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EL DIMORFISMO EN LA PRODUCCIÓN DE NECTAR: UN ACERCAMIENTO AL PROCESO EVOLUTIVO DE CARACTERES FLORALES

TESIS

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Indice

RESUMEN

La producción de néctar es un atributo que es considerado costoso en términos energéticos y por lo tanto en muchos casos se ha considerado como un atributo adaptativo. El mesquite mielero es una planta importante y en algunos casos dominante de las zonas áridas de América y juega un papel significativo en las interacciones con otros organismos y a nivel de ecosistema, modificando la distribución de los nutrientes. En la Reserva de la Bósfera de Mapimí, Durango México, las poblaciones de mesquite tienen proporciones 1:1 de productores y no productores de néctar en condiciones naturales. En esta tesis, buscamos las posibles consecuencias que tiene la producción de néctar en varios atributos tanto de plantas productoras como no productoras de néctar. Realizamos censos de abejas durante dos periodos de floración (marzo de 1994 y 1995) para saber cual era el efecto de producir néctar sobre el tipo de visitante. Al mismo tiempo, evaluamos la fenología de ambos morfos (1994–1996) y algunos aspectos de la viabilidad y captura de polen de cada morfo. Además evaluamos la efectividad de algunos de los polinizadores más comunes. Para evaluar la función femenina con más cuidado, evaluamos el éxito de la fructificación de la población, y medimos aspectos morfológicos de la flor, analizamos las tasas de entrecruzamiento de las semillas de cada morfo, y evaluamos el éxito en la germinación de semillas. Para poder acercarnos a evaluar el costo de producción de néctar, utilizamos un modelo demográfico modular en donde describimos de manera muy fina el comportamiento demográfico de ambos morfos tomando en cuenta un aspecto ambiental y el otro de producción de néctar. La producción de néctar en el mesquite mielero *Prosopis glandulosa* además de mantenerse en proporciones 1:1 no ha cambiado entre años sugiriendo que tiene una base genética. Las consecuencias sobre los polinizadores es clara, con un mayor en el número de individuos y de especies en las plantas que lo producen. Como consecuencia de esta mayor tasa de visita, el número de granos de polen y el número de semillas producidas fué mayor, sin embargo el tipo de visitante es importante ya que algunos de estos no son tan eficientes en el deposito de polen sobre estigmas como otros. En contraparte, el número de granos de polen es mayor en las plantas que no producen néctar sugiriendo una inversión mayor a la función masculina. La consecuencia del incremento en el número de visitas no conlleva a un incremento en las tasas de entrecruzamiento ($t = 1$ para amboos morfos) ni sobre el peso y la tasa de germinación de las semillas. Demográficamente, la producción de néctar no juega un papel importante y la dinámica de la población de módulos se encuentra limitada por recursos y por la variación interanual. Las posibles rutas evolutivas que pueden mantener este dimorfismo se discuten en donde se proponen modelos inestables (sustitución de un morfo por el otro, y evolución al dioicismo) y modelos estables (EEE y genes ligados al sexo) en donde se puede mantener el dimorfismo de producción de néctar a largo plazo.

ABSTRACT

Nectar production has often been considered a costly attribute in energetic terms and in many cases it has been described as an adaptive trait. The honey mesquite is an important and sometimes dominant species of American arid environments and plays a significant role in plant–animal interactions as well as at an ecosystem level, where it influences the distribution of nutrients. In the Mapimi Biosphere Reserve, Durango, Mexico, a 1:1 proportion of nectarful and nectarless individuals can be found in the populations of the honey mesquite. In this thesis, we describe the consequences of nectar production on several attributes of both nectarful and nectarless individuals. For this purpose, we performed bee censuses during two flowering periods (March 1994 and 1995) to determine the effect of nectar production on pollinator visitation. We also determined plant phenological characteristics for both nectar morphs (1994–1996) as well as some aspects of pollen viability and pollen capture on stigmas and evaluated the effectiveness of the most common visitors. Do determine the effect of nectar production on female function, we determined fruit sets over a three year period, as well as floral morphology, outcrossing rates, seed weights and seed germination rates. To determine the cost of nectar production we used a demographic approach of modular growth for both nectar morphs. Nectar production in *Prosopis glandulosa* was constant throughout the study period and proportions of nectarless to nectarful individuals did not change between years, suggesting that nectar morph could have a genetic basis. The consequences on pollinators was clear, with an increase in the number and species of pollinators on nectarful individuals. As a consequence of this increase, a larger number of pollen grains were deposited on stigmas and a larger number of seeds were produced by nectarful individuals over long time perids, however, the type of floral visitor played an important role as not all floral visitors were as efficient in depositing pollen. On the contrary, the number of pollen grains on nectarless individuals was higher, suggesting a higher investment towards male function. The increase in the number of visitors did not have an effect on the outcrossing rates ($t = 1$ for both nectar morphs), nor in seed weight nor germination rates. Demographically, nectar production does not pose an important drain of resources and modular dynamics was mostly influenced by resources (water availability) and inter–annual variation. The possible evolutionary routes that can be followed by this nectar:nectarless system are discussed whereby models leading to instability (substitution of one nectar morph by the other, and the evolution of dioicism) and stable models in which the dimorphism can be maintained (ESS and sex–linked genes) are described.

Capítulo 1

Introducción

El dimorfismo en la producción de néctar: Un acercamiento al proceso adaptativo de caracteres florales

The first question which has to be answered
on investigating any flower is whether it is a
nectar flower or not because if one regards a
nectar flower as lacking nectar, one will not quite
possibly be in a position to give in any reason why
it has this particular structure but not other.
Christian Konrad Sprengel (1793)

1. Introducción.

Desde la época de C. K. Sprengel (1750–1816), las flores han sido consideradas un elemento para la atracción de polinizadores, y una manera de promover el entrecruzamiento entre plantas (Sprengel, 1793; Darwin, 1862). Las flores presentan varios atributos como el color (Delph & Lively, 1989), la forma (Delph *et al.*, 1996), el tamaño, la presencia de néctar y/o polen (López-Portillo *et al.*, 1993), fragancias (Williams, 1983), aceites (Simpson *et al.*, 1977; Buchmann, 1987) que atraen e influyen el comportamiento de los visitantes a las flores. La expresión de cada uno de estos componentes florales va a tener un efecto sobre la adecuación de las plantas, por varias razones como el número de visitas recibidas, la calidad de la visita, el patrón de forrajeo, y el costo de producir el atributo entre otros. Por ejemplo, un cambio en el número de visitas puede incrementar la probabilidad de exportación e importación de polen (Zimmmerman, 1988; Rush *et al.*, 1995) y además, la planta puede seleccionar la mejor calidad de polen para la fertilización (Stanton *et al.*, 1986; Niesenbaum, 1999). Como estos atributos tienen efectos tan importantes en el éxito reproductivo de las plantas, podremos considerar que la selección natural es la principal fuerza que los modifica. En el caso específico de la polinización, podemos encontrar varios procesos, cada uno con dinámica compleja, que afectan la adecuación de las plantas. Por ejemplo, el efecto que el número de visitas de un polinizador tenga en la dinámica del flujo de polen va a afectar de manera diferencial el éxito reproductivo de la función hembra (recepción de polen) asi como de la función macho (donación de polen). Aunque la dinámica de estos factores es muy compleja, podemos subdividir el proceso global de la polinización en factores que contribuyen a la adecuación total de una planta, de tal manera que podemos analizar modelos más sencillos que al final puedan ser integrados para formar un modelo más general. Al simplificar cada proceso podemos considerar los factores que influyan en los costos y beneficios involucrados en producir y mantener un atributo para después poder generar hipótesis acerca de su evolución. En particular, los sistemas de polinización, además de los atributos que se han considerado como adaptativos (aceites, nectar, forma de la flor; Baker, 1983), hay muchos otros factores no adaptativos (e.g., restricciones genéticas) que deben ser considerados. Entendemos como adaptación: (1) caracteres que promueven la adecuación y además fueron "construidos" para esa función, y (2) una variante fenotípica que goza de una mayor adecuación entre otras variantes, en un ambiente definido y sin considerar el componente histórico (Herrera, 1996; Reeve & Sherman, 1993; Williams, 1966). Por lo tanto, al estudiar la evolución de las flores y la función de la polinización, no solo se necesita información acerca de cada proceso; sino que además necesitaríamos incluir un componente histórico (filogenético) y/o un componente experimental (Armbruster, 1996).

2. Efectos y Consecuencias de los Atributos Florales.

2.1. Los Efectos de la Interacción con los Polinizadores.

Los atributos florales tienen varios efectos sobre la conducta de los visitantes que a su vez afectan la adecuación de las plantas (ver Fig. 1) (Waser, 1983; Mitchell *et al.*, 1999). Los atributos florales afectan la conducta de polinizadores de varias maneras :

- Determinan la probabilidad de visita de los visitantes florales. Esto se puede observar por un incremento en el número de visitas conforme aumenta el despliegue floral (Gori, 1989; Ohashi & Yahara, 1998).
- Influyen en la secuencia de forrajeo de los visitantes dentro de cada inflorescencia. El mecanismo conductual se basa en la probabilidad de encontrar recursos, dado el nivel del recurso encontrado. La conducta se modifica de tal manera que disminuyen la probabilidad de visitar la misma flor dentro de la inflorescencia por medio de patrones regulares (e.g. movimientos basales o apicales constantes).
- Modifican el patrón de forrajeo de los polinizadores después de visitar una planta. Cuando un visitante floral encuentra una flor o planta con recompensas, lo más probable es que en promedio las flores o plantas de la zona van a dar recompensas de la misma calidad, por lo tanto tiende a quedarse dentro del parche de recursos, haciendo vuelos cortos y vuelos en ángulos agudos. En cambio, cuando un polinizador visita una flor sin recompensas, tendería a volar distancias más largas

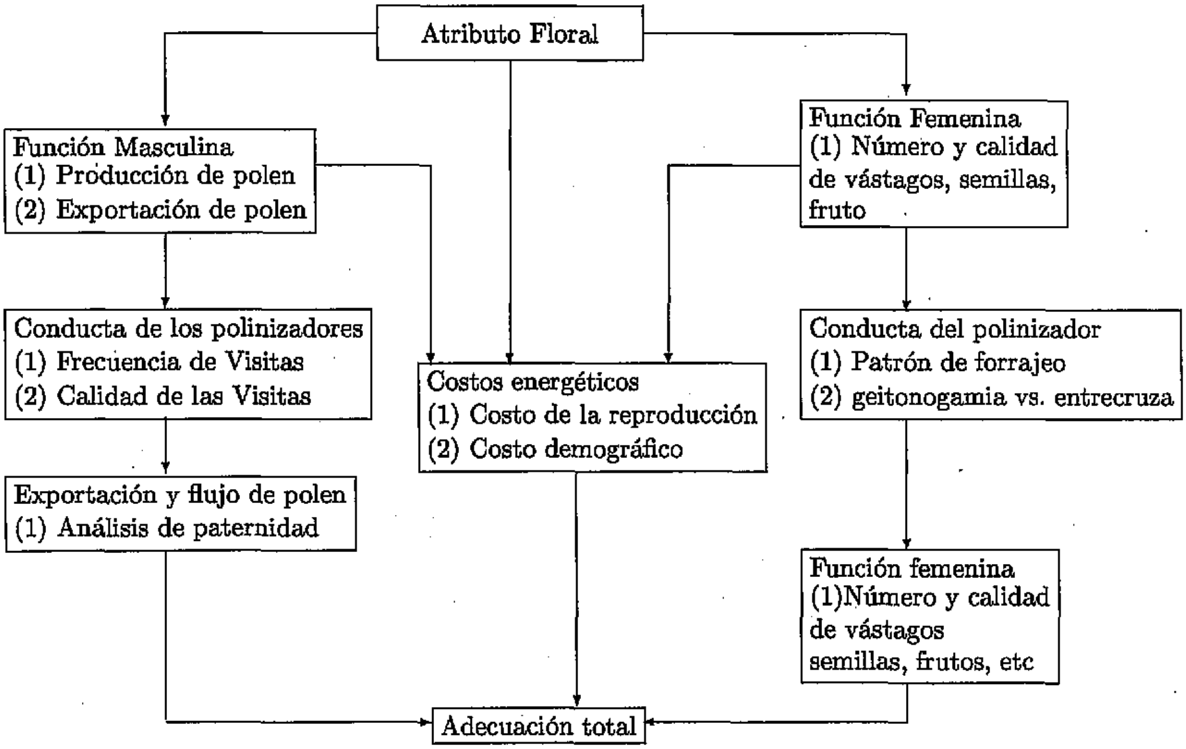

Figura 1: Factores asociados a la producción de atributos florales que afectan la adecuación de las plantas. Por un lado tenemos los componentes reproductivos que son afectados por la producción de néctar y por otro los costos asociados a la producción de néctar

con ángulos de vuelo obtusos en busca de un parche con recursos (Heinrich, 1983; Gill & Wolf, 1977).

- Determinan cómo y cuánto polen se deposita en el cuerpo del polinizador. Los ejemplos más sorprendentes de estos mecanismos se encuentran en orquídeas. Las polinias son insertadas en posiciones específicas del cuerpo del polinizador para incrementar la probabilidad del contacto entre la polinia y la superficie estigmática de otra inflorescencia.

- La interacción de la planta con su visitante determinan en gran medida la dispersión del polen en el espacio. Tanto el patrón de forrajeo inter–planta como el intra–planta van a tener efectos importantes en las tasas de entrecruzamiento (un efecto de acarreo de polen o "pollen carry–over") y autofertilización (geitonogamia).

La polinización genera una disyuntiva importante entre el visitante floral y la planta. En el caso de la producción de polen, el conflicto es especialmente importante, ya que el polen es usado como alimento de las larvas de algunos polinizadores pero es también la función masculina de la planta. Por lo tanto un incremento en el consumo de polen por polinizadores es un secuestro de genes y recursos de la poza génica de la población de plantas. Sin embargo, plantas en donde no existe una producción de atrayentes como el néctar, se ha sugerido que hay un incremento en la producción de polen que funciona como atrayente (Simpson & Neff, 1983). Desde el punto de vista del polinizador, las visitas a las flores están limitadas a encontrar recursos suficientes (que pueden ser aceites, néctar, polen, etc) que maximizen la función costo–beneficio en términos de recursos para el visitante. Desde el punto de vista de la planta, también se va a maximizar la función costo–beneficio (Fig. 2), pero en términos de garantizar la reproducción (Bell, 1986). Estos tres componentes de la interacción con el polinizador son, en buena parte, determinantes de la dispersión del polen (la adecuación por vía masculina). Por ejemplo, un incremento en la producción de néctar incrementa la probabilidad de dispersión y depósito del polen (Aizen & Basilio, 1998), pero también puede provocar un incremento en la tasa de autofertilización y una disminución del flujo de polen por la conducta del polinizador (Klinkhamer *et al.*, 1994; Mitchell *et al.*, 1999).

2.2. Costos Energéticos de los Atributos Florales.

La producción de atributos florales es costosa en términos energéticos, por lo que se debe considerar que cada atributo va a ser optimizado (Cody, 1974; Pyke, 1991)(Fig. 2). El valor óptimo del atributo sería aquel en el cual la distancia entre la curva de beneficios y costos sea la mayor. Estos costos no solo son en términos energéticos, sino también en términos de recursos utilizados como el agua, y nutrientes necesarios para mantener los atributos florales (Ashman & Schoen, 1996). En algunos casos la flores pueden generar fotosintatos que de alguna manera subsidian el costo floral, y en otros casos, puede haber una reabsorción de productos que pueden ser costosos como el néctar (Koopowitz & Marchant, 1998; Búrquez & Corbet, 1991). Los costos pueden llegar a ser tan altos que tienen consecuencias en otros atributos, como en muchos casos que involucran "trade–offs" con varias características de los frutos (Ashman & Schoen, 1996). De manera indirecta, la producción de atributos florales también tienen efectos en atraer polinizadores que no siempre son adecuados, especialmente si incrementan la autofertilización o dañan las partes florales (Renner, 1983). En el caso del néctar, se ha demostrado que hay una correlación positiva entre su producción y alguna medida relacionada con la adecuación (e.g., número de visitas, cantidad de polen exportado e importado, calidad del polen, etc). Esto se debe a que un incremento en la producción de néctar provoca un incremento en la tasa de visita que lleva a un incremento en la exportación e importación de polen. Estos incrementos en polen permiten una mayor fertilización de óvulos (vía masculina) y una mejor selección de la calidad de las semillas (vía femenina), aumentando así la adecuación por ambas vías. Como consecuencia de la atracción el costo tanto energético (Southwick, 1984; Pyke, 1991) como del incremento en la geitonogamia (Klinkhamer *et al.*, 1994) provoca una disminución en la adecuación (Fig. 2).

En algunos casos, individuos dentro de una población y hasta en especies diferentes han desarrollado sistemas de polinización por engaño (Little, 1983) en donde se incrementa la adecuación al reducir los costos de producir recompensas. Ejemplos de estos sistemas son frecuentes en orquídeas (Meiland & Wilcock, 1998), en donde los mimetas que no producen néctar por lo general tienen una menor producción de frutos pero no tienen el costo de producir el recurso. En los sistemas en donde hay plantas que no producen néctar, por lo general hay una sustitución de la recompensa por fragancias y/o polen (Meiland & Wilcock, 1998). Estos sistemas casi siempre son mantenidos por algún proceso de selección (e.g., selección dependiente de las frecuencias). Por ejemplo, la orquídea mimeta *Orchis israelitica* es más exitosa (48,6 %) en presencia de la Liliaceae modelo *Bellevalia flexuosa* que produce néctar que en la ausencia (3,8 %) del modelo (Dafni & Ivri, 1981)

2.3. Función Femenina y Masculina.

La presencia o ausencia de atributos florales va a tener consecuencias principalmente en la función masculina de la flor (Bell, 1986). Los modelos teóricos sugieren que la inversión en caracteres florales esta asociada a la función macho. Si solo consideramos la asignación secundaria a las

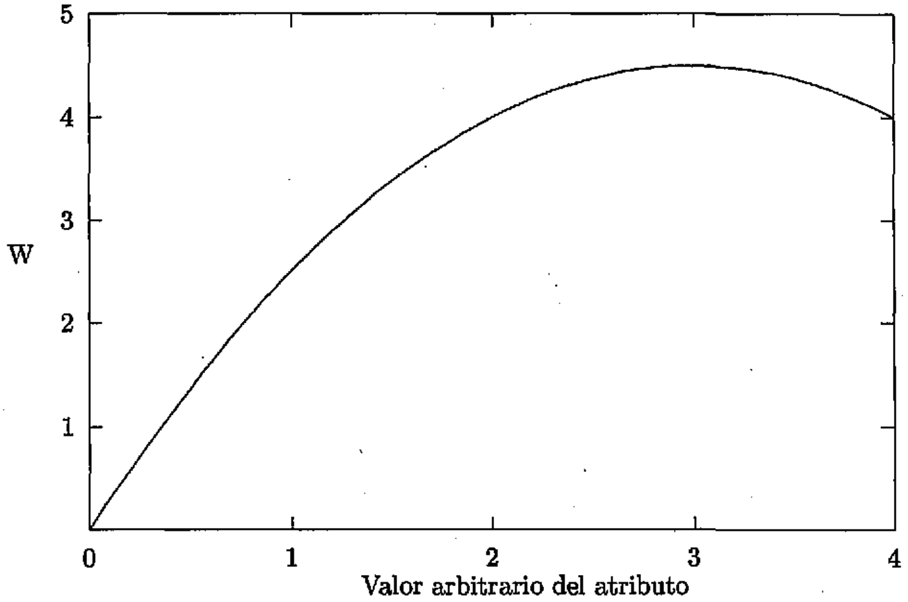

Figura 2: Función de optimización para un atributo floral como el néctar

estructuras de atracción como iguales entre masculino y femenino, en las flores perfectas necesariamente habría una asignación a la parte femenina mucho mayor que a la masculina (Bell, 1986). Cierta evidencia empírica también apoya hacia este hecho. En sistemas dioicos en donde hay productores y no productores de néctar, la producción de néctar se encuentra asociada a las plantas masculinas. Por ejemplo, en muchas orquídeas la producción de néctar esta asociada a las flores masculinas mientras que las flores femeninas son mimetas (Bino *et al.*, 1982). En sistemas protrándricos como en el caso de algunas especies del género *Agave* (Schaffer & Schaffer, 1977), y en *Aplistoema aurea* (Aizen & Basilio, 1998), la producción de néctar esta asociada a la función masculina dentro de la fenología floral.

