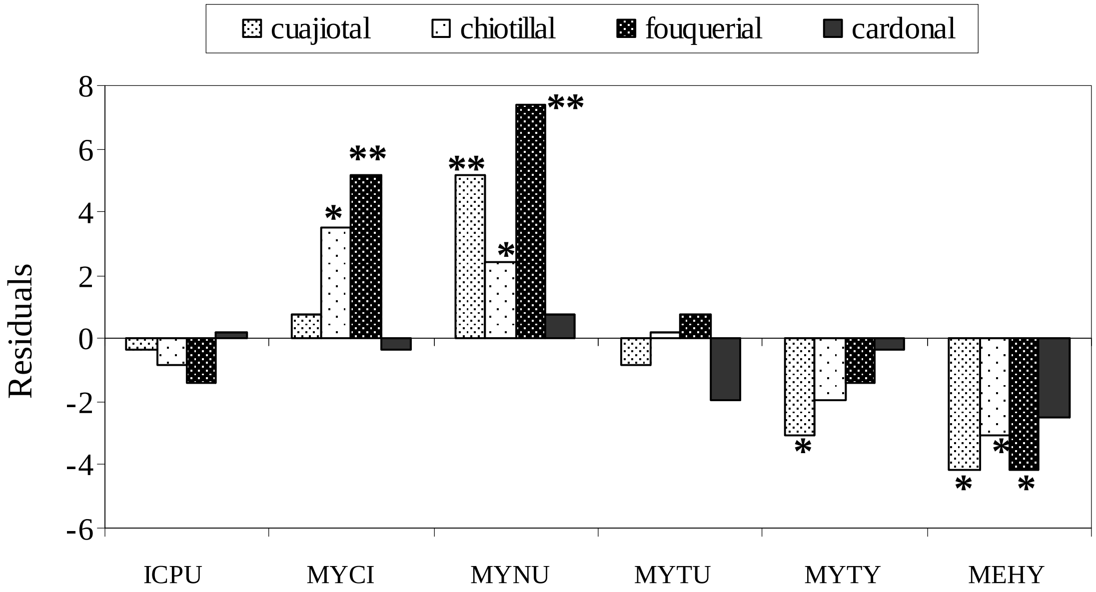
Time (days)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CAPITULO V. DISCUSIÓN Y CONCLUSIONES GENERALES

La propuesta general de este trabajo fue abordar la dispersión biótica de semillas de *Bursera morelensis*, una especie caducifolia endémica de México que produce frutos con y sin semilla. La dispersión de semillas juega un papel importante en la dinámica poblacional de esta especie (Capítulo IV de este trabajo), como se ha mencionado para otras plantas características de ambientes áridos y semiáridos (i.e. Hutto et al. 1986, McAuliffe 1988, Godínez-Alvarez et al. 2002, Spiegel & Nathan 2007). Sin embargo, para comprender este proceso primero fue necesario resolver varias incógnitas básicas de la historia natural de la planta como son: la producción de estructuras reproductivas, el origen de las semillas (sexual o asexual), las características de los frutos y la depredación de semillas previa a la dispersión.

En *B. morelensis* encontramos una serie de características que muestran la importancia de la producción de semillas en la reproducción de esta especie, tales como una sincronía en la fenología de la floración la cual se traduce en una adaptación para disminuir la competencia por polinizadores. También se encontró un proceso de aborción escalonado de las estructuras reproductivas (flores, frutos y semillas) el cual está relacionado con una adaptación ante la escasez de recursos, y por último se evidenció que el origen sexual de las semillas involucra una adaptación para mantener una alta variabilidad genética en la población, y frutos adaptados a la dispersión de semillas por aves (Ramos-Ordoñez et al. 2008). Sin embargo la presencia de partenocarpia pareciera ser una incongruencia, ya que no era clara la razón por la cual una planta con las características mencionadas, produce también frutos sin semilla en proporciones que pueden alcanzar hasta el 50% de la cosecha.

La partenocarpia en *Bursera morelensis* ya había sido mencionada por Verdú & García-Fayos (1998), pero es hasta este trabajo en que se proporciona evidencia sobre este fenómeno. El crecimiento inusual de las paredes del ovario es algo que no se había reportado en las especies partenocárpicas naturales, aunque si se presenta en varios cultivos manipulados artificialmente como los cítricos. Este hecho permite de inicio especular que la causa y desarrollo de la partenocarpia en *B. morelensis* obedece a errores en el equilibrio hormonal como sucede en esos cultivos (Gillaspy et al. 1993, Varoquaux et al. 2000). Otro dato importante es que la partenocarpia suele presentarse en especies con un gran número de óvulos por fruto, tales como los cítricos y tomates (Weiss et al. 1993), siendo menos frecuente en especies que desarrollan una sola semilla como las de Anacardiaceae y Burseraceae. Aunque estas dos familias están fuertemente emparentadas (Soltis et al. 2000), el desarrollo de la partenocarpia aparentemente es diferente ya que en el género *Pistacia* no se ha reportado el crecimiento de las paredes del ovario (Jordano 1988, Traveset 1993, Verdú & García-Fayos 1998) como sucede en *B. morelensis* (Ramos-Ordoñez et al. 2008). Sin embargo hace falta comparar con otros géneros de anacardiáceas como *Spondias*, *Toxicodendron*, *Rhus*, y *Manguifera* (Jordano 1988, Verdú & García-Fayos 1998) sobre los cuales no se ha generado tal información.