Como hemos visto, la presencia/ausencia de atributos florales tiene consecuencias en varios aspectos relacionados con la adecuación de las plantas. Para poder determinar la importancia en adecuación de algún atributo, debemos analizar las consecuencias sobre la historia de vida de las plantas (como el crecimiento y la reproducción) para poder generar hipótesis que puedan aproximarnos a explicar la evolución de sistemas biológicos. Esto hace que los modelos de optimización tengan que incluir todos lo factores que involucran la adecuación de la planta (Fig. 1). Para esto, necesitamos conocer la mayoría de los factores causales en el proceso, para poder determinar la importancia relativa de cada factor y así evaluar las consecuencias generales involucradas en el proceso. Partimos del supuesto de que un atributo tiene algún efecto sobre los polinizadores (incrementa el número de visitas, el tiempo de cada visita, etc). Estos a su vez modifican la dinámica del flujo de polen y la función femenina, que se traduce en adecuación por las dos vías. Por otro lado, tenemos los costos asociados de producir el atributo que pueden negar los beneficios obtenidos. Al juntar estas dos vertientes, podríamos aproximarnos a evaluar como afecta el atributo en la adecuación final de manera integrada.

3. El caso de *Prosopis glandulosa.*

Esta tesis trata de explicar la evolución de un sistema dimórfico de producción de néctar. Se centra en encontrar las consecuencias de producir néctar sobre aspectos genéticos, reproductivos y demográficos de los individuos. Para este fin, usamos a *Prosopis gandulosa* var. *torreyana* (mesquite mielero) que es una planta sumamente importante en las zonas áridas de Norte América al tener asociaciones con un número grande de especies tanto artrópodos como mammíferos (ver Apéndice 3). El género *Prosopis* se encuentra ampliamente distribuido en América. La expansión de las especies leñosas a pastizales ha geerado una serie de metodologías para el control de estas plagas, sin embargo la importancia y el papel ecológico que juegan las especies de mesquite en las zonas áridas es raramente discutido. Por ejemplo, se ha demostrado que suelos asociados a mesquite se encuentran enriquecidos de Nitrogeno y Carbono libre, generando así islas de fertilidad en los ambientes desérticos. Sin embargo, el mesquite sigue siendo considerado como una especie invasiva de pastizales. Esta invasión se atibuye principalmente a sequías, supresión de fuegos naturales, sobrepastoreo de ganado y concentraciones elevadas de CO_2. Aunado a estas características ambientales, el mesqite posee atributos demográficos que lo hace ser una especie invasora muy eficiente. Por un lado es capaz de mantener poblaciones al equilibrio en épocas de sequía comportandose como una planta leñosa perenne, mientras que también aprovecha los pulsos de recursos para la invasión de los ambientes de pastizales. Demográficamente, el mesquite puede comportarse como una planta invasora cuando los recursos son adecuados (ver apéndice 2). Los factores más importantes que determinan la demografía del mesquite mielero se componen de dos aspectos, el primero es la cantidad de agua disponible en un sitio y en segundo término, la variabilidad entre años que afecta las tasas de reclutamiento por un lado y el crecimiento por el otro. En años malos (precipitación por debajo del promedio), la demografía del mesquite mielero esta determinada por la sobreviviencia más que cualquier otro proceso demograáfico.

Estudiamos una población de mesquite mielero en la cual se ha descrito un dimorfismo de producción de néctar (proporción 1 : 1 entre morfos productores y no productores) en varias poblaciones dentro de la Reserva de la Biósfera de Mapimí (Durango, México López-Portillo *et al.*, 1993). Este sistema dimórfico de producir/no producir néctar en proporciones tan semejantes es único en condiciones naturales y permite explorar las consecuencias en varios aspectos biológicos que genera éste atributo floral.

4. Organización de la tesis.

La tesis esta dividida en 5 capítulos y cuatro apéndices, siguiendo el marco teórico planteado anteriormente (Fig. 1). En el capítulo 2 se describe cómo la producción de néctar afecta la conducta de los polinizadores, tanto en el número de visitas como en la calidad de la visita. Esta parte es esencial para la planta, ya que la interacción con el polinizador es una relación crítica de la reproducción y por ende de su adecuación (Wilson & Thompson, 1996). Para este capítulo se realizaron censos durante dos años en individuos que producen y que no producen néctar, para describir el comportamiento de los polinizadores en cada morfo, y analizar la calidad de los diferentes visitantes florales. El capítulo 3 se acerca al problema del dimorfismo en la producción de néctar desde un punto de vista de caracteres florales, producción de frutos y tasas de entrecruzamiento, tratando de entender cómo es alterada la estructura floral y un componente de la adecuación (función hembra) de la planta. Para esto usamos marcadores moleculares (isoenzimas) para determinar las tasas de entrecruzamiento, y realizamos una descripción de los caracteres florales, y un seguimiento de la producción de frutos a través del tiempo. En el capítulo 4 determinamos las consecuencias de producir néctar en ambientes desérticos, tratando de evaluar los costos demográficos a nivel modular. Utilizamos tanto modelos matriciales como log-lineales para poder describir la importancia del néctar, la variación anual y la disponibilidad de agua (factores importantes en zonas áridas) en los procesos demográficos modulares de *P. glandulosa.* El quinto capítulo es un análisis global de la evolución de la producción de néctar en el mesquite mielero. En especial trato de resumir todo lo encontrado durante el transcurso de estos últimos años acerca de la influencia que tiene el néctar en los individuos de *P. glandulosa.* Intento explorar varios modelos que puedan explicar el dimorfismo, para poder llegar a una hipótesis de la evolución de este atributo floral. En el apéndice 1 se describe la metodología que seguimos para empezar a cuantificar el flujo de polen, que aunque mencionado brevemente en el capítulo 3, amplía la explicación del componente masculino más allá de solo la parte temprana del desarrollo. Para esto, describimos el uso de marcadores moleculares más específicos (microsatélites) para poder cuantificar el flujo de polen dentro de la población. El apéndice dos describe la demografía del mesquite en ambientes desérticos y la estrategia demográfica que sigue para adecuarse a cambios en el ambiente. El apéndice 3 resume características del género *Prosopis* que le permiten ser uno de los componentes florísticos más importantes de las zonas áridas de América. Trata de resaltar la importancia del mesquite en áreas donde los ambientes son muy fluctuantes e incluyo algunos aspectos demográficos que ayudaron a entender las características que hacen de *Prosopis glandulosa* una especie tan importante de las zonas áridas de norteamérica. Finalmente, los anexos del final son los códigos de los programas que utilicé para el análisis demográfico y un programa de modelos de selección que fué utilizado brevemente en el cuarto capítulo.

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Capítulo 2

Reproductive Ecology and the role of pollinators in nectarful and nectarless honey mesquites *Prosopis glandulosa*

PAGINACIÓN DESCONTINUA

Reproductive ecology and the efect of pollinators on nectarful and nectarless honey mesquites

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Running title: Floral visitors in nectarful and nectarless trees.

Abstract

We investigated the plant-pollinator interactions between nectar and nectarless plants of *Prosopis glandulósa* var. *torreyana* in the Chihuahuan desert. Nectar production has been proposed as an adaptation to attract pollinators that benefit from this resource, while plants gain in fitness through pollination. As mesquite species are bee pollinated, we explored how differences of visitor species diversity and visitor frequency affect several aspects of female function in nectar and nectarless trees. During the flowering season of 1994 and 1995, for both nectarful and nectarless individuals, floral visitors were captured at three different times of day. Flowering phenology (over a three year period), rates of nectar production, effects of visitation on pollen receipt and pollen germination rates were recorded. Nectar production rates were constant throughout the day but differed between days. No differences were found in flowering phenology between nectar morphs, and proportions of nectarful and nectarless individuals within the population remained constant throughout the study period. Bee species diversity and frequency of visitors were significantly larger on nectarful than on nectarless plants and only 10% of bee species were shared by both plant morphs. Our results suggest clear differences in the function played by the plant rewards (i.e. nectar and pollen) to attract visitors, but no significant differences in fruit set were found between nectar morphs. Even though flowering phenologies overlap in time and space, the kind of pollinators between nectar morphs are clearly distinct. The quality of visitation and the sexual identity of the pollinators could probably be affecting the frequency of selfing. In addition, the visitation of several generalist bee species results in the same pollination success as few constant bee visitors that collect pollen. Very low fruit sets are found despite the

high amount of bee species that visit *P. glandulosa.* These low fruit sets could be due to pollen limitation and inbreeding depression as a result of selfing or unsuccessful cross–pollination.

Introduction

Plant-pollinator interactions have been extensively studied in the literature (Bierzychudek, 1981; Cruden et al., 1983), and pollinator "decisions" with respect to resource acquisition have generated both an empirical and theoretical framework (Waser, 1983; Gilbert et al., 1991; Bell, 1986). Formerly, nectar was generally ineterpeted interpreted as an adaptation to attract pollinators, that benefit from a carbohydrate rich resource while plants gain in fitness through pollination (Baker and Baker, 1983; Heinrich, 1975), but this has been recently undermined (Herrera and Soriguer, 1983).

In spite of this relationship, a large amount of visitors take advantage of plant resources which can either positively or negatively affect plant fitness. Positive effects on plant fitness in large visitor coteries often occurs when pollination is achieved by a large number of "bad pollinators" as compared to an "optimum" or more specialized visitor (Burd, 1995; Arizmendi et al., 1996; Fishbein and Venable, 1996). Negative effects occur when nectar robbers damage or alter the flowering structure, eliminating the possibility of fruit development (Roubik, 1982, 1989), although nectar robbers might not necessarily reduce fruit sets (Inouye, 1980; Morris, 1996; Arizmendi et al., 1996).

Maintaining large pollinator coteries could be beneficial if and when the expended resource does not prove costly (Harder and Barrett, 1992). If resources such as nectar prove costly, then robbers or "poor" pollinators should be discouraged, leading to the possible evolution of restricted plant-pollinator interactions. Pollinators have been shown to respond to resource-rich patches and have the capacity of discriminating between these, depending on the energetic source that is being searched (Falque et al., 1995). Pollinator visitation frequencies and flight patterns have been largely analyzed in terms of energetics and optimality theory (Heinrich, 1975, 1976) and their activities largely depend on the benefits gained after probing or scents left behind by previous visitors (Wetherwax, 1986). Optimum plant–pollinator interactions have evolved in several ways (Herrera and Soriguer, 1983; Gilbert et al., 1991; Nilsson, 1992; Pleasants and Zimmerman, 1979), such as "Bonanza-Blank" resource offering (Brink, 1982; Feinsinger, 1983), flower color changes (Delph and Lively, 1989) and variable nectar secretion patterns (Brink and de Wet, 1980).

It is thus important, from the plants perspective, to guarantee actual reproductive success with available pollinators, especially when pollinator guild variability has been shown on a daily, seasonal and yearly basis (Fishbein and Venable, 1996; Herrera, 1996) or when flower constancy is absent (Waser et al., 1996). Both systems can be found in arid environments where there are large amounts of possible pollinators and low availability of resources for both plants and pollinators (Linsley and MacSwain, 1957; Mandujano et al., 1996; Simpson et al., 1977; Keys et al., 1996; Waser et al., 1996). *Prosopis* is a genus that has a characteristic bee pollinator syndrome (Simpson et al., 1977). Due to the large floral display and regular phenology, trees have a large amount of visitors, and are often used as sites for other activities such as mating sites, areas were predator-prey interactions occur, as well as growth sites for different animal taxa (Simpson et al., 1977). In particular, a dimorphic system of nectar production between plants has been described for *Prosopis glandulosa* var. *torreyana* (López-Portillo et al., 1993; Golubov et al., 1999) of the southern Chihuahuan desert, where 1:1 proportions of nectarful to nectarless individuals are intermingled, forming dense scrublands and vegetation arcs.

The dimorphic system of nectar production provides a means of describing nectar variation patterns, availability and changing community of pollinators, and their influence on plant fitness in the same species.

The aim of this study was to determine the guild of pollinators that visit *P. glandulosa* and in particular we describe 1) differences in visitor guilds between nectar morphs?, 2) assess the differences and identity of visitors in nectar and nectarless morphs between and within years? and 3) determine if there is an effect of nectar production on pollen viability and on female function?

Methods

Study area–Research was conducted in the Mapimi Biosphere Reserve (MBR), southern Chihuahuan desert (26° N 104° W, 1100 m altitude, 264 mm yearly average rainfall, 21°C mean temperature). Yearly rainfall during the study period was 138.5 mm in 1994 and 198.4 mm in 1995 (MBR climatic station). Field work was concentrated in a 1 ha plot of desert scrubland with *P. glandulosa* var. *torreyana* surrounding a temporal water-catchment site. In the plot, all reproductive individuals have been tagged and their nectar condition determined since 1994 (Golubov et al., 1999).

Flowering Phenology–General plant phenological state was recorded every second day during the 1995 and 1996 flowering season following the same methods described previously for the 1994 flowering season (Golubov et al., 1999). We tested if nectarful and nectarless plants differed in the number of reproductive individuals between years (1994–96) by means of Chi–square on a 2 x 3 contingency table (2 nectar states and 3 years) and tested for independence.

Nectar Production–During the 1994 flowering season, 11 nectarful reproductive individuals of *P. glandulosa* var. *torreyana* were randomly selected. Of these, two individual branches containing mature inflorescences were also randomly chosen and fresh individual inflorescences were bagged at dawn with 15 x 20 cm paper bags, to avoid pollinator visitation. Nectar production curves (accumulated nectar per flower vs. time) were measured at regular 4 hr intervals from 8:00 hr to 20:00 hr by probing at least 5 individual flowers per tree, sampled on 6 consecutive days. To determine the rate of nectar production, we fit linear regression models of accumulated nectar at different times of day. As no differences were found between individual plants with respect to nectar production, data were pooled. We used an ANOVA to assess the influence of hour on the volume of nectar production (Kirk, 1995).

Visitor Surveys–During the 1995 flowering season, we performed fixed–time capture efforts on 12 trees at three times of day (8.00-10.00, 12.00-2.00 and 16.00-18.00 hr) every second day following the methodology described previously (Golubov et al., 1999). The sample size was determined by the time that could be covered in 2 hr intervals (5 minute capture efforts per plant) on nectar and nectarless morphs by a single collector. All visitors that were found were captured using 15 x 20 cm plastic bags (thorns preclude the use of nets) or directly in lethal chambers. Captured individuals were identified at the Museo de Zoología, Facultad de Ciencias, UNAM, Mexico. This methodology was done for a second sampling year, and the full list of visitors has now been identified. Chi-square analysis was performed to assess the influence of time of day on pollinator abundance (Everitt, 1977).

Pollinator efficiency–During the 1996 flowering season, we bagged new inflorescences of nectarful and nectarless individuals and 1 visitor per inflorescence was monitored for each nectar morph ($N = 20$ visitors). The inflorescences where visitation had occurred were immediately collected after visitation, and a sample of 10–15 styles were excised, stained with methylene blue, and number of pollen grains counted. In addition, to assess the levels of natural pollination, during the same period, 3 flowers of each of 6 trees were tagged while immature. Once the inflorescence matured, we randomly collected one of the tagged inflorescences on each of 3 consecutive days. Styles of at least 10 flowers per inflorescence were collected and stained with methylene blue. The presence and number of pollen grains was determined for each stigma. Data analysis was performed with an ANOVA having day, and nectar morph as factors.

Pollen performance–The success of pollen germination was assessed by germinating pollen grains of a single inflorescence in a 10 % sucrose solution and kept for 6 hrs in a humid chamber. We sampled 10 inflorescences per plant of 11 plants per nectar morph. The viability of pollen grains was then determined by staining with Alexanders medium (Kearns and Inouye, 1993). We analyzed the importance of individual trees and nectar morph on the proportion of viability by means of GLIM ver 3.77 (Royal Statistical Society) assuming a binomial error distribution (Crawley, 1993).

Results

The number of flowering individuals during the reproductive season was similar for both nectar morphs (Table 1), resulting in an equal proportion of nectar to nectarless morphs in the study site that did not change between years (Table 1; $\chi^2 = 0.02, df = 2$).

With respect to nectar, the rate of production of *P. glandulosa* flowers is constant during the day (Fig. 1), with individual flowers starting to produce nectar in the morning ($0.063\mu l \pm SE$ 0.065 by 8 am) and on average producing $0.16\mu l \pm SE$ 0.01 of nectar per flower per day. We found no significant difference of nectar production between plants ($N = 11$, $P = 0.194$), but there were significant differences in standing crop of nectar at different times of day ($F_{3,43} = 26.75$, $P < 0.01$, Fig. 1). Contrast t-tests showed the only non-significant difference was between 12:00 and 16:00 hr ($P = 0.06$). However, we found differences in nectar production between days ($N = 6$ days; $F_{5,43} = 4.09, P = 0.01$) probably due to the environmental conditions that prevailed during the study period. For nectarless individuals of *P. glandulosa*, no nectar production was observed and this character has remained stable in consecutive years (Golubov et al., 1999).

During the two–year period, a total of 64 species of bees were identified visiting *P. glandulosa*. After taxonomic classification to the species level, 55 species (distributed in 21 genera) were collected during the first year and only 44 (distributed in 17 genera) were collected during the second year. However, during the second year, 9 new species were identified visiting *Prosopis* flowers (Table 2). Bee diversity was strongly biased towards the Megachilidae in both 1994 and 1995 (47.11% and 53.68% of all captured individuals, respectively) and Colletidae (35.54% and 31.1%) families followed by Apidae (7.85% and 5.69%), Andrenidae (6.2% and 9.36%), and Halictidae (3.31% and 1.17%). The most abundant genera changed between years: during 1994, *Colletes* was the most common genus (30.72%) followed by *Ashmeadiella* (22.18%), while during 1995, *Colletes* decreased in importance (24.41%) and *Ashmeadiella* increased (30.43%). The genus *Megachile* remained constant in both years (18.87% and 17.56%, respectively). *Perdita* followed in abundance with less than 10 % and the rest of genera contributed in less than 5% to total bee abundance. Species abundance during 1994 was clearly characterized by more genera (and species) in low frequency that were not sampled in 1995 (30 vs. 24 species, respectively). The high abundance category was consistent between years for only 8 species, the rest of the species varied in abundance between years (Table 2). It is thus clear that of the 19 genera visiting *P. glandulosa*, only the most abundant species visit nectarless individuals. The number of species that visit each tree accounts for close to 50 % of total species diversity found within a given year.

Visitors differ greatly between nectar morphs. Nectarful trees had 97.11% of total captures and nectarless trees had only 2.89% of total captures during 1994. This changed in 1995, where nectarful trees had close to 92.81% of total captures and nectarless trees had 7.19%. In addition, for female bees, the captures on nectarless trees remained constant in both years (2.89% and 2.84% of total captures, respectively). However, male individuals were an important component on nectarless trees during 1995 (4.34% of total captures). With respect to time of day, the proportion of bees was greater at midday during 1994 but this changed towards the afternoon census in 1995 ($\chi^2 = 498, df = 2, P < 0.01$). For both years however, bees were rarely found before 10 am despite abundant nectar availability, probably as a consequence of their physiological requirement of temperature for activity.

Sex abundance differed with respect to flowering period. Males largely visit at the beginning of the flowering period and preferably on nectarful plants, while female bees are found on both nectarful and nectarless individuals, but their abundance is found a few days later with respect to male bees (Fig. 2). The abundance of species was independent of the specific year ($\chi^2 = 0.076$, $P > 0.01$), as was reflected in the similar abundances of 17 species between years. There were 8 species that had high abundance in both years, 3 species with intermediate and 6 species with low abundance (Table 2). The data suggest that the abundance of these species on *Prosopis* flowers is constant over time (at least during these two study periods), and *Prosopis* can depend on at least these species to be present for pollination. The rest of the species differed in their abundance between years. Similar results were found by (López-Portillo et al., 1993) where species differed between years and only a few were found in both years. As fruit sets and outcrossing rates are similar between nectar morphs (Golubov et al., 1999), the low visitation frequency by the captured species are affecting pollination. Considering female bees exclusively, these comprised 5 families in 1994 and 4 families in 1995 (excluding Apidae). In both years the species that visited nectarless individuals in the majority of the cases corresponded to the most abundant genera (mentioned above) which were also found on nectarful plants (Table 2).

Pollen viability was greatly affected by the specific tree the sample came from ($X^2 = 62.43, gl = 10, P < 0.01$), however we found no differences between nectar morphs ($\bar{X}_{nectarful} = 0.50, \bar{X}_{nectarless} = 0.52$; $X^2 = 1.711, gl = 1, P > 0.05$), suggesting that both nectar morphs provide viable pollen in the same proportion, with high variability between individuals.

There were significant differences in the number of pollen grains deposited between nectar morphs and between consecutive days. Pollen grains accumulated progressively on the stigmas of flowers (Table 3) and the mean number of pollen grains differed between the first two days and the third ($P < 0.01$). The amount of pollen grains deposited on stigmas also differed between nectar morphs, nectarful individuals significantly ($P < 0.01$) increased (by approximately 30%) the number of pollen grains deposited on stigmas ($F_1, 1304 = 83.2, P < 0.01$), suggesting that female function is being benefitted by nectar production ($\bar{X} = 10$ pollen grains per flower over the three days period on nectarless trees vs. $\bar{X} = 15$ pollen grains per flower on nectarful individuals; Table 3).

The honey mesquite *P. glandulosa* has a mean of 18 ovules per flower (Golubov et al., 1999), but mean seed set was lower ($\bar{X} = 11$). This suggests that 30% of the ovules of flowers are not fertilized or are aborted. The variance between flowers of the number of pollen grains received (range = 0–40) varied greatly, but saturated with time ($CV_{(day1)} = 113.82$, $CV_{(day3)} = 61.93$). The amount of pollen deposited was also a function of the type of visitor, on average large bees of the Apidae and *Apis* deposited large amount of pollen per visit (5.38 and 6.39 pollen grains $^{-1}$ flower $^{-1}$ visit $^{-1}$), while smaller bees also of the Anthophoridae such as *Melissodes tristis* deposited less pollen (Table 4). Flies were poor pollinators, depositing less than 1 grain of pollen per visit per flower while *Megachilide* had intermediate values of pollen deposition (2.34 pollen grains^{-1} flower^{-1} visit^{-1}).

Discussion

Nectar production is often associated to male function, as a consequence of Batmen's principle, which states that female fitness is resource limited, while male fitness is limited by access to females (Wilson et al., 1994). In contrast, nectar production has been associated to female function in dioecious species (Pyke et al., 1988; Greco et al., 1996), as a means of attracting pollinators and is associated to male function in monoecious and hermaphrodite species. In the honey mesquite, a hermaphrodite species, nectar production positively affected visitation and as a consequence it also played a role in the female fitness function by increasing the number of pollen grains received. The proportion of pollen grains that are deposited (30% more) could be one of the factors that is increasing the fitness of nectarful individuals by 25% as found peviously (Golubov et al., 1999). The increase in visitation could also suggest an increase in male function through pollen export, as has been found for other plant species (Zimmerman, 1988; Rush et al., 1995). However, under closer scrutiny, the sexual characteristics of the higher visitation frequency on nectarful individuals may play an important role in the fitness gained through male function. On one hand, nectarful individuals provide resources for a wide range of visitors, and on the other, nectarless individuals provide resources only to a limited number of visiting species. In addition to attracting female bees, nectarless morphs during the 1995 flowering season attracted male bees which could possibly have been naive pollinators. The actual success of pollen transfer by bees other than female bees must be assessed, as males generally do not possess the structures needed for pollen transfer but may be causing pollination in a more haphazard manner. The high outcrossing rates and limited self–fertilization found for *P. glandulosa* (Golubov et al., 1999) and *P. velutina* (Keys and Smith, 1996) suggest the need for cross–pollination, especially as the resulting cross–pollinated seeds are, on one hand, highly heterozygous (Golubov et al., 1999) and on the other also benefit from better germination rates (Martínez, 1996).

Attraction of pollinators is also affected by plant phenology, especially as the size and density of floral display can positively or negatively affect plant fitness through male and female functions (Fritz and Nilsson, 1996).

Large floral displays would seem to benefit plant fitness, however, it has been shown to decrease the efficiency of pollen export, with an increase in geitonogamy (DeJong et al., 1993). In mesquites, flowering phenology among the different plants is similar within a year (Golubov et al., 1999) and is also similar between years (this study), supporting the idea that both nectar and pollen resources are available at the same time period for access by foragers. Comparing the data with those described previously (López-Portillo et al., 1993) the proportion of nectarful to nectarless individuals seems to remain relatively constant between years (±46% nectarful and ±54% nectarless). Even when nectar production rates in *P. glandulosa* are constant throughout the day, it also seems to be constant between years (López-Portillo et al., 1993), nectar resource availability is variable between trees, which is often associated to bee pollination (Cruden et al., 1983; López-Portillo et al., 1993). This high variation is probably coupled to prevailing environmental conditions, giving a patchy nature to resource availability. In addition, the lack of nectar production on nectarless trees suggests a genetic basis underlying the system which also contributed to the segmented nature of resources that are offered to pollinators. This patchiness could in fact optimize outcrossing rates as the high frequency of nectarless to nectarful trees causes pollinators to seek for resources between trees.

The adaptive value of floral traits has been reconsidered, especially regarding pollinator syndromes (Herrera, 1996). The evidence suggests low floral specialization to particular pollinators (Herrera, 1996) even though some examples of specificity do occur (e.g. the *Yucca Yucca*–moth associations). Mesquites seem to have a low floral specialization and we identified two aspects that could contribute to this fact: (1) Floral morphology allowed visitation by a wide range of insect orders (Golubov et al., 1999), and when considering a specific order (Hymenoptera in this case), a wide range of visitors were found. (2) The spatio–temporal variation in pollinators undermines the plants possibility to specialization (Herrera, 1996; Eckart, 1992) as floral traits are subject to varying selection regimes (Schemske and Horvitz, 1989; Waser et al., 1996).

In the honey mesquite, bee coteries varied widely between both morphs and between years. On one hand, nectarless individuals were benefited by the most abundant pollinators and on the other, nectarful individuals increased visitation and quite possibly geitonogamy. Of all species studied, 8 genera seem to be abundant and constant year to year visitors of *Prosopis glandulosa* at MBR, while 5 genera (especially females) are found on nectarless morphs during the two studied years. The data suggest that the abundance of these species on *Prosopis* flowers is constant over time (at least during these two study periods), and *Prosopis* possibly depends on these species for pollination. The rest of the species differed in their abundance between years making them unpredictable pollinators. Similar results were found by (López-Portillo et al., 1993) where species differed between years and only a few were found in both years. As fruit sets and outcrossing rates are similar between nectar morphs (Golubov et al., 1999), the low visitation frequency by the captured species are affecting pollination. In both years the species that visited nectarless individuals in the majority of the cases corresponded to the most abundant genera (mentioned above) which were also found on nectarful plants. In arid environments, oligolecty (specialization) is particularly dominant (66 % of bee species Waser et al., 1996). In the case of *P. glandulosa*, some species seem to be oligolectic (e. g. *Colletes prosopidis* and *C. algarobiae*) but many others such as *Diadasia* are generally considered to be specific to the Cactaceae (notably *Opuntia* Mandujano et al., 1996) but may require the energetic resources provided by *P. glandulosa* during the dry period. Regardless of specialization, the visitors to the nectarless morph are considered good pollinators especially as fruit sets and outcrossing rates do not differ between nectarful and nectarless morphs.

With respect to individual visitors, given the large amount of pollen grains produced by flowers ($\approx 3,600$ flower $^{-1}$), pollinators such as *Perdita* and smaller bees will obtain full pollen loads in a single visit, reducing the possibility of inter-flower movements. On the contrary, larger bees such as *Megachile* would be better pollinators as pollen loads accumulate after several visits to different flowers, possibly increasing cross-pollination and therefore fruit sets. Our data suggest that larger bees do in fact deposit large amounts of pollen on stigmatic surfaces, and flowers need only 2–3 visits to complete seed sets. Other visitors such as flies may only land on flowers and insert proboscis on each flower, but the amount of pollen that is transported by these species is one order of magnitude less than those deposited by solitary bees, and therefore generates low fruit sets. An example of this inefficient pollination is that of the fly *Volucella* on the velvet mesquite (*Prosopis velutina*), leading to relatively low fruit sets (Keys et al., 1996). In addition to bad pollination, wasps and flies are consumers of nectar, mainly acting as nectar robbers and reducing the resources of the more effective pollinators. Our results suggest that the Megachilidae are the most important visitors of mesquite, because they have high densities, have more or less constant abundance between years and are efficient pollen carriers.

Nectar production has consequences on several aspects of mesquite biology. The increase in female function associated to nectarful individuals could be a first step towards the evolution of separate sexes in this species, however, the changing pollinator coteries can undermine the selection pressure towards dioecy.

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Table 1: Number of flowering nectarful and nectarless individuals during the three year study period 1994–96 (N = 358).

Nectar morph	1994	1995	1996
Nectarful	140	129	109
Nectarless	170	160	135
No flowering	48	69	114

Table 2: Number of individuals of each bee species captured on nectarful and nectarless individuals of *Prosopis glandulosa* during the 1994 and 1995 flowering seasons.

Family	Genus	Species	Number of bees 1994		Number of bees 1995	
			Nectarful 1994	Nectarless 1995	Nectarful 1994	Nectarless 1995
Andrenidae	Perdita	callicerata			1	
Andrenidae	Perdita	sp. 1	4		10	
Andrenidae	Perdita	sp. 2	2			
Andrenidae	Perdita	sp. 3	1		3	
Andrenidae	Perdita	sp. 4	30		11	3
Andrenidae	Perdita	sp. 5	3	2	24	
Andrenidae	Perdita	sp. 6			2	
Andrenidae	Perdita	sp. 7	3		2	
Apidae	Apis	mellifera	2	1		
Apidae	Centris	pallida			1	
Apidae	Centris	rhodopus	1			
Apidae	Ceratina	sp. 1			4	
Apidae	Diadasia	sphaeralcearum	8	1		
Apidae	Epeolus	mesillae	5		11	2
Apidae	Epeolus	sp. 1	2		3	
Apidae	Epeolus	sp. 2	5		4	2
Apidae	Melissodes	tristis	26	1	6	
Apidae	Nomada	sp. 1	1			
Apidae	Xeromelecta	larreae			1	
Apidae	Zacosmia	maculata	4			
Colletidae	Colletes	aff. perilencus	78		26	1
Colletidae	Colletes	aff. scopiventri			1	
Colletidae	Colletes	algarobiae	91	4	54	2
Colletidae	Colletes	deserticola	3			
Colletidae	Colletes	louisiae	1		8	1
Colletidae	Colletes	prosopidis	1			
Colletidae	Colletes	salicicola	41	1	40	2
Colletidae	Colletes	wickhami	3		11	
Colletidae	Hylaeus	asininus	34		38	2
Colletidae	Hylaeus	sp. 1	1			
Halictidae	Agapostemon	melliventris	4		2	
Halictidae	Agapostemon	sp. 1	6			
Halictidae	Agapostemon	sp. 2	1			
Halictidae	Agapostemon	tyreli				1
Halictidae	Dialictus	spp	8	2	4	
Halictidae	Lassioglosum	sp. 1		1		
Halictidae	Lassioglosum	sp. 2	1			
Halictidae	Lassioglosum	sp. 3	1			
Megachilidae	Anthidium	cochimi	23		1	1
Megachilidae	Anthidium	cockerelli	1			
Megachilidae	Anthidium	paroselae	7			
Megachilidae	Ashmeadiella	bigeloviae	6		1	
Megachilidae	Ashmeadiella	breviceps	10		13	
Megachilidae	Ashmeadiella	clypeadentata	23	1	5	1
Megachilidae	Ashmeadiella	gilletei	8		5	
Megachilidae	Ashmeadiella	leuconzona	95	3	99	7
Megachilidae	Ashmeadiella	meliloti	1		1	2
Megachilidae	Ashmeadiella	prosopidis	1		3	
Megachilidae	Ashmeadiella	rhodognatha	12	1	41	4
Megachilidae	Coelioxys	aff hunteri	2		2	
Megachilidae	Coelioxys	menthae			2	
Megachilidae	Dioxys	productus	1			1
Megachilidae	Dolichostelis	perpulchea	1			
Megachilidae	Megachile	chilopsida	7			
Megachilidae	Megachile	discorhina	6		2	
Megachilidae	Megachile	lippiae	11		2	
Megachilidae	Megachile	newberryae	95	1	84	8
Megachilidae	Megachile	odonstostoma	7		5	2
Megachilidae	Megachile	sidalceae	7	2	2	
Megachilidae	Megachile	spinotulata	1			
Megachilidae	Osmia	subfasciata	1			
Megachilidae	Stelis	elongaventris	5		15	1
Megachilidae	Stelis	xerophila nv	3		4	
Megachilidae	Trachusa	larreae			1	
Total	24	64	705	21	555	43

Table 3: Number of pollen grains (± SE) deposited on stigmas of nectarless and nectarful individuals during a 3–day period.

Nectar morph	Day 1	Day 2	Day 3
Nectarful	12 (0.78)	13 (0.77)	19 (0.82)
Nectarless	8 (0.61)	10 (0.62)	11 (0.69)

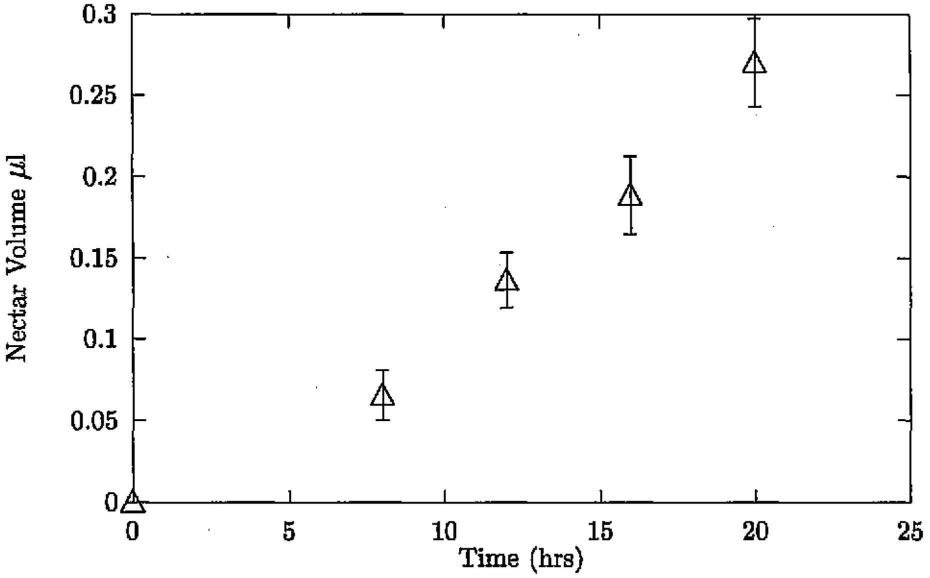
Table 4: Average number of pollen grains deposited per visit for different types of visitors

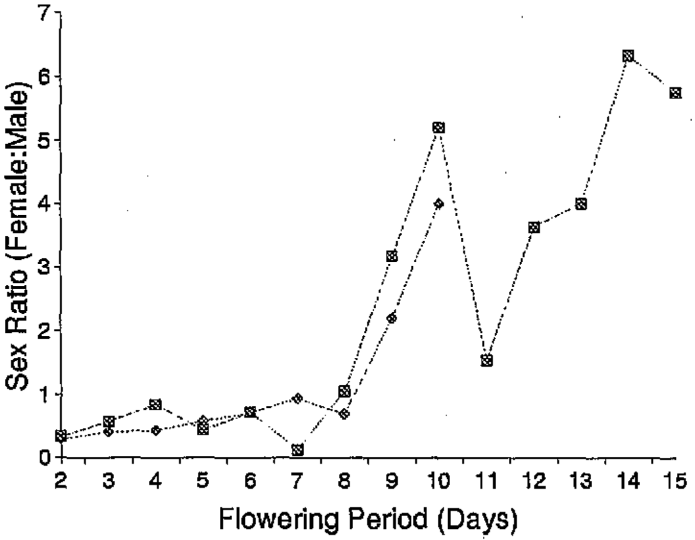
Family	Bee species	X pollen grains visit $^{-1}$
Apidae	sp. 1	5.38
Apidae	*Apis mellifera*	6.16
Apidae	*Melissodes tristis*	0.87
Halictidae	*Dialuctus*	0
Megachilidae	*Megachile*	2.34
Diptera	sp. 1	0.39

Figure Legends

Figure 1. Mean volume of accumulated nectar (μl $\pm SE$) in inflorescences of *Prosopis glandulosa* in the MBR.