Uno de los hallazgos más importantes de este trabajo fue que la producción de frutos partenocárpicos en *Bursera morelensis* representa un ahorro energético para la planta madre (Capítulo II), ya que por un lado la partenocarpia se desarrolla tempranamente en la ontogenia del fruto y por otro, en estos frutos no se forman los cristales de oxalato de calcio necesarios para la protección de la semilla (Janzen 1971, Franceschi & Horner 1980, Lee et al. 1991, Webb 1999, Molano-Flores 2001). Bajo este contexto, la presencia de la partenocarpia toma un mejor sentido, ya que entonces encontramos que *B. morelensis* produce frutos armados química y mecánicamente para proteger la semilla y otros frutos desprotegidos que tienen una estrategia de engaño, de bajo costo energético que disminuye la depredación de semillas por insectos (Ramos-Ordoñez et al. 2008).

Aun con esta información, todavía hacia falta definir el papel de la partenocarpia en el proceso de la dispersión de semillas. Para este fin se tomaron en cuenta las características de los frutos tales como el tamaño y la cantidad de nutrientes, los requerimientos energéticos, la conducta de forrajeo y características anatómicas y fisiológicas del animal, la fenología de la fructificación, las características del hábitat, y el tamaño de la cosecha producida son algunos factores que determinan la remoción de semillas y la tasa de visitas por los frugívoros (Moermond & Denslow 1985, Korine et al. 2000, Bleher & Böhning-Gaese 2001, McCarty 2002, Saracco et al. 2005). En el Capítulo III de este trabajo se muestra como los frutos partenocárpicos producidos por *B. morelensis* incrementan el tamaño de la cosecha y la tasa de visitas por las aves, mediante un efecto de coloración y densidad (Wilson and Melampy 1983, Wilson and Hoppes 1986, Willson et al. 1990, Facelli 1993, Fuentes 1995).

Como se mencionó en el Capítulo I, los trabajos sobre frugivoría realizados en plantas partenocárpicas (género *Pistacia*) han tenido la limitante de que no era posible distinguir los frutos con semilla de los partenocárpicos, aun cuando ya han madurado (Jordano 1988, Traveset 1993, Fuentes & Schupp 1998, Verdú & García-Fayos 1998, 2001). Hasta este punto, los resultados mostrados en esta tesis hacen referencia a la proporción de frutos partenocárpicos producidos por *B. morelensis* como en los estudios mencionados. Sin embargo, uno de los objetivos planteados fue generar información que permitiera definir que tipo de fruto es removido tanto por los depredadores, como por los dispersores de semillas (Ramos-Ordoñez et al. 2008, Tabla 2). Estos datos permitieron ver que la función de la partenocarpia no solo se limita a la disminución de la depredación de semillas por insectos o a atraer frugívoros que remuevan las semillas, sino también involucra una adaptación de la planta que sirve para disminuir la depredación de semillas por aves granívoras (Capítulo III), como sucede en *Pistacia lentiscus* (Verdú & García-Fayos 2001). En conjunto, estos resultados resuelven la paradoja de porque los frutos partenocárpicos son producidos (y en cantidades tan altas) en una planta que invierte una gran cantidad de recursos y estrategias en la producción de semillas como unidad de dispersión.

En el Capítulo IV, se muestra la importancia de los papamoscas (género *Myiarchus*) como dispersores legítimos de *B. morelensis*. Este resultado ya había sido sugerido por Bates (1992), pero además la importancia de estas aves aumenta cuando consideramos que son especies migratorias en la zona estudiada (Arizmendi & Espinosa de los Monteros 1996), de modo que el rompimiento o desfase temporal de este mutualismo podría tener consecuencias importantes en la conservación tanto de la planta como de los papamoscas, afectando también el mantenimiento de la diversidad del ecosistema (Herrera 2001, Traveset 2002). Finalmente, la información recabada hasta el momento no es suficiente para comprender hasta que punto la dispersión de semillas influye en la dinámica poblacional de *B. morelensis*. Para comprender en toda su extensión esta situación es necesario realizar experimentos a largo plazo que determinen bajo que especies de plantas hay un mayor establecimiento de plántulas y caracterizar los patrones de reclutamiento y la probabilidad de sobrevivencia de *B. morelensis* en los diferentes tipos de vegetación y bajo las diferentes plantas nodriza, de modo que se pueda complementar la efectividad como la contribución del agente dispersor a la futura reproducción de la planta (Schupp 1993).