Figure 2. Sex ratio of bee visitors to flowers of *Prosopis glandulosa*. Squares indicate 1994 and cirlces indicate 1995 flowering seasons.


Nectar Volume μl
0.3
0.25
0.2
0.15
0.1
0.05
0
0
5
10
15
20
25
Time (hrs)



Sex Ratio (Female:Male)
0
1
2
3
4
5
6
7
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Flowering Period (Days)

PAGINACIÓN
DESCONTINUA

Capítulo 3

Why be a honeyless honey mesquite? Reproduction and mating system of nectarful and nectarless individuals

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WHY BE A HONEYLESS HONEY MESQUITE? REPRODUCTION AND MATING SYSTEM OF NECTARFUL AND NECTARLESS INDIVIDUALS[1]

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Populations of *Prosopis glandulosa* var. *torreyana* in the Chihuahuan desert have a fixed dimorphic system of nectar production in which half the individuals produce nectar (are nectarful) and the other half are nectarless. We analyzed the impact of nectar production on different estimates of fitness, comparing nectarful against nectarless individuals in size, mating system, seed traits, and fruit set in a 1-ha scrubland. Of the reproductive individuals (358), 46% were nectarful and 54% were nectarless. Neither tree size nor flowering phenology differed between nectar morphs. Fixation indices (F) for both progeny ($F = -0.2$) and adults ($F = -0.45$) were negative, and high heterozygosities were found in adults and progeny ($H = 0.45$). No differences were found between nectar morphs for F, H, and single ($t_s = 1.1$) and multilocus ($t_m = 1.03$) outcrossing rates. Controlled pollinations showed differences between selfing and control treatments with no differences between nectar morphs. Nectarless individuals produced significantly more pollen grains than did nectar producers, but all other measured floral traits showed no differences. Nectarful trees were visited by pollinators 21 times more often and had a significantly higher overall fruit set than did nectarless trees. No differences between nectar morphs in seed mass or in percentage seed germination were found, but heavier seeds tended to have higher heterozygosities. Both morphs had similar success as females, but nectarless trees had ~7% higher male function. We discuss three possible scenarios for the evolution of the fixed dimorphism in nectar production, two involving unstable phases (substitution of one morph by the other, and evolution towards dioecy) and one stable scenario (maintenance of the dimorphic system).

Key words: floral traits; Leguminosae; mating systems; nectar production; outcrossing rates; pollination; polymorphism; *Prosopis glandulosa* var. *torreyana*; seed traits.

Pollination of most angiosperms depends on visitation by animals seeking rewards found within flowers (Kevan and Baker, 1983). Of all floral rewards, nectar is the most commonly found in angiosperms (Kevan and Baker, 1983; Simpson and Neff, 1983). Its provision within flowers influences components of pollinator visitation, including plant choice, foraging time, and foraging movements (Zimmerman, 1983, 1988; Hodges, 1993). Plants might be expected to evolve optimal allocation towards floral rewards to attract visitors, as increased visitation rates might prove beneficial in two ways: (1) the probabilities of pollen import and export may increase with visitation rates (Zimmerman, 1988; Harder and Barrett, 1996), and (2) the plant can become selective as to which pollen grains fertilize the ovules, leading to higher seed quality (Stanton, Snow, and Handel, 1986). However, increased visitation rate does not always increase seed set (Klinkhamer, De Jong, and Metz, 1994; Mitchell, 1994). Excess visitation may lead to lower seed set, because of higher levels of selfing, clogging of stigmatic surfaces with self pollen, and an overall decrease of pollen export (de Jong et al., 1992; de Jong, Waser, and Klinkhamer, 1993; Klinkhamer, De Jong, and Metz, 1994). In addition, greater allocation to nectar involves an energy investment (Pleasants and Chaplin, 1983; Southwick, 1984), which can entail a reproductive cost (Pyke, 1991). Some plants, however, show strategies to avoid some of the costs associated with floral displays. These include food deception mimicries. Within a population in which most individuals produce a food reward such as nectar, nectarless individuals would have an advantage if they received floral visitors attracted by nectarful individuals while avoiding the costs of nectar production (Little, 1983; Gilbert, Haines, and Dickson, 1991; Dafni, 1992). The consequence of such deceptive pollination is conspecific deceit mimicry (automimicry) or mimicry based on naiveté, as described by Little (1983). In such a case, the fitness of nectarful and nectarless plants would be frequency dependent: if nectarless individuals increased in number, pollination rates for all individuals in the population would be expected to diminish significantly (Bell, 1986; Gilbert, Haines, and Dickson, 1991). However, few food deception mimicries have yet been examined; in

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particular studies that quantify the effects of deception mimicries are not common.

Populations of honey mesquite, *Prosopis glandulosa* var. *torreyana* Benson (Mimosoideae), in the Mapimi Biosphere Reserve of Mexico have a fixed intrapopulation dimorphic system of nectar production (López-Portillo, Eguiarte, and Montaña, 1993). Half of the individuals within a mesquite population are nectarful, producing on average 0.51 mg of sucrose equivalents per millilitre of nectar, while the other half produce no nectar at all (López-Portillo, Eguiarte, and Montaña, 1993). Nectarful flowers are visited between 2 and 4 times more often by a larger diversity of pollinators (29 vs. 5, respectively) compared to nectarless individuals. Both nectar morphs have been shown to be self-compatible, but both display a high degree of inbreeding depression (López-Portillo, Eguiarte, and Montaña, 1993). Two observations suggest that nectar production in mesquites has a genetic basis. (1) Nectar production appears to be uncorrelated with environmental factors. During 4 yr (1994–1997), none of the studied plants has changed nectar morph (Golubov et al., unpublished data), even under varying rainfall regimes. This suggests genetic determination of nectar morph. (2) Nectarful and nectarless trees at various Chihuahuan desert sites are randomly distributed in space; even when found surrounding water supplies, proportions do not differ from 1:1 (López-Portillo, Eguiarte, and Montaña, 1993; López-Portillo, unpublished data). This species, therefore, provides a system in which the relative fitness values of traits associated with nectar production can be assessed under natural conditions.

Our study examines the relative costs and benefits of nectar production by comparing traits of nectarful vs. nectarless plants, specifically addressing the following question: (1) How is nectar production related with plant size, outcrossing rates, and seed traits? (2) What is the relative importance of floral traits and pollinator visitation on the reproductive success of each nectar morph? and (3) Do plants that provide nectar have higher fitness than those that do not?

MATERIALS AND METHODS

Study site—The study was made in the Mapimi Biosphere Reserve (MBR), southern Chihuahuan Desert (26°N104° W, 1100 m altitude, 264 mm yearly average rainfall mainly in summer, 21°C mean annual temperature, Mexico). Yearly rainfall during the study period was 138 mm for 1994, 198.4 mm for 1995, and 234.7 mm for 1996 (MBR climatic station). Fieldwork was done on a 1-ha area of desert scrubland dominated by *Prosopis glandulosa* var. *torreyana* surrounding a seasonal water-catchment site.

Study species—The honey mesquite, *Prosopis glandulosa* var. *torreyana* Benson (Mimosoideae) (hereafter *P. glandulosa*), is a woody perennial tree widely distributed in northern Mexico and southeastern United States (Rzedowski, 1988). This species is a dominant element in different communities of the Chihuahuan Desert. At MBR, *P. glandulosa* is found in the bajadas, playas, and arroyos and is the dominant species that surrounds all water catchments (López-Portillo, Eguiarte, and Montaña, 1993). Flowering at the study site starts in mid-March (before the summer rains) and ends in mid-May. *Prosopis glandulosa* is mainly pollinated by bees (López-Portillo, Eguiarte, and Montaña, 1993), like other species of *Prosopis* (e.g., Simpson, Neff, and Moldenke, 1977; Keys, Buchmann, and Smith, 1995).

Study population—In 1994, we censused, tagged, measured, and mapped all individuals of *P. glandulosa* within the 1-ha area of desert scrubland. Tree dimensions were taken as two canopy widths and height. Spatial distribution was analyzed with contingency tables (100 squares, each 10 × 10 m). Within the study site, the density of individuals was 0.13 ind./m^2, and of these 0.035 ind./m^2 were reproductive. The study site was subdivided into three plots of contrasting plant densities (low density [LD] 0.07 ind./m^2, medium density [MD] 0.22 ind./m^2, and high density [HD] 0.48 ind./m^2).

During the flowering seasons of 1994 and 1995, we measured nectar presence of all reproductive individuals ($N = 358$). In each plant, we bagged five first-day open inflorescences of two separate branches at dawn. Nectar presence–absence was determined at dusk after collecting and probing five flowers per inflorescence with graduated 2-μL micropipettes.

The following traits were measured to assess any possible difference between nectar morphs other than the production of nectar. Tree size was calculated as the volume of the tree (using a spherical model of plant size) and cube-root transformed for further analyses (Sokal and Rohlf, 1981). Tree size was ranked into five categories, and possible differences in size between nectar morphs were analyzed by means of a 2 × 5 contingency table (Everitt, 1977). To assess differences between morphs in flowering phenology, we recorded the presence–absence of mature inflorescences every 2 d between 14 and 30 March 1994 on nine consecutive observation dates and differences were tested with a 2 × 9 contingency table (Everitt, 1977). Finally, to characterize water availability between nectar morphs, in each of the three plots with different plant densities, we measured predawn water potentials (Scholander et al., 1965) for five randomly selected trees from each morph (5 trees × 2 morphs × 3 plots, $N = 30$). During March 1994, predawn water potentials were measured on two randomly selected shoots per tree using a pressure chamber (PMS model 1000, Corvallis, Oregon).

Mating system—Outcrossing and population genetics—We estimated heterozygosity and outcrossing rate of each nectar morph using starch-gel electrophoresis of progeny arrays. Fresh cotyledons of 10-d-old emerging seedlings ($N = 10$ seeds per tree of 30 trees per nectar morph) from the germination experiments (see Seed traits below) were ground on Tris-citrate buffer (pH 8.3) (Keys and Smith, 1994) and placed on a 10% starch gel Tris-citrate pH 8.3 substrate (Soltis et al., 1983). Specific staining and interpretation were done on glutamate oxaloacetate transaminase (E.C. [Enzyme Commission number] 2.6.1.1.; Saidman, 1986), leucine aminopeptidase (E.C. 3.4.11.1.; Solbrig and Bawa, 1975), esterase (E.C. 3.1.1.1.1.; Saidman and Naranjo, 1982), and the malic enzyme (E.C. 1.1.1.40.; Murphy et al., 1990). Single (t_s) and multiloci (t_m) outcrossing rates, maternal genotypes, and maternal and progeny fixation indices were obtained using the multilocus estimation program (MLT; Ritland, 1990).

Controlled pollination experiments—We tested the importance of selfing and the effectiveness of floral visitors through hand-pollination, using a completely randomized partial hierarchical design (Kirk, 1995). Hand-pollinations were done on ten randomly selected trees (main plot) per nectar morph in March 1996, during the peak flowering period. On each tree, 15 24 × 12 cm cotton bags (to avoid insect and wind pollination) were used to cover selected branches having immature inflorescences. When inflorescences reached maturity, we randomly assigned five bagged branches to each of the following treatments: (1) automatic self-pollination—bagged inflorescences with no further manipulation, (2) forced self-pollination—inflorescences manually self-pollinated every 2 d, and (3) open-pollination (control)—mature inflorescences left open for 5 d and then bagged. As the number of inflorescences varied between samples, each bagged branch assigned to a pollination treatment was considered the subplot experimental unit. Bags were sprayed with insecticide every 2nd d to avoid flower loss from various larvae that consume flower parts.

We assessed fruit set (pods/inflorescence) on 15 May 1996, once pods were almost fully developed. Fruit set was arcsine-transformed (Sokal and Rohlf, 1981), and data were analyzed using nested ANOVA for completely randomized partial hierarchical designs (Kirk, 1995). The experimental model is nectar morph as the main treatment, trees (nested in nectar morph), and the pollination treatment crossed with nectar morph and tree (nested in morph). Differences between selfing and control pollination treatments were analyzed with orthogonal contrasts (Sokal and Rohlf, 1981).

Floral traits and visitors—To address the possibility of differences in flower traits between nectar morphs, we selected ten nectarful and ten nectarless trees of similar sizes within the study site during the 1996 flowering season. From these, we collected ten first-day inflorescences per tree. Total rachis length was measured, and total number of flowers per inflorescence were counted. Then, one flower per inflorescence was selected randomly, and we measured style and stamen length and counted the number of ovules and pollen grains. Given the symmetry of the two-parted anther, pollen counts were recorded from half an anther (Cruden, 1977. We stained ovules and pollen grains with methylene blue (0.01 g/mL) and counted them under a stereomicroscope at 80×. Floral measures that did not conform to Shapiro-Wilk normality tests (for $N < 1000$) were log transformed (Sokal and Rohlf, 1981). All floral measurements were analyzed using nested ANOVA (JMP statistical package, version 3.1.2; SAS, 1995), considering nectar morph and tree as factors (Kirk, 1995). Finally, as further indirect evidence of the mating system, we calculated pollen:ovule ratios according to Cruden (1977).

We evaluated the abundance and diversity of floral visitors on both nectarful and nectarless individuals during the 1994 flowering peak (21 March–6 April). Every 2nd d, on six randomly selected trees per nectar morph, 5-min fixed-capture efforts were made three times a day (0800, 1200, and 1600). Visitors were captured by using plastic bags (10 × 20 cm), as plant architecture and thorns prevent the use of mesh nets and visitors to this species are easily captured. Plants were randomized on a daily basis, to avoid temporal and observer-biased errors. Captured specimens were identified, sexed, and measured (head to tip of abdomen), using four size classes: <2, 2–3, 3–4 and >4 cm. Data sets include only bees (Apoidea, Hymenoptera), as they are the main pollinators of *Prosopis* (Simpson, Neff, and Moldenke, 1977; López-Portillo, Eguiarte, and Montaña, 1993; Golubov et al., unpublished data). Differential activity of bees with respect to time of day was analyzed using contingency tables (Everitt, 1977).

Flowering and fruit set—To determine differences and variability in pod production between nectar morphs, we tagged three widely spaced branches around the canopy of each reproductive tree in 1994. Total numbers of flowers, nodes, and fruits were recorded for each branch during two consecutive years. To avoid losses in counts from dehiscence and predispersal predation, pods were counted before fully mature (May). Fruits set was calculated as the total number of developed pods per total number of inflorescences. To obtain a single estimate of reproductive success per tree, we averaged and arcsine transformed (Sokal and Rohlf, 1981) flower and pod counts of all three branches. Fruit set was analyzed through multivariate analysis of variance (MANOVA) with the 3 yr as repeated measures (von Ende, 1993), taking nectar morph, site, and tree (nested in morph) as factors (JMP, version 3.1.2; SAS, 1995). Statistical significance was assessed using exact F contrast tests, and F adjusted with the Greenhouse-Geisser (G-G) method (SAS, 1995).

Seed traits—To assess differences in seed mass and germination success between nectar morphs, we collected pods from all reproductive individuals from the site in June 1994 (plants having <20 pods were excluded from further manipulations). Ten pods from 30 nectarful and 30 nectarless trees were randomly chosen. To reduce the probability of sampling consanguineous progeny, only one seed (also randomly selected) per pod was used ($N = 300$ seeds for each morph). Selected seeds were weighed to the nearest 0.001 g, scarified mechanically, sown in soil from the original site, and grown in a greenhouse at the Instituto de Ecología, UNAM, Mexico. Germination was considered successful when the seedlings had a developed radicle and fully expanded cotyledons.

Differences in seed mass were analyzed using nested ANCOVA with three factors: nectar morph, plot, and parent tree (nested in plot) and one covariate (tree size; Kirk, 1995). Differences in germination success associated with nectar morph and parent tree were analyzed using contingency tables (Everitt, 1977). The relationship between seed mass and germination was calculated using a logistic regression model (Sokal and Rohlf, 1981; JMP version 3.1.2; SAS, 1995).

In addition, we related genetic information (see section outcrossing rates and population genetics) to seed mass by means of multiway ANOVAs, considering the number of heterozygous loci (0–7; pooling loci 0 and 1 as well as 6 and 7), nectar morph, and tree as factors. Contrast t tests were performed to analyze the effect of heterozygous loci on seed mass Sokal and Rohlf, 1981).

Cumulative effects of nectar production on plant fitness—To obtain an approximate and relative value of female and male function for each nectar morph, we multiplied all characters contributing to each function (Arnold and Wade, 1984). Among the values measured, we considered number of flowers, number of ovules, fruit set (1994–1996, see Flowering and fruit set above), and seed set to be components of female function. Numbers of flowers and pollen grains were considered as the components of male function. Numbers of flowers, ovules, and pollen grains were recorded from one flower per inflorescence ($N = 100$, ten trees per nectar morph). Given the symmetry of the two-parted anther, pollen counts were recorded from half an anther. Fruit sets were taken from tagged branches around the canopy of nectar and nectarless trees during the 3-yr period (1994–1996). Seed sets were taken as number of viable seeds from 20 pods of five trees per nectar morph. All components are multiplicative and, therefore, the error associated to relative fitness was calculated as: $Z = A_0 B_0 \pm (A_0 \Delta B_0 + B_0 \Delta A_0 + \Delta A_0 \Delta B_0)$, where Δ's are SE associated to each mean value. This estimate of male fitness is approximate, because pollen flow and the proportion of seeds fathered were not estimated.

RESULTS

Of all reproductive individuals at the study site (358), 46% were nectarful and 54% nectarless; these numbers were not significantly different from a 1:1 proportion ($\chi^2 = 2.51$; $P = 0.113$). Neither tree size ($P = 0.211$; Fig. 1A) nor flowering phenology ($P = 0.7$; Fig. 1B) differed between morphs.

Water availability (measured as predawn water potentials) did not differ between nectar morphs ($P = 0.1259$) but was significantly different among plots ($F = 5.69$, $P = 0.009$), being lowest in the LD ($\bar{\chi} = -0.82 \pm 0.08$ MPa), as compared to MD ($\bar{\chi} = -0.58 \pm 0.046$ MPa) and HD plots ($\bar{\chi} = -0.55 \pm 0.046$ MPa). Nectarful and nectarless tress were distributed randomly throughout the whole 1-ha site ($\chi^2 = 23.2$, df = 99, $P > 0.05$).

Mating system—Outcrossing and population genetics—Seven polymorphic loci were resolved: LAP 1 (three alleles), EST1 and EST2 (three alleles each), EST3 (two alleles), ME (two alleles), and GOT1 and GOT2

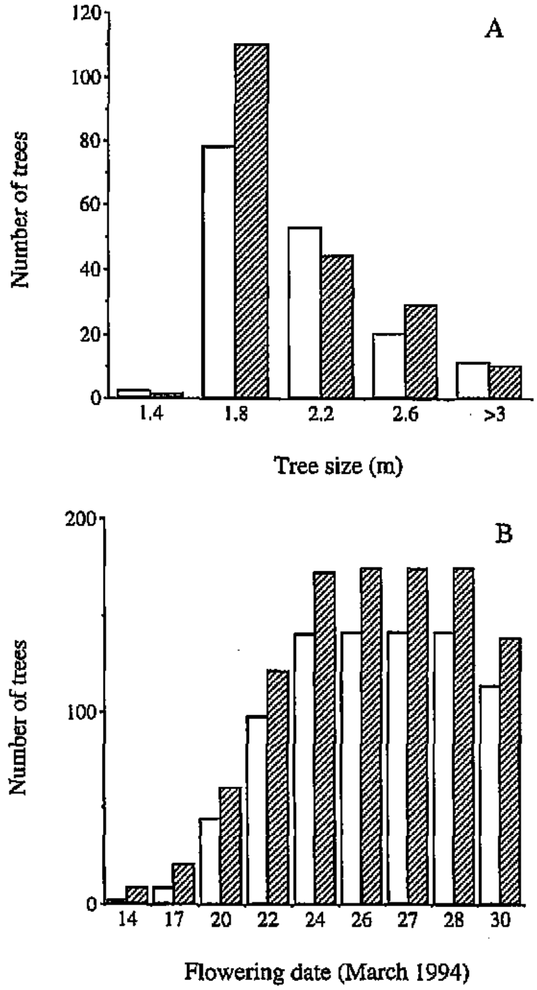

Fig. 1. (A) Size (as a radius in metres, $N = 358$) and (B) flowering phenology of adult ($N = 310$) individuals of nectarful (empty bars) and nectarless (hatched bars) trees during the 1994 reproductive season.

(two alleles), while GOT3 resulted in a monomorphic band. The fixation indices (F), excluding monomorphic loci, were negative in progeny and adults, indicating an excess of heterozygous individuals at both stages. F was lower in parents compared to their progeny, but we found no significant differences in F between morphs at either stage. Heterozygosities were high in both stages, and no difference were found either (Table 1).

Single and multiloci outcrossing rate estimates (Table 1) indicate no detectable selfing, no biparental inbreeding (no positive differences between t_m and t_s; Ritland, 1984), and especially no differences between nectar morphs. This indicates that both nectar morphs are outcrossers in spite of the unrealistic values of t (i.e., >1) obtained, probably caused by the multiple heterozygosity of parental genotypes.

Controlled pollination experiments—We found differences between pollination treatments with respect to fruit set ($P < 0.001$; Table 2). The lowest fruit set was for automatic self-pollination ($\bar{\chi} = 0.0008 \pm 0.002$), followed by forced self-pollination ($\bar{\chi} = 0.015 \pm 0.012$), and finally open pollination ($\bar{\chi} = 0.058 \pm 0.023$). Both self-pollination treatments showed a marked decrease in fruit set with respect to the control ($P > 0.05$). On the other hand, fruit set did not differ between nectar morphs ($P = 0.2824$, Table 2). The significant treatment × tree interactions indicated the high variability between trees ($P = 0.0278$, Table 2), but all other interactions were not significant.

Floral traits and visitors—Nectarless trees produced, on average, slightly more pollen grains than did nectarful trees ($P = 0.05$; Table 3). No other measured floral trait differed significantly between nectar morphs. However, for all floral traits, there was great variation between trees within each morph ($P < 0.0001$). Comparing pollen: ovule ratios (Table 3) to those reported by Cruden (1977), the breeding system of *P. glandulosa* falls between facultative autogamy and facultative xenogamy.

The most abundant bee genera visiting both nectar morphs (Table 4) included *Colletes, Ashmeadiella*, and *Megachile*, with smaller numbers of *Melissodes, Exomalopsis, Apis, Lasioglossum*, and *Perdita*. Of all genera, only one species of *Perdita* and one of *Lasioglossum* were only found on the nectarless morph, and then only in low frequencies (one recorded visit per bee species). Considering total bee visits to both nectar morphs, there were no significant differences in bee activity between different times of day ($\chi^2 = 4.61$, df = 2, $P = 0.1$) or between size classes of bees ($\chi^2 = 5.11$, df = 3, $P = 0.16$). Despite these similarities between nectar morphs, the number of visits differed dramatically, as the number of bees on nectarless trees comprised only 4.5% of total

TABLE 1. Levels of heterozygosity, fixation index (F), and outcrossing rates based on seven polymorphic loci (1 SE in parentheses). All estimates were calculated using MLT (Ritland, 1990).

		Overall[a]	Nectarful[b]	Nectarless[b]
Heterozygosity	Progeny	0.4507 (0.02)	0.4458 (0.03)	0.4533 (0.03)
	Parents	0.4507 (0.06)	0.4627 (0.1)	0.4577 (0.1)
Fixation index	Parents[c]	−0.4463 (0.2)	−0.4658 (0.1)	−0.4565 (0.1)
	Progeny	−0.2124 (0.048)	−0.2085 (0.003)	−0.2162 (0.004)
Outcrossing rate	t_m[d]	1.033 (0.023)	1.101 (0.087)	1.023 (0.04)
	t_s[d]	1.186 (0.028)	1.232 (0.050)	1.173 (0.044)

[a] Progeny of 60 parents, ten seeds per parent ($N = 600$).
[b] Progeny of 30 parents, ten seeds per parent ($N = 300$).
[c] Inferred from MLT.
[d] Based on 1000 bootstraps.

TABLE 2. Summary of F statistics and significance levels for ANOVA in a completely randomized partial hierarchical design testing the effect of different pollination treatments (open-pollinated control, forced self-pollination, and automatic self-pollination), nectar morph (nectarful or nectarless), and tree ($N = 20$) on fruit set. The pollination treatment factor was decomposed into orthogonal contrasts: (1) control (C) vs. both selfing treatments (FS and S), and (2) automatic self (S) vs. forced self-pollination (FS). Fruit set was arcsine transformed.

Source of variation	SS	df	F	P
Nectar morph	0.099	1	1.22	0.2824
$\text{Tree}_{[\text{morph}]}$	1.457	18	1.17	0.3304
Treatment	2.332	2	16.91	0.0001
C vs. SF + S	1.865	1	27.05	<0.001
S vs. SF	0.467	1	6.77	0.013
Nectar morph × Treatment	0.0015	2	0.01	0.9890
$\text{Tree}_{[\text{morph}]}$ × Treatment	2.482	36	1.56	0.0278
Error	10.610	240		
Total	16.985	299		

captures. Nectarful trees were visited, on average, 21 times more often than were nectarless trees. Taking into account only the eight genera that are shared by both nectar morphs, the visiting ratio is reduced somewhat to 10:1 (nectarful: nectarless). Wasps and files were seen constantly, but only on the nectarful morph. Both sexes of bees visited nectarful individuals, while females alone visited nectarless trees (Table 4).

Flowering and fruit set—Fruit set was very low in all years (range = 0.08–0.17 fruits per inflorescence; Table 5). Fruit set varied significantly between years (Tables 5, 6) and was highest in 1995. Nectar morph and plot had a significant effect on fruit set (Table 6), and there was a nonsignificant trend towards a tree effect (Table 6). Nectar producers had a higher overall fruit set than did nectarless trees (Tables 5, 6). The highest fruit set was in the plot MD ($\bar{x} = 0.1977 \pm 0.056$) followed by plot HD ($\bar{x} = 0.1662 \pm 0.053$), the plots with the highest water availability; plants in plot LD ($\bar{x} = 0.116 \pm 0.038$) had significantly lower fruit set ($P < 0.0001$). Variation in fruit set between plots and nectar morphs among years resulted in the only significant interaction (Table 6).

Seed traits—In 1994, we found no differences between nectarful and nectarless trees in seed mass (Table 7), but there was wide variation within morphs ($\bar{x} = 30.16 \pm 0.27$ mg, range = 12–58 mg). The main influence on seed mass related to maternal effects ($P < 0.0001$; 40% of total variance, Table 7). Seed mass of both nectar morphs did not vary among plots, but nectarless trees showed a slightly reduced seed mass in plot LD, giving a significant plot × nectar morph interaction (Table 7). The orthogonal contrasts showed seed mass in plot LD to be different from those in plot MD and HD ($P < 0.001$), but plots MD and HD did not differ from each other ($P = 0.66$).

TABLE 3. Mean values (1 SE) of measured floral traits for nectarful and nectarless trees. Significance levels correspond to a nested ANOVA with factors nectar morph and tree ($N = 100$ flowers per nectar morph). The pollen : ovule (P:O) ratio was calculated by dividing the estimate of pollen grains per flower by the number of ovules per flower.

Floral trait	Nectarful (SE)	Nectarless (SE)	P
Pollen grains (½ anther)[a]	391 (12)	420 (10)	0.05
Ovules per flower	17.88 (0.28)	18.34 (0.27)	0.578
Flowers per inflorescence	92.76 (0.12)	92.38 (0.26)	0.967
Length of anther (mm)	4.98 (0.12)	4.88 (0.12)	0.772
Length of style (mm)	4.75 (0.09)	4.89 (0.08)	0.647
Corolla diameter (mm)	2.3 (0.04)	2.28 (0.04)	0.838
Length of pedicel (mm)	39.59 (0.12)	38.07 (0.13)	0.661
P:O ratio	441 (18)	461 (33)	0.602

[a] Each flower has ten stamens.

We found no significant differences in germination success between nectar morphs ($P > 0.05$). Both seed mass ($\chi^2 = 6.43$, df = 1, $P = 0.0112$) and parent tree ($\chi^2 = 73.944$, df = 29, $P < 0.001$) had significant effects on germination success. The mass of seeds was influenced by both seed heterozygosity (taken as the number of heterozygote loci over the six possible; $F = 3.2106$, $P = 0.0009$) and tree-related effects ($F = 8.395$, $P < 0.001$), but nectar morph had no significant effect ($F = 0.6525$, $P = 0.32$). Contrast t tests after a significant ANOVA divided the sampled population of seeds into two categories (Fig. 2), those having fewer than three heterozygote loci and those having more. There was a slight tendency for heavier seeds to have higher heterozygosities, but little total variation is explained by this factor ($r^2 = 0.03$, df = 598, $P < 0.001$).

Cumulative effects of nectar production on plant fitness—The analyses revealed little difference between nectar morphs. Thus, to include an overall measure of plant fitness through either female or male functions, the mean values of some characters important for plant fitness from both nectarful and nectarless morphs are described in Table 8. In terms of female function, there is a large variation associated with each trait; overall, nectarful and nectarless tress did not differ. In contrast, nectarless individuals had a higher relative male function (Table 8), and the error associated indicates the difference to be significant (Table 3).

DISCUSSION

Our results suggest there are benefits and costs associated with the lack of nectar production in *P. glandulosa*. Nectar production has been proposed to be expensive, both in terms of total energy investment (>30%; Pleasants and Chaplin, 1983; Southwick, 1984) and in reproductive costs (Pyke, 1991). We would expect these costs to be reflected in nectarful trees having decreased reproductive output (i.e., fewer flowers, shorter flowering times) and/or decreased plant growth (resulting in smaller plants). However, we found no differences in plant size, flower production, or phenology between nectar morphs. This could be, in part, because nectar production represents a low energy cost for *P. glandulosa*. Negligible costs of nectar production have also been found by Harder and Barrett (1992) in the bee-pollinated *Pontederia cordata*.

Nectar production variability has been shown to affect pollinator foraging bouts and patterns (Waddington, 1983). In *P. glandulosa*, nectar production clearly affects the number, species, and sex of bees that visit each nectar

TABLE 4. Number of bees and other floral visitors, bee sex ratios, and visitor densities on nectarful and nectarless plants. Data set obtained from nine census dates (21 March–6 April 1994) of six trees per nectar morph at three times of day (0800, 1200, and 1600).

Traits of floral visitors	Nectarful	Nectarless
Total no. of bee visits	423	20
Sex ratio (female : male)	2:1	1:0
No. of bee species	58	15
Andrenidae	*Andrena* 2 spp., *Perdita* 5 spp.	*Perdita* 2 sp.
Anthophoridae	*Epeolus* 2 spp., *Exomalopsis* 1 sp., *Melissodes* 2 sp., *Neopasites* 1 sp., *Nomada* 1 sp., *Triepeolus* 1 sp., *Zacosmia* 2 sp.	*Exomalopsis* 1 sp., *Melissodes* 1 sp.
Apidae	*Apis* 1 sp.	*Apis* 1 sp.
Colletidae	*Colletes* 8 spp., *Hylaeus* 3 spp.	*Colletes* 2 spp.
Halictidae	*Agapostemon* 1 sp., *Lasioglossum* 4 spp.	*Lasioglossum* 4 spp.
Megachilidae	*Anthidium* 3 spp., *Ashmeadiella* 12 spp., *Coelioxys* 2 spp., *Megachile* 5 spp., *Stelis* 2 spp.	*Ashmeadiella* 3 spp., *Megachile* 1 sp.
Other orders of visitors	Coleoptera 4 spp., Diptera 6 spp., Hemiptera 2 spp., Hymenoptera (Vespoidea) 3 spp. (Formicidae) 2 spp., Lepidoptera 4 spp., Thysanoptera 2 spp.	Diptera 1 sp., Thysanoptera 2 spp.

morph. Nectar production enhanced visitation frequencies by at least one order of magnitude, as compared to nectarless trees. Similar patterns have been found in dioecious plants in which nectar is associated with female function (Pyke, Day, and Wale, 1988; Greco, Holland, and Kevan, 1996). However, the increase in visitation to nectarful individuals was not reflected in a corresponding increase in fruit set. Nectarful trees produced outcrossed progeny, and these did not differ from nectarless ones. Probably, nectar collection is increasing rates of selfing and consequently lowering both fruit and seed set. The possible cost of increased geitonogamy incurred by nectar production (Klinkhamer, de Jong, and Metz, 1994) seems to be high for nectarful *P. glandulosa* plants, especially when a single effective pollinator visit is sufficient to pollinate a flower, as has been found for the closely related velvet mesquite, *P. velutina* (Keys, Buchmann, and Smith, 1995). Few but effective pollinators (i.e., female bees that collect pollen to feed larvae) were the main visitors of nectarless trees providing a service by dispersing pollen and pollinating during their foraging bouts.

Nectar production does not seen to affect the mating system of the honey mesquite, even considering the differential visitation rates. *Prosopis glandulosa*, although capable of selfing, is mainly an outcrosser, producing a higher than expected proportion of heterozygote seeds. Previous pollination experiments on *P. glandulosa* (López-Portillo, Eguiarte, and Montaña, 1993) have also shown higher fruit set for cross- than for self-pollinations. Similar estimates of the mating system were found by Keys and Smith (1994) for the velvet mesquite, *P. velutina*. In *P. glandulosa*, high fruit abortion rates (up to four fruits/inflorescence) could mean selection against homozygote progeny (<1% of seeds sampled were homozygous for all loci) or selection favoring the more heterozygous individuals (Eguiarte, Perez-Nasser, and Piñero, 1992), although these aspects must be fully explored. We found that fruit set, especially of nectarless morphs, is affected by environmental factors. Felker and Lee (1992) also found an environmental influence on fruit set of *P. glandulosa* var. *glandulosa*, although they did not describe a nectar dimorphism.

Seed mass is an important component of plant fitness, through its effects on time of germination, seedling establishment, competitive ability, survival, and fecundity (Stanton, 1984; Kalisz, 1989). In our study, germination and mass of *P. glandulosa* seeds were unaffected by nectar morph but seemed to be partially influenced by maternal and environmental effects. Maternal effects can be ascribed in part to environmental conditions that determine the amount of resource invested in the seeds by the parent (Roach and Wulff, 1987), such as those found for nectarless trees in the low water availability areas (plot LD). These maternal and environmental effects on seed traits (e.g., mass) have been found for other species as well (Kalisz, 1989; Waser, Shaw, and Price, 1995) and usually affect a large percentage of total variation (40% in this study). We also found negative F estimates (even

TABLE 5. Mean fruit set per inflorescence (1 SE) for three sampling years (1994–1996). *N* = number of trees sampled.

Year	Tree morph	
	Nectarful (*N* = 149)	Nectarless (*N* = 172)
1994	0.16 (0.106)	0.11 (0.08)
1995	0.17 (0.165)	0.17 (0.18)
1996	0.14 (0.143)	0.08 (0.10)
Average	0.156 (0.05)	0.12 (0.04)

TABLE 6. Multivariate nested analysis of variance with repeated measures in time (1994–1996) of the fruit set (arcsine transformed) of nectarful and nectarless individuals. Data correspond to three plots of contrasting densities in 1-ha scrubland of the Chihuahuan Desert.

Source of variation	df	*F*	*P*
Between subjects[a]			
Nectar morph	1, 146	4.82	0.0296
Plot	62, 146	8.12	0.0004
$\text{Tree}_{[\text{plot}]}$	169, 146	1.26	0.0703
Nectar morph × Plot	2, 146	2.08	0.1274
Within subjects[b]			
Year	1.8837, 275.02	6.04	0.0033
Year × Nectar morph	1.8837, 275.02	0.18	0.8207
Year × Plot	3.7674, 275.02	0.97	0.4167
Year × $\text{Tree}_{[\text{plot}]}$	311.41, 275.02	1.20	0.0558
Year × Nectar morph × Plot	3.7674, 275.02	3.23	0.0148

[a] Exact *F*.

[b] G-G adjusted *F*.

TABLE 7. Analysis of covariance of seed mass of nectarful and nectarless plants, using plant size as a covariate. Data correspond to three plots of contrasting densities.