En términos generales, este trabajo muestra como la partenocarpia, un fenómeno común pero poco conocido en los sistemas naturales afecta diferentes procesos de la historia natural de una planta, tales como la dispersión y depredación de semillas. Sobre todo en el caso de las especies de las familias Burseraceae y Anacardiaceae para las cuales se han reportado al menos 22 especies partenocárpicas (26.1% de las eudicotas reportadas, Fig. 1), dispersadas por animales (de acuerdo con una revisión bibliográfica realizada abarcando los años 1965 a 2007), en futuros trabajos se debe contemplar la necesidad de conocer a fondo la unidad de dispersión y la posibilidad de que la especie este produciendo este tipo de frutos, ya que la partenocarpia se podría considerar como un factor que afecta la ecología e historia evolutiva de estas especies.

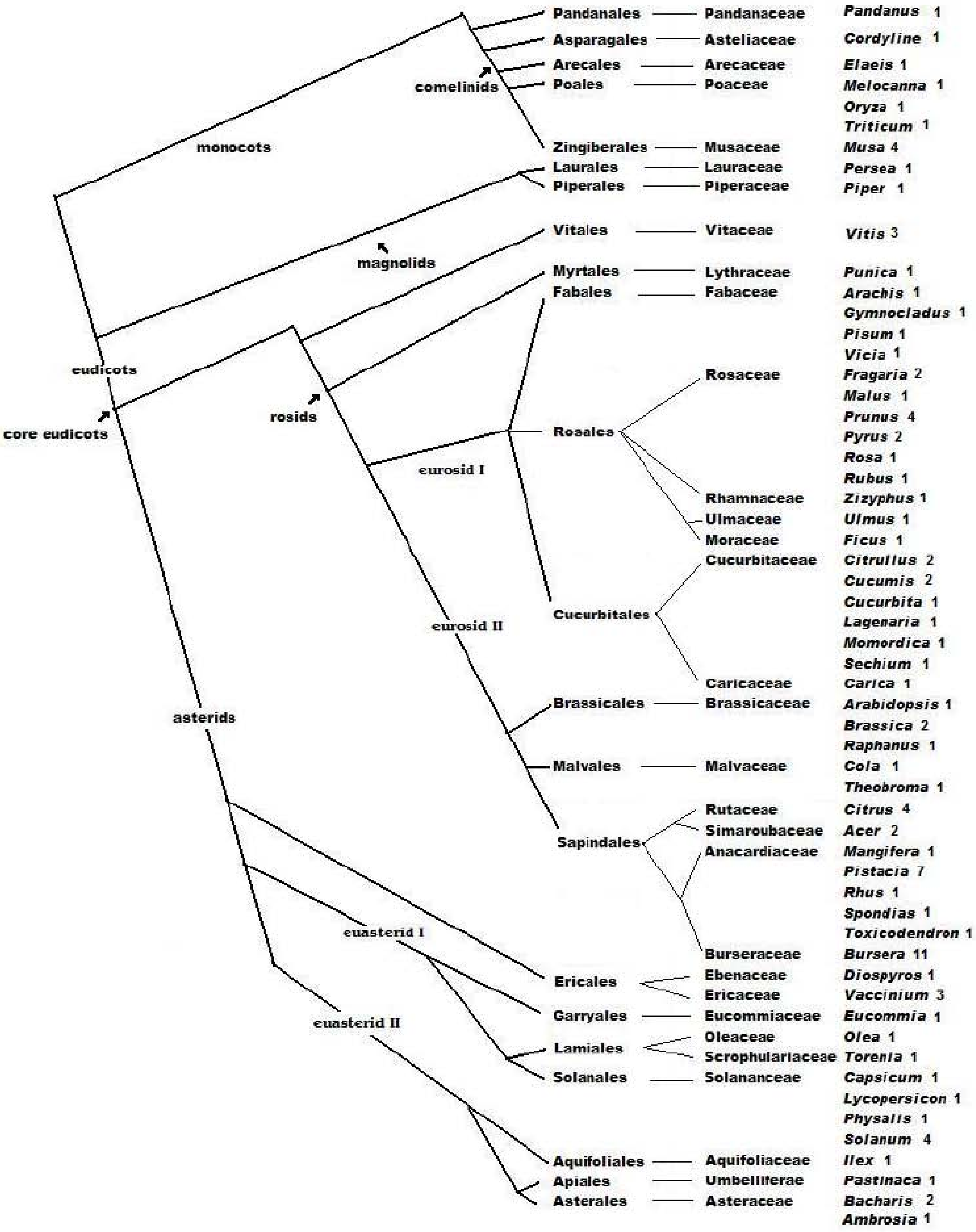

Fig. 1. Géneros partenocárpicos encontrados en la literatura, el número indica la cantidad de especies en las que la partenocarpia se reporta como un fenómeno natural. La revisión bibliográfica abarca los años 1965 a 2007. El árbol fue creado sobreponiendo el carácter partenocárpico al árbol filogenético generado por Soltis et al. (2000) y Stevens (2001).

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