Source of variation	SS	df	F	P
Nectar morph	1.805	1	0.0666	0.7965
Plot	309.758	2	0.6509	0.5282
$\text{Tree}_{[\text{plot}]}$	10 720.71	30	13.1869	0.00001
Tree size	4.926	1	0.1818	0.67
Plot × Morph	180.798	2	3.3358	0.0363
Error	15 256.941	563		
Total	26 476.212	599		

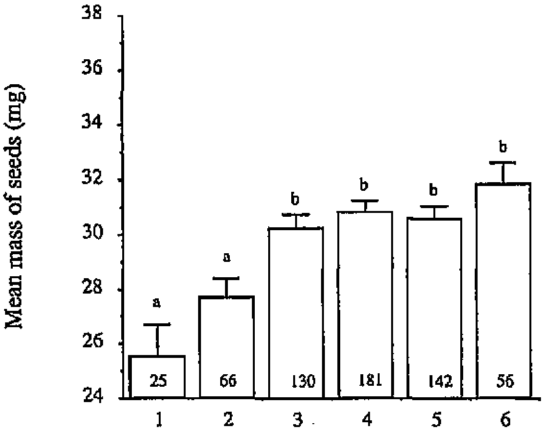

Fig. 2. Seed mass frequency with respect to heterozygote loci. Values having the same letter did not differ significantly in contrast comparison t tests ($P < 0.05$). Bars indicate 1 SE, and numbers within bars indicate number of seeds in each locus category ($N = 600$).

in seeds) and strong heterosis, correlated with seed mass, similar to those described in several long-lived perennials, mainly conifers (Ledig, 1986) and tropical palms (Eguiarte, Perez-Nasser, and Piñero, 1992; Eguiarte et al., 1993). The advantages of generating outcrossed progeny in relation to selfed progeny have been documented for many plant species (Charlesworth and Charlesworth, 1987; Mandujano, Montaña, and Eguiarte, 1996). This is especially important when heterosis is coupled to seed mass and the latter associated with higher germination rates (A. Martínez, Instituto de Ecología, A. C. unpublished data).

We found higher fruit set and lower pollen counts on nectarful morphs. These two components of fitness are pivotal for understanding total reproductive success in plants (Bell, 1985; Zimmerman, 1988). In relation to female function, the nectarful morph had higher success only in fruit set, but overall, female function did not differ between nectar morphs. Higher fruit sets have been found to be associated with higher nectar production (Pyke, Day, and Wale, 1988). Nonetheless, the nectarless morphs had higher pollen counts, which suggest a slightly (7%) higher male function. This "fitness accounting" is a crude approximation and must be interpreted carefully. Nevertheless, it is still surprising to find differences in male function between nectar morphs. Ongoing research is quantifying pollen flow, in order to estimate a more realistic component of male function (Golubov et al., unpublished data).

The evolutionary forces involved in the origin and maintenance of the nectar dimorphism in *P. glandulosa* are still unknown. We can rule out a possible relation with resource availability for several reasons. Firstly, if nectar production were associated with water condition, measured water potentials should be different between nectar morphs, and we found that the plots having different water availability still maintained a 1:1 proportion of nectarless to nectarful trees. Secondly, both nectar morphs have a spatially random distribution, and if the morph depended on microsite conditions, we would find different proportions at different sites and in different years. In all studied sites, the proportions of nectar morphs are the same, and individuals have not shifted between nectar morphs during the study period. We consider that there is enough evidence to conclude that the nectar dimorphism has a genetic basis. Three main sets of scenarios could be proposed for the evolution of the nectar dimorphism in *P. glandulosa*: (1) the population is an unstable phase in the evolution of nectar production. This scenario would result in populations with varying proportions of nectarful to nectarless trees. However, the empirical evidence presented here does not support the hypothesis that nectarful plants have higher fitness, so we would not expect them to displace nectarless tress. We could also consider that nectar production as a relatively cheap expense and this selectively neutral, however, this seems unlikely given the large difference in pollinator behavior. If we consider a case of floral automimicry, we would not expect the morphs to be in equal proportions (López-Portillo, Eguiarte, and Montaña, 1993). (2) The population is in an early stage of sexual differentiation. In this respect, nectarless plants would be evolving toward males (higher pollen) and nectarful trees towards females (higher fruit set). While we found differences in one component of female function (fruit set), there are no overall differences between morphs. Fruit set was higher for nectarful trees, but the overall female function

TABLE 8. Mean values (± 1 SE) for traits contributing to plant fitness through female and male functions in nectarful and nectarless individuals.

Morph	No. of flowers per inflorescence	No. of ovules or pollen grains per flower	Fruit set (3 yr) per inflorescence	Seed set per fruit	Relative fitness
Female function					
Nectarful	92.76 (0.12)	17.88 (0.28)	0.156 (0.05)	11.09 (0.3)	1 (0.38)
Nectarless	92.38 (0.26)	18.34 (0.27)	0.123 (0.04)	10.38 (0.3)	0.75 (0.29)
Male function					
Nectarful	92.76 (0.12)	391 (12)			0.93 (0.032)
Nectarless	92.38 (0.26)	420 (10)			1 (0.033)

did not differ between nectar morphs and even though male function did differ, the component we measured (pollen production) only represents a fraction of total male success; the proportion of pollen that reaches receptive stigmas has not been evaluated. In addition, nectar production is generally expected in males when there is sexual dimorphism, as a consequence of Bateman's principle, which states that female fitness is resource limited, while male fitness is limited by access to females (Wilson et al., 1994). Even though nectar production has been associated with female function in dioecious species as a means of attracting pollinators, it is associated with male fitness in monoecious species. Comparative studies of pollen flow and paternity analysis between nectar morphs will help estimate the relative contributions of male and female function of each nectar morph. (3) The populations are in a stable dimorphic state. This scenario would be the result of a complex balance between the different evolutionary forces mentioned in the above scenarios. This nectar dimorphism could be analogous to other sexual or morphological dimorphisms (dioecism and heteromorphy; Smith, 1963; Richards, 1986).

Additional experimental manipulation may help determine whether the differences found between nectarful and nectarless trees are directly associated with the presence of nectar, or are associated with correlated characters such as age (e.g., Zimmerman, 1988; Mitchell, 1994). Unfortunately, the heritability of nectar production is difficult to assess through progeny, as age at maturity is probably ~20 yr. However, ongoing studies measuring the costs of floral nectar production, monitoring pollinator activities, and quantifying pollen flow should help reveal how this dimorphism is maintained.

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Capítulo 4

The demographic costs of nectar production in the desert perennial *Prosopis glandulosa* (Mimosoideae): a modular approach

PAGINACIÓN
DESCONTINUA

The demographic costs of nectar production in the desert perennial *Prosopis glandulosa* (Mimosoideae): a modular approach

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Abstract.

Nectar production in angiosperms is considered to represent a reproductive cost, and has been associated to a decrease in fruit set or an overall decrease in the energetic budget of the plant. Populations of *Prosopis glandulosa* var. *torreyana* (honey mesquite) are a suitable system to evaluate the demographic costs of nectar production, as populations are composed of a 1:1 proportion of nectarful to nectarless individuals. The study was carried out in a population of 404 individuals of *Prosopis glandulosa* var. *torreyana* found in an area with differing water availability in the Southern Chihuahuan Desert. The possible costs of nectar production was assessed on 1212 shoots of the honey mesquite that were tagged in 1994 and followed until 1998. We used two methods of analysis to describe the effect of nectar production on modular population dynamics: matrix analysis and log–likelihood models. Water availability and the varying environmental conditions affected plant growth, but nectar production did not have an effect on the demographic parameters we measured. The values of λ did not differ between

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nectar morphs and the only important effects we detected were the year to year variation and water availability. Furthermore, the elasticity of each demographic process (growth, fecundity, retrogression and stasis) between nectar morphs did not differ. The log–likelihood models suggested a similar pattern but could discriminate the importance of each factor (nectar morph, year and site) on module fate. We were not able to detect a demographic cost of nectar production in the honey mesquite. The absence of a demographic response could be due to the negligible cost of producing nectar for this species or the resources allocated for growth are different from those allocated for reproduction. Our results suggest that the modular fates of mesquites are mainly determined by environmental factors.

Keywords: cost of nectar, effects on nectar production, desert plants, matrix and log–linear models, modular analysis of demographic parameters

1. Introduction

Nectar production has been suggested to be a costly floral attribute (Southwick, 1984) and under the principle of allocation, the energy and/or resources devoted to nectar production would not be available for other functions, such as growth or other floral attributes (Zimmerman, 1988; Zimmerman and Pyke, 1988). These costs would decrease growth and/or survival in the plants producing this floral resource, compared to plants not investing in its production. It is difficult to find systems in which the cost of nectar production can be assessed under natural conditions. However, because populations of *Prosopis glandulosa* var. *torreyana* at the Mapimi Biosphere Reserve have a dimorphic system of nectar production (whereby half the individuals of any given population produce nectar while the other half never produce nectar, López-Portillo et al., 1993, Golubov et al., 1999a), this species is ideal to assess the cost of nectar production. Furthermore, flowering and growth occur simultaneously in *Prosopis* (Simpson et al., 1977; Golubov et al., 1999a), suggesting that common resources may be involved in the production of both reproductive and vegetative structures.

Incorporating reproductive attributes into the demographic behavior of plants is of importance because floral traits are related to plant reproductive fitness through male and female functions (Bell, 1985). However, floral attributes, which are part of the cost of reproduction are quite often neglected (Zimmerman, 1988), even though they may represent a high energetic cost (Southwick, 1984; Pyke, 1991). For example, a positive correlation between successive reproduction events coupled with an eventual decrease in plant size was demonstrated using matrix models on modular growth (McGraw and Antonovics, 1983) and specifically, the cost of nectar production has been associated to a decrease in growth (Pyke, 1991). However, there have been no studies that interpret the cost of a floral attribute in demographic terms, even though nectar is the most ubiquitous attractant among angiosperms and constitutes part of the rewards usually sought by the majority of pollinators (Kevan and Baker, 1983).

Individual plants may be considered a population of repeated parts or modules (Bazzaz and Harper, 1977), which can be defined as a countable, iterated unit of construction. The interpretation of the demographic behavior of modules (i.e., a node, an internode and its associated meristem,Harper, 1977) can be considered equivalent to the demographic processes (growth, survival and reproduction) occurring within an individual. The modular approach to plant demography has been previously used to study intraspecific and interspecific competition (Jones, 1985; Flores-Martínez et al., 1994), to determine the ecological effects on module demography of competition with nurse plants, to understand growth in extreme environments (Maillete, 1987; López-Portillo et al., 1996), and to assess the effects of herbivory (Whitham and Mopper, 1985; Haukioja et al., 1990). However, only a few studies have implemented an explicit matrix population model (Maillete, 1982; Flores-Martínez et al., 1994; Lehtilä et al., 1994) despite the benefits of being able to describe fine scale growth in terms of age or stage (Caswell, 1989), specially as age is not a good predictor of plant performance and in many cases is difficult to determine (Mandujano et al., 2001). Furthermore, sensitivity and elasticity analyses can also be done at the modular level, increasing the potential of this tool to understand the processes involved in modular dynamics and to determine the causal factors behind the demographic behavior, both at the modular and at the individual level.

For the purpose of this paper, we studied the consequences of nectar production on the modular dynamics of mesquites over a 4–year period to assess the cost of nectar production in the dimorphic system. Additionally, we investigated the effect of environmental factors and nectar production on modular dynamics, employing log–linear models.

2. Methods

Field work was conducted within a 1–ha plot of desert scrubland in the Mapimí Biosphere Reserve MBR (26 °N, 104 °W, 1100 m altitude, 264 mm yearly average rainfall mainly in summer, 21 °C mean annual temperature), surrounding a temporal water–catchment area. Annual rainfall for the period 1994–1998 was 138.5 mm, 198.4 mm, 234.7 mm, 210.4 mm and 157 mm respectively. During the 1994 flowering season, we tagged three branches in each of 404 reproductive individuals in a N, SE and SW orientation (*ca.* 120° separation between branches). On each branch, we counted the number of modular units and the number of newly produced shoots (Fig. 1), which are easily distinguished by the soft bright green tissue. This recording method was repeated yearly for the 1995–98 reproductive seasons. Nectar presence was determined by sampling 5 flowers of each of two inflorescences per tree using 2 μl micropippettes. Nectar sampling was done at dusk, in inflorescences bagged for at least 8 hr. In addition to demographic data, our 1–ha study site site was subdivided into three sub–plots according to water conditions (humid site HS, intermediate site IS, and dry site DS) inferred from the measurement of predawn water potentials (Golubov et al., 1999b). We tagged a total of 1212 shoots, 46% of which corresponded to the nectarful condition and 54% corresponded to the nectarless condition. Of all individuals, 62 were in site HS (humid site), 281 were in site IS (intermediate site) and 61 were found in site DS (dry site).

2.1. MATRIX MODELS

To compare modular growth of nectarful and nectarless individuals, we constructed size–structured transition matrices (M) for each annual transition, using the following size–class limits in number of modular units (MU): 1–20, 21–40, 41–60, and > 60. Fecundity was defined as the number of new shoots produced per size–class at time

t. Two demographic processes were considered in the first row of each matrix, fecundity (F_{1j}=sum of new shoots produced in a given year by a shoot in size class j/ total number of shoots in size–class j), and the probability of retrogression to the smallest size class (R_{ij}=number of shoots of size i at time $t+1$, which were in category j at time t/total number of shoots in size j at time t, when $i < j$). The main diagonal contains the probability of stasis or survival in the same class (S_{ij}= number of shoots in size–class i at time $t+1$, which were already in this size–class at time t/total number of shoots in this same class at time t), the lower diagonals contained transition probabilities of growth to higher size classes (G_{ij}=number of shoots in size–class i at time $t+1$ which were in size–class j at time t/total number of shoots in size class j at time t, when $i > j$), and the upper diagonals contained retrogression in size by death of MU's (R_{ij}). This yielded a matrix of the form:

$$\mathbf{M} = \begin{pmatrix} S_{11}+F_{11} & R_{12}+F_{12} & R_{13}+F13 & R_{14}+F14 \\ G_{21} & S_{22} & R_{23} & R_{24} \\ G_{31} & G_{32} & S_{33} & R_{34} \\ G_{41} & G_{42} & G_{43} & S_{44} \end{pmatrix}$$

The resulting transition matrices were constructed according to the three factors year, nectar conditions and water status: four study years (Y, 1994–98), two nectar conditions (N, nectarful and nectarless) and three water status sub plots or sites (HS, IS and DS). Thus, there were a total of 24 transition matrices. For each matrix, we calculated the dominant eigenvalue λ, and its associated right and left eigenvectors (w, v). We also conducted standard sensitivity and elasticity analyses (Caswell, 1989; deKroon et al., 1986). As transition probabilities and fecundities are measured in different scales, the sensitivity analysis is difficult to interpret, so we used an analysis of

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elasticity that measures the proportional change in λ given a proportional change in in each cell entry of **M** (deKroon et al., 1986) which allows the interpretation of relative contribution of each demographic process to λ in each sub plot (Caswell, 1989). This analysis was used to determine the routes and importance of demographic processes. We assigned confidence intervals on λ by performing 1000 bootstraps estimates and determining the 95% percentile limits (Meyer et al., 1986; Caswell, 1989).

2.2. LOG–LINEAR MODELS

To determine whether the fates of modules varied between years, sites and nectar conditions we conducted comparisons employing log–linear models (Caswell, 2000). This method provided a means of testing specific hypotheses by comparing the results to a null model. In general, the method adjusts a log–linear model to the transition frequencies, after adding 0.5 to each cell (Fingleton, 1984). The effect of initial module condition (I, the frequency of shoots in size–class i at time t) on the final state of modules (F, frequency of shoots in size–class j at time $t+1$) was evaluated. In addition, we tested the effect of nectar condition (N), site (S) and year (Y) employing a 5–dimensional contingency table. The full model assumes that all terms and all higher order interactions contribute to predict cell frequencies. The null hypothesis is therefore a reduced model in which terms that are assumed not to be important for predicting cell frequencies are set to 0. In our specific case, this was done by setting the FN, FY and FS interaction terms to 0 as well as all higher order–interactions that involved these terms (Bishop et al., 1975). We then tested the effect of nectar condition, year and site on the fate of modules. This was done by assessing the goodness–of–fit of models that corresponded to each hypothesis, that resulted in the models that assessed the effect of nectar condition, site and year on module fates. In addition, we fitted models that included the interaction terms between FY and FS. A lack of fit of the model would suggest an important effect of one or more of the parameters tested (Bishop et al., 1975; Caswell, 1989). The significant models were then collapsed by initial states in order to determine how each factor affected the fate of each module belonging to a specific initial state. All log–linear analyses were conducted with GLIM (Society, 1993).

3. Results

3.1. MATRIX MODELS AND ELASTICITY ANALYSES

The finite rate of population increase (λ) was consistently lower in nectarless trees compared to their nectarful counterparts in the four yearly intervals (Fig. 2, Table 1), but, confidence intervals obtained through 1000 bootstraps indicated that such differences were not significant (Table 1). Overall, the population of mesquite modules is growing at a high rate, even though this growth rate may vary considerably between sites and nectar morphs ($\lambda = 1.69 - 2.64$, Table 1). Both nectar morphs had similar demographic behaviors between sites and years (Fig. 2 and 3), but the value of λ was highest in site IS, and lowest in site DS. Between years, the highest growth rate corresponded to the first year (1994–95, Table 1), probably because of the influence of higher rainfall during the previous season (293.4 mm, the highest during the study period).

There was no correspondence between water availability and the elasticity of demographic processes. Water availability was similar between sites HS and IS ($\bar{X} = -0.55 \pm 0.046 MPa$ and $\bar{X} = -0.58 \pm 0.046 MPa$) and both of these differed significantly from DS ($\bar{X} = -0.82 \pm 0.08 MPa$). These water conditions were found to be consistent between years (C. Montaña unpublished data). Site HS had particularly low values for retrogression (shoot death) and the lowest values for growth causing the elasticity of stasis to be the highest (Fig. 2). This behaviour, together with intermediate fecundity values suggest that these modules are growing at slow rates with decreased growth and death rates. On the contrary, the site IS had the highest fecundity and growth, but the highest mortality of modules (retrogression). The combination of high growth and retrogression caused the values of stasis to be the lowest. As expected, site DS had the lowest values of fecundity, but contrary to our expectations, had intermediate values of the other three demographic processes (growth, stasis and retrogression).

The year 1994–95 was characterized by intermediate values of fecundity, retrogression, stasis and growth (Fig. 3). The lowest rainfall found during this period (138.5 mm) resulted in the low growth, fecundity and high stasis recorded during the 1995–96 season (Fig. 3). Even though low fecundity was observed during this period, a higher rainfall was recorded which probably affected modular dynamics by increasing growth and retrogression and reflecting in a decrease in stasis. The highest rainfall recorded during the study period (234.7 mm, 1996–97 study period) also corresponded to an increase in fecundity during the following year (1997–98 season), with a consequent decrease in stasis, growth and retrogression. The values of

λ for both nectar morphs were negatively and significantly correlated with retrogression (branch death $r = 0.36, P < 0.05$) and positively correlated with fecundity ($r = 0.37, P < 0.05$), suggesting that new shoot growth and death are important processes in our estimation of growth.

Growth was consistently lower in site DS. The nectarful population had slightly higher elasticity values for growth and fecundity, and lower mortality (retrogression) than those of the nectarless population for site IS; however, this pattern was inverted in site DS. Although these demographic processes were reversed, the importance of stasis affected the pattern of demographic processes buffering the possible effects of the other processes and maintaining the values of λ for the nectarless morph below those of the nectarful morph (Fig. 2), even though these values were not significant. The largest difference in mortality rates occurred during the 1997–98 season when the nectarless morph was strongly affected by module mortality. The resulting decrease in retrogression for the nectarful morph was probably responsible for the increase in λ found during this period. Contrary to what would be expected if nectar production were costly, the nectarful subpopulation of modules had consistently higher values of λ in the driest site (DS). Our results indicate that the importance of different demographic processes vary between years and sites but are not significantly different between nectar morphs.

3.2. LOG–LINEAR MODELS

The reduction in deviance from the first log–linear analysis involving the effect of initial state (I) on the final condition (F) suggested that modular behavior is strongly determined by initial modular size ($\chi^2 =$

3522, df=12, $P < 0.01$). The appropriate null model of conditional independence was therefore NSYF, IF (N=nectar morph, S=site, Y=year, F=fate and I=initial state). To determine the effect of nectar condition (N) on module fate, we fitted the model NSYF, YSFI (Table 2). In addition, to test the effect of year (FY) and site (FS) we fitted the models NSYF, NSFI and NSYF, NYFI respectively. The test that involved nectar condition fit the data, suggesting that nectar condition is not important in determining modular fate. The lack of fit of the models that had either year or site suggested that one or both of these factors were responsible for the lack of fit. In order to determine if these factors interacted, we fitted models that contained the interaction term FY x FS. These models, containing the site and year interaction fit the data, suggesting that both year and site contribute significantly and independently to the fate of modules (NSYF,YSFI; Table 2).

The most important effects on modular fate were both site and year (Table 2). When we decomposed the significant models to determine the relative importance of each of these factors on the initial states, these models suggested that the smaller size classes were affected by both the site (S) and the year (Y) (Table 3), and the largest size–class (> 60 modules) were unaffected. Significance of the site was given by size–class 2 (21–40 modules) during 1995–96, by size–classes 2 and 4 during 1996–97, and by size–classes 1 to 3 during the 1997–98 season. The only consistent effect of site was for stage 2 that affected modular fate in three out of four transitions. With respect to year, fate of modules in size–classes 1 (1–20 modules) and 2 were consistently affected throughout the study period, with a decreasing effect for larger modules (Table 4). Year to year variation affected modules in size classes 1 and 2, by means of modular death (Table 5), suggesting that these branches are affected to a larger extent by lack of resources. This model is consistent with the results provided by the matrix models, a significant effect of site and year–to–year variation on module fates.

4. Discussion

Nectar has been thought to represent a significant cost to reproduction in plants (Pleasants and Chaplin, 1983; Southwick, 1984; Pyke, 1991), but evidence suggests small energetic costs of nectar production (Harder and Barrett, 1992). Our results employing both matrix and log–linear analyses also suggest that nectar production does not conflict with plant growth (modular dynamics). Both matrix and log–linear analyses showed similar patterns: an important effect of year to year variation, due to the varying rainfall regimes, as well as an important effect of the microclimatic conditions within each site. The effects of environmental heterogeneity are similar to those found when measuring complete individuals of mesquite (Golubov et al., 1999b). However, the values of λ (always above equilibrium) when studying modules were consistently higher than those for the demography of individual plants of adults for both nectar morphs. When comparing their demographic processes, however both modular and individual tree elasticity analyses show that mesquites behave as perennial trees (Silvertown et al., 1992; Golubov et al., 1999b) in terms of the sensitivity of λ to the different matrix elements, and this contribution is dominated by stasis (Golubov et al., 1999b). The results presented here suggest that nectar production in honey mesquites does not represent a cost in terms of vegetative growth. If this were not the case, we would expect a negative relationship between the presence of nectar and modular growth which would be reflected in lower values of λ for nectarful, as compared to nectarless individuals. Surprisingly, however, λ was consistently lower in the nectarless population, and in DS (assuming water–resource limitation). This was remarkable, particularly because the study period experienced below average rainfall.

The lack of evidence to support a significant cost of nectar production could be due to several characteristics of mesquites. The production of foliage in *Prosopis* coincides with the reproductive season, and they both rely on resources (mainly rainfall) that were most likely obtained the previous season (Golubov et al., 1999b). This makes the energetic expenditure on nectar and growth to be in part supported by resources, generated by foliage, that are being produced during the current reproductive season. This was demonstrated in part by the differences between sites, by the important site specific effects that contributed to differences in modular fates. The effects of different site specific conditions has been previously documented for different factors such as the importance of large environmental conditions (Horvitz and Schemske, 1995; Mandujano et al., 2001), interspecific competition (Flores-Martínez et al., 1994), year to year variation (Golubov et al., 1999b; Mandujano et al., 2001) and density effects (Harvell et al., 1990).

Nectar production does not pose a significant drain on plant resources as suggested by the results or does not have the same limiting factor underlying the activities of growth and reproduction. Unfortunately it is difficult to discriminate between these two possible explanations. Mesquites are well known to be adapted to arid environments (Simpson et al., 1977; DeSoyza et al., 1996), being facultative phreatophytes that exploit water resources from areas that are 0.3 m deep, regardless of individual size (Ansley et al., 1990; DeSoyza et al., 1996). In addition shoot growth, the production of foliage, and reproductive events (where nectar is involved) are all temporally equal, suggesting that resources such as water can be considered to be coming from a common pool. This effect was in part a result that water availability had a significant effect on canopy growth, probably due to the extreme arid conditions found during the study period that clearly affected modular dynamics. The environmental effect was especially true for branches in the smallest size classes (branches having < 40 modules), that were usually affected more often in varying environmental conditions. Contrary to what (López-Portillo et al., 1996) reported, we found a significant effect of site on the demographic behavior of modules. However, this difference could be due to higher water availability in our study because the site is surrounded by a water catchment that accumulates water after heavy rainy seasons. However, water availability did not entirely explain the demographic processes involved in the population as λ was consistently lower in HS than in IS. Further studies regarding other aspects of modular growth (such as the investment of modules to sexual reproduction, by the production of flowers) would be important.

Arid environments pose important constraints on resources, because of the unpredictable rainfall periods and extreme temperatures (Noy-Meir, 1973). Heterogeneity of resources can be due to abiotic factors such as temporal and spatial variability and to biotic factors such as the creation of *islands of fertility* by the effect of certain species (e.g. mesquite). The unpredictable nature of arid environments can make the demographic processes to be dependent on environmental cues and therefore unpredictable too (Golubov et al., 1999b). Studies that use matrix models that span several years or habitats have now tried to incorporate environmental heterogeneity into the models (Bierzychudeck, 1982; Oostermeijer et al., 1996; Mandujano et al., 2001). In the case of mesquites, year to year environmental variation was an important component of modular dynamics. We have previously shown that mesquites are particularly able to change demographic behaviors between years (Golubov et al., 1999b). In addition to year to year variation, ecological conditions specific to certain sites also play an important role in modular dynamics. These can be due not only to different water availability but also to other factors such as competition and herbivory. We can therefore conclude that modular fates in mesquites are determined by factors other than nectar condition, and that prevailing environmental conditions the prime determinants of modular fate in *P. glandulosa.*

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Tables

Table I. Values of λ (upper and lower 95% confidence intervals after 1000 bootstraps) for modules of nectarful and nectarless individuals over a four year study period.

Study period	Nectarful	Nectarless
1994–95	2.64 (2.10–3.39)	2.34 (2.08–2.64)
1995–96	2.36 (2.06–2.71)	1.90 (1.74–2.12)
1996–97	1.69 (1.56–1.84)	1.58 (1.43–1.80)
1997–98	2.14 (1.97–2.33)	2.01 (1.87–2.17)

Table II. Log–linear analysis of nectarful and nectarless mesquite module transition frequencies for a four–year period at 3 sites. Parameters in the models stand for N=nectar morph, I = initial module state, F= final module state, Y = year and S = site

Model	Deviance	df	p
NSYI, IF (null model)	611.49	368	< 0.01
NSYI, FISY (nectar)	162.40	192	0.9408
NSYI, FINS (year)	434.27	288	< 0.01
NSYI, FINY (site)	246.34	256	< 0.01
NSYI, FINS, FIYN (year x site)	186.53	192	0.597

Table III. Deviance of the collapsed models that take into account the effect of site (S) and year (Y) on modular fate depending on initial modular states (I). * significant at $P < 0.05$, ** significant at $p < 0.01$

Stage (I)	Site (FS)	Year (FY)
1	89.916*	115.24**
2	102.12**	131.63**
3	97.026**	109.2 **
4	60.278	78.206

Table IV. Significance of the effect of site on fate for each initial module state (FS) for each of four initial states (I) and in each sampling year (Y). Numbers in bold are significant at $\alpha = 0.05$

Initial Module State (I)	Year(Y)			
	1994–95	1995–96	1996–97	1997–98
1	0.813	0.854	0.337	**0.001**
2	0.616	0.052	**0.007**	**0.001**
3	0.549	0.339	0.708	**0.001**
4	0.943	0.292	**0.034**	0.11

Table V. Significance of the effect of year (Y) on modular fate (F) for each initial state (I) and each site (S). Numbers in bold are significant at $\alpha = 0.05$

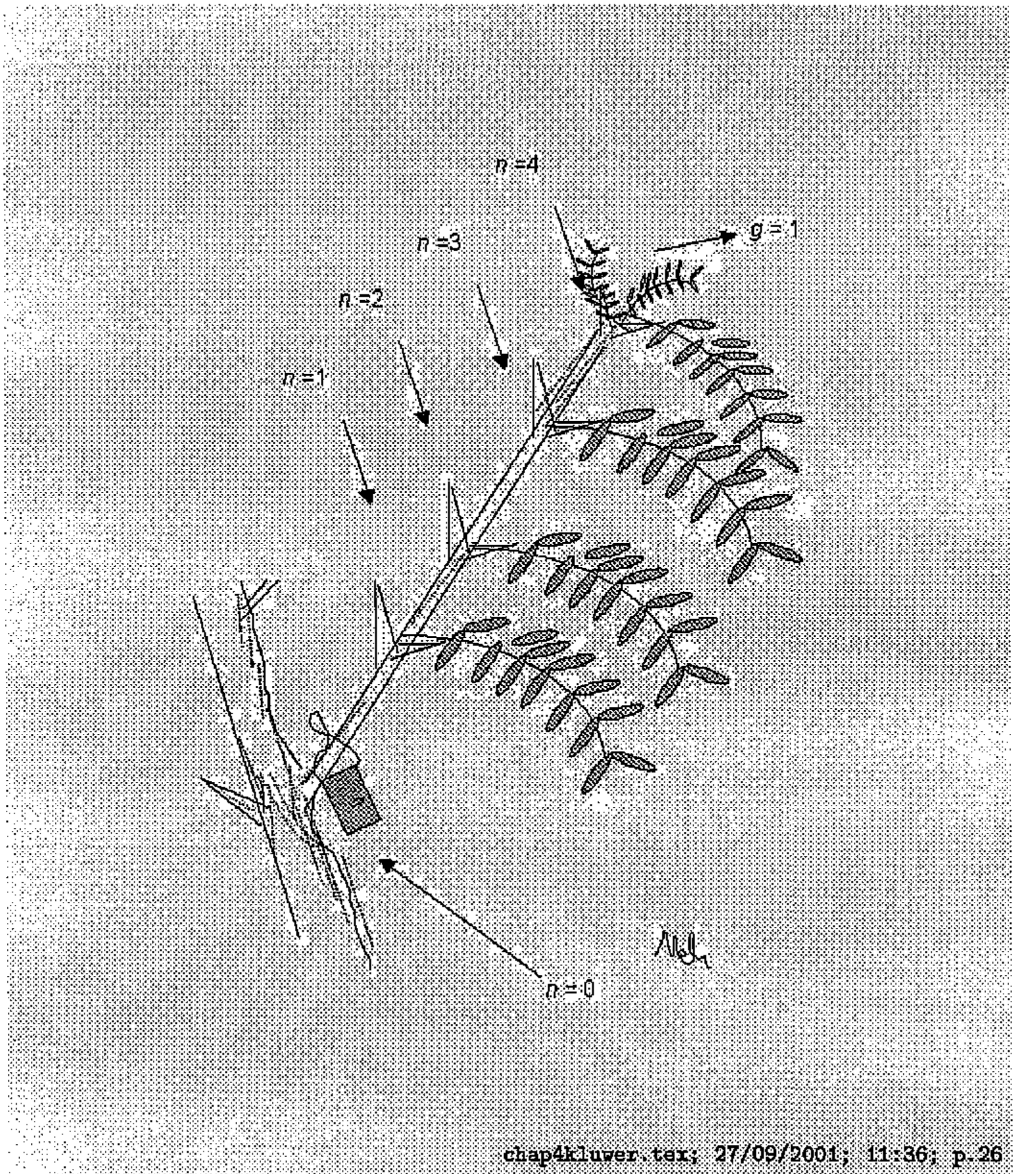
Initial Module State (I)	Site(S)		
	1(Humid)	2(Intermediate)	3(Dry)
1	**0.017**	**0.001**	**0.002**
2	**0.015**	**0.001**	**0.027**
3	0.661	**0.001**	0.093
4	0.918	**0.001**	0.765

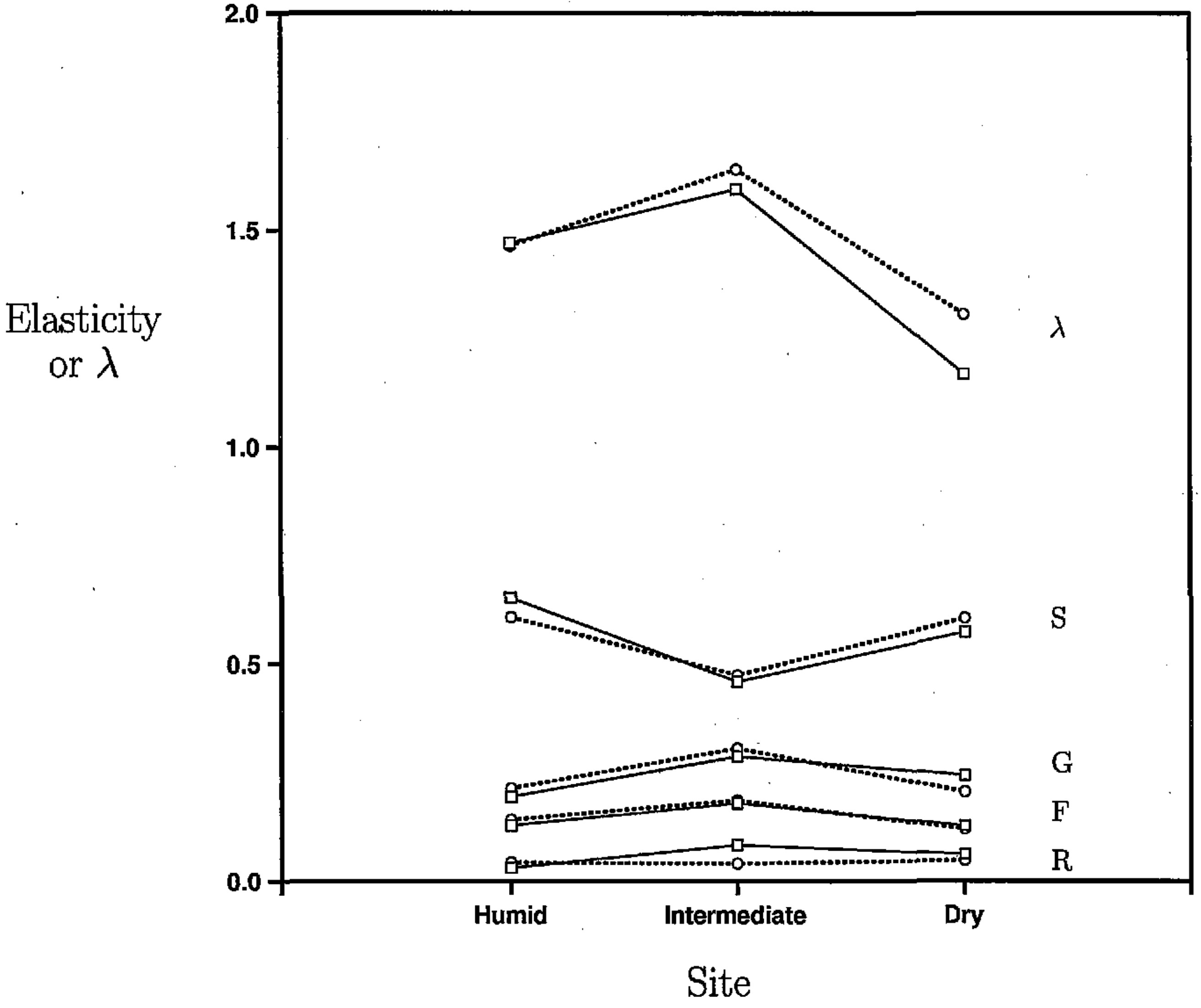
Figure Legends

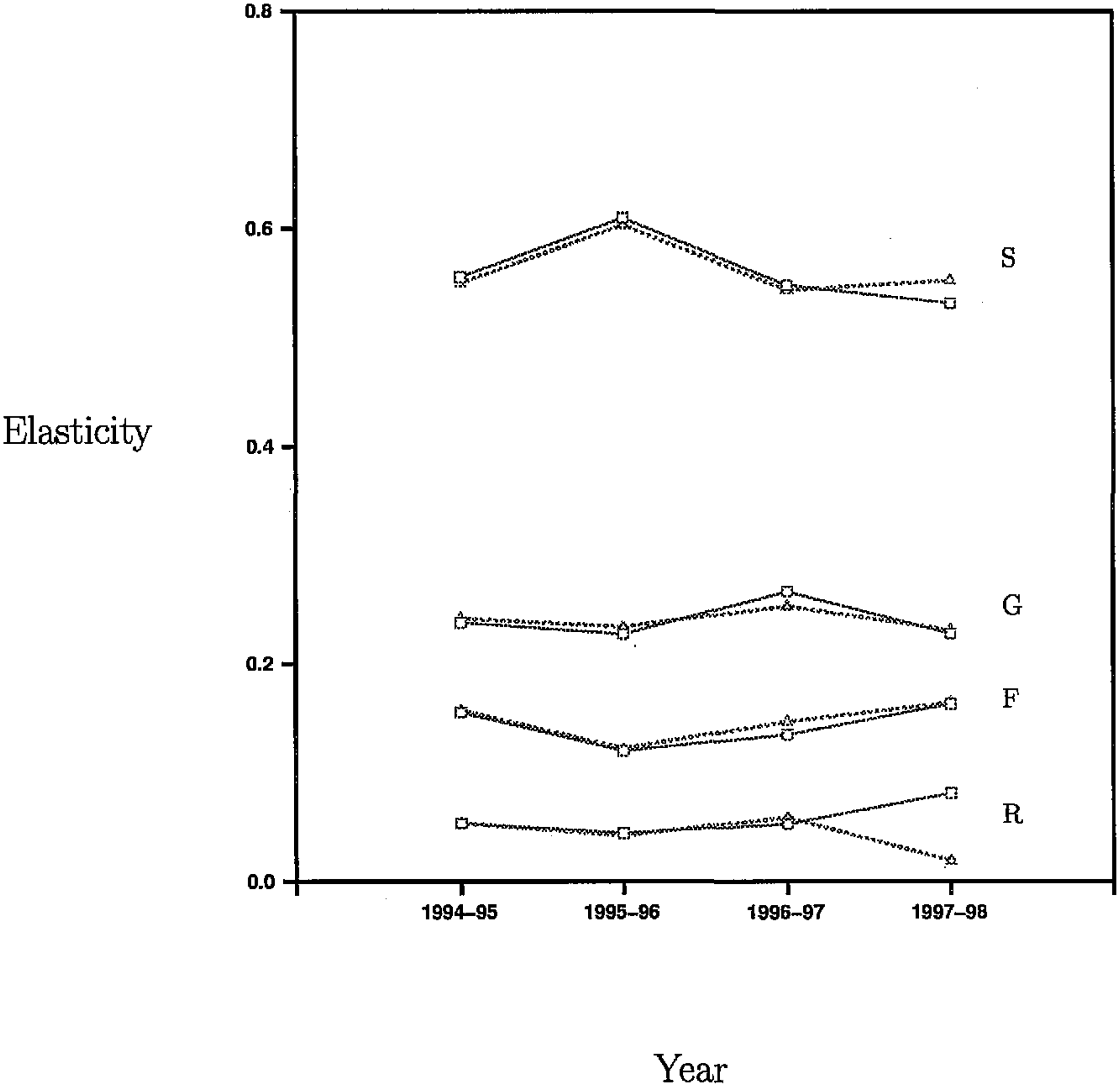
Figure 1. Honey mesquite shoot. n indicates nodes counted, and g indicates new growth in terms of number of shoots. In this case, $n = 4$ and $g = 1$.

Figure 2. Mean values of elasticity for different demographic processes (growth, fecundity, retrogression and stasis) for the three sites. The symbols stand for S=stasis, R=retrogression, G=growth and F=fecundity. The top portion of the graph corresponds to the values of λ for the three sites. The solid lines correspond to the nectarless morph, and the dotted lines correspond to the nectarful morph.

Figure 3. Mean values of elasticity for the different demographic processes (growth, stasis, fecundity and retrogression) during the 4 year study period (1994–98). The symbols stand for S=stasis, R=retrogression, G=growth and F=fecundity. The top portion of the graph corresponds to the values of λ for the three sites. The solid lines correspond to the nectarless morph while the broken lines correspond to the nectarful morph.


n =4
g = 1
n =3
n =2
n =1
n = 0


Elasticity or λ
2.0
1.5
1.0
0.5
0.0
λ
S
G
F
R
Humid
Intermediate
Dry
Site


Elasticity
0.8
0.6
0.4
0.2
0.0
S
G
F
R
1994–95
1995–96
1996–97
1997–98
Year

PAGINACIÓN DESCONTINUA

Capítulo 5

Discusión y Conclusiones Generales

Discusión y Conclusiones Generales

Se ha propuesto que la producción de néctar tiene consecuencias sobre la adecuación de las plantas. Aún cuando el atributo de producción de néctar sea muy común, en condiciones naturales es rara la condición de no producirlo, simplemente por la presión selectiva tan fuerte en contra de los no productores que ráapidamente serían eliminados de la población.

En los 7 años de seguimiento de la población de mesquite mielero, hemos encontrado que la producción de néctar genera algunas diferencias. En primer término, las proporciones de productores y no productores de néctar son similares en varios sitios dentro de la Reserva de la Biósfera de Mapimí. La condición de producir néctar se ha mantenido constante a lo largo del estudio, las plantas productoras de néctar no han dejado de producirlo, sugiriendo que no es un carácter plástico que cambie en el tiempo o dependiendo de los recursos, y que es un atributo que tiene un origen genético. Aún con diferencias de agua generada por el presón (diferencias en potenciales hídricos) las plantas han mantenido su morfo.

Hay muchos estudios en donde demuestran la existencia de plantas que producen néctar y plantas que no producen néctar (p. ej. *Begonia*, varias especies de orquídeas). Se han postulado varias hipótesis acerca de las características genéticas de la producción de néctar y su interacción con el ambiente. Por un lado, existe una gran variabilidad de producción de néctar que tiene una influencia ambiental, por ejemplo, la temperatura, la humedad relativa y la tasa de visita determinan la tasa producción de néctar. Por otro lado, los estudios que han tratado de descriminar el componente genético de la variación de producción de néctar han encontrado que la heredabilidad (h^2) de la producción de néctar puede ser de hasta 0.65, pero presenta mucha variación (Boose, 1997). Los estudios genéticos en algunos casos han encontrado varios loci del atributo por medio de modelos de genética cuantitativa (quantitative trait loci, QTL) de tal modo que la producción de néctar y otros atributos florales (tamaño de los pétalos, heterostilia, genes de autoincompatibilidad) son generados por un grupo de genes que tienen una interacción importante con el ambiente (Bradshaw *et al.*, 1998).

Fenológicamente ambos morfos de *P. glandulosa* se comportan se manera similar, permitiendo el intercambio genético entre ambos. La presencia del recurso néctar en las plantas generó cerca de 20 veces más visitantes florales y mayor número de especies (63 especies vs. 25 especies), y de todos los polinizadores, solo se comparten el 10 % (2 son exclusivas del morfo sin néctar). Además, existe variación temporal en el tipo de visitantes (55 especies en 1994 y 44 especies en 1995). La calidad de los visitantes es claramente diferente, las moscas y algunas abejas como *Melissodes tristis* que aunque pueden ser muy abundantes son relativamente peores polinizadores que otras especies de abejas (e.g., *Megachile*, *Apis mellifera*). La función femenina es mayor en las plantas productoras de néctar, y esta dado por un incremento en el número de granos de polen recibidos. Este incremento puede además ser la causa del incremento en el número de semillas producidas por este morfo. Por el contrario, las plantas que no producen néctar, producen un mayor número de granos de polen favoreciendo así la función masculina. Sin embargo, aunque las tasas de visitas florales son tan diferentes entre morfos, la tasa de entrecruzamiento de los dos morfos es igual, produciendose un exceso de heterócigos, que se encuentra ligeramente correlacionado con el peso de la semilla.

Genéticamente, no parece haber un efecto de la producción de néctar, sin embargo se requiere de una análsis más fino para determinar cómo es el flujo de polen en la población. Para esto, el uso de marcadores moleculares hipervariables parece ser una herramienta prometedora (Ver Apéndice I). Demográficamente, tanto a un nivel modular como de los individuos, la producción de néctar no parecer ser una fuga de recursos o que le imponga limitantes al crecimiento o reproducción, como se ha sugerido para otros sistemas (e.g., Southwick, 1984). Desde el punto de vista modular, los factores más importantes son la cantidad de recursos (en este caso el agua), y los cambios entre años. Los módulos más afectados fueron los de tamaños pequeños, mientras que los módulos de tamaños grandes raramente fueron afectados por recursos o variaciones interanuales. Un factor (no incluido en este trabajo) que esta en seguimiento es la importancia de los depredadores (p. ej. *Oncyderes* spp.). Estas especies llegan a matar hasta un 30 % de las ramas de la población.

En especial, un sistema dimórfico de producción de néctar como el descrito en *Prosopis glandulosa* es raro en condiciones naturales, y como hemos encontrado, la produccón de néctar en el mesquite mielero tiene varias posibles explicaciones. En general propongo dos posibles escenarios para la evolución del dimorfismo en *Prosopis glandulosa*, uno estable y el otro inestable. Es difícil encajonar todas las variantes posibles para obtener los resultados que tenemos en condiciones naturales, sin embargo traté de abarcar los modelos posibles de tal manera que cada escenario contiene vías alernatvas que pueden dar el mismo resultado. En cada caso trato de explicar el razonamiento que seguí, lo que se esperaría ver bajo el supuesto del escenario que se propone, y una explicación de porqué lo podemos rechazar o aceptar como posible ruta evolutiva. Cada escenario tiene una explicación, ya sea por medios experimentales descritos en los capítulos de la tesis o por simulaciones que desarrollé. En las siguientes secciones se presentan estos posibles escenarios y se describen posibles rutas a seguir en el futuro.

1. Las funciones de adecuación y la teoría de la asignación sexual

La evolución del dimorfismo de caracteres sexuales de plantas se basa principalmente en la teoría de la asignación sexual. El suspuesto pincipal de esta teoría se encuentra centrado en la idea de una disyuntiva (*trade-off*) entre la asignación de los recursos hacia la función femenina y la función masculina. Por lo tanto, una dismunición en la inversión hacia una función podría estar compensado por un incremento en la otra función (principio de la compensación de Darwin; Charlesworth & Charlesworth, 1978a). Esta teoría de la asignación del sexo ha generado hipótesis acerca de la evolución de los sistemas de apareamiento en plantas. Una parte central de los modelos son las curvas de ganancia en adecuación (*fitness gain curves*) que describen la inversión a funciones masculina y femenina y la ganancia en adecuación por cada vía. Por lo general la inversión representa una proporción de recursos invertidos (a) a una función en particular. Las curvas de ganancia en adecuación son funciones de tipo exponencial, en donde:

$$W_m = ba^{v_m} \tag{1}$$

a es la proporción de recursos asignados a la función, b = una constante que define la proporción sexual de la población, W_m la adecuación vía masculina y v_m es una tasa a la cual se gana o se pierde adecuación. Dado que los recursos son limitados y por el principio de compensación, la proporción de recursos asignados a la función hembra se calculan como $1 - a$ por lo que:

$$W_f = b(1-a)^{v_f} \tag{2}$$

Por lo tanto, la adecuación total de una planta hermafrodita (o bien monoica) está definida por:

$$W_{total} = W_m + W_f \tag{3}$$

que quiere decir que la adecuación total esta determinada por la contribución por vía femenina (W_f) y la contribución por vía masculina (W_m) (Charnov, 1982). En flores dioicas, alguna de las funciones no se encuentra, por lo que $a = 1$ para ambas asignaciones y las funciones se reducen a una sola función de ganancia de adecuación:

$$W = ba^v \tag{4}$$

Para poder determinar los valores optimizados y las estrategias estables, es necesario poner la adecuación de una función sexual en relación a la función contraria, de tal manera que:

$$W_f = b\left(1-\left(\frac{W_m}{b}\right)^{\frac{1}{v_m}}\right)^{v_f} \tag{5}$$

La forma de las curvas de ganancia de adecuación van a determinar la estabilidad evolutiva de los sistemas de apareamiento. El hermafroditismo siempre es estable si las dos curvas muestran una saturación ($v < 1$, *diminishing returns*, Fig. 1 D y E) y el dioicismo es estable si los dos se aceleran ($v > 1$, Fig. 1 C). Si la curva masculina es lineal (ó $v < 1$) y la femenina se satura, entonces el hermafroditismo sería estable (Fig. 1 E). Con especies cosexuales de plantas, las formas de las curvas determinan la asignación sexual a nivel poblacional. Los individuos dentro de la población deben de ajustar su asignación sexual de tal manera que incrementen su adecuación.

Las proporciones sexuales en todos los tipos de sistemas reproductivos en plantas parten de una pregunta principal: ¿cuál es el equilibrio bajo selección natural donde los posibles genotipos tienen diferentes contribuciones genéticas por vía masculina y femenina? Las situaciones estables de un atributo son estrategias evolutivamente estables (EEE). Suponiendo que hay una población de individuos con un atributo Z e introducimos a la población un genotipo raro con un atributo alternativo $\hat{Z}$, podemos ver si $\hat{Z}$ se seleccionan a favor o en contra. Si para algún atributo existe una Z tal que todas las variantes son seleccionadas en contra, entonces a Z se le denomina una EEE. Dentro de las EEE pueden haber estrategias puras (el caso arriba mencionado) o estrategias mixtas en donde el atributo cambia de Z a $\hat{Z}$ con cierta probabilidad, dando como resultado polimorfismos estables (Charnov, 1982).

La derivada de la curva (ecuación 5) de adecuaciones entre una función y la otra da el resultado de las estrategias evolutivamente estables de la población en donde se maximiza la adecuación. En la figura 2 se muestran diferentes modelos en donde se cambió el coeficiente de la asignación a los recursos (femenino y masculino) para generar cuatro posibles situaciones estables: 1) Poblaciones en donde la ganancia en adecuación es una función lineal de la asignación, hace una estrategia estable para cualquier asignación (Fig. 1 A) , 2) La EEE es el hermafroditismo en donde puede variar la asignación de los recursos dependiendo de los coeficientes (Fig. 1 D y E), 3) La EEE es el dioicismo en donde los individuos que tienen cualquier estrategia diferente a las puras (flores femeninas o flores masculinas) tendrían una adecuación menor (Fig. 1 C y D) poblaciones en las cuales hay más de una estrategia estable (Fig. 1 B). Estos modelos sugieren que la forma de la asignación de los recursos determina los puntos estables de la EEE.

2. Escenario Inestable

En casi todos los escenarios inestables, las proporciones de productores de néctar y no productores de néctar van a ser alteradas de las proporciones que observamos (1:1). Esperariamos una desviación de las proporciones para favorecer a uno u otro morfo. En cualquier situación de inestabilidad individuos que posean un caracter (como en nuestro caso el néctar) que le confiera una ventaja (o desventaja) a los individuos, va a incrementar (o diminuir) en frecuencia en la población. Dentro de esta categoría, hay varias posibilidades por las que se pueda dar una separación, y discuto las razones por las cuales he descartado.

2.1. El néctar como atributo lábil

En primer término, podríamos considerar que la producción de néctar es un sistema que depende de los recursos (lábil), similar a lo que se reporta para cambios sexuales en plantas (Freeman *et al.*, 1980; Klinkhamer *et al.*, 1997). Si suponemos que la producción de néctar le confiere un costo a los individuos (especialmente en zonas áridas donde el agua es un recurso muy limitado), esperaríamos, por lo tanto que en sitios en donde hay mas recursos exista una mayor proporción de productores de néctar y en zonas pobres haya una menor proporción de productores de néctar como se encuentra en otras especies (Bowker *et al.*, 2000). La mayor parte de la evidencia empírica indica que los cambios en atributos sexuales están relacionadas en su mayoría a efectos ambientales tales como la

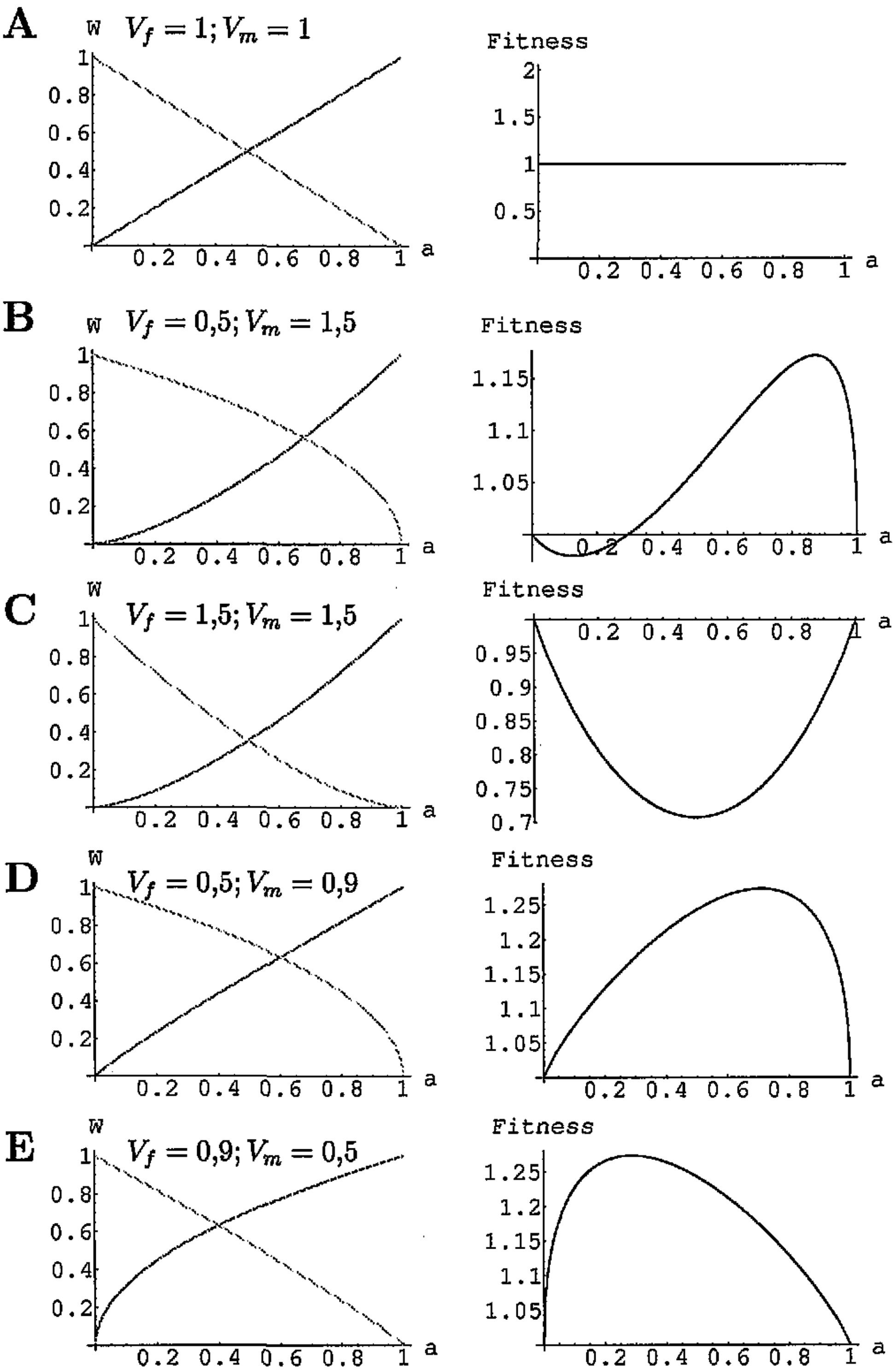


Figura 1: **Funciones de adecuación por las dos vías sexuales en relación a la asignación de recursos de la función masculina a, con diferentes valores de V_m y V_f. A la izquierda, las líneas gruesas corresponden a la función masculina (ecuación 1) y las líneas claras a la función femenina (ecuación 2) con respecto a la asignación a. Las gráficas de la derecha corresponden a la suma de las adecuaciones para cada caso (ecuacion 3).**

precipitación, temperatura, humedad y tamaño (Klinkhamer *et al.*, 1997). La evidencia que obtuvimos no muestra esta tendencia. Por un lado, si el atributo de producir néctar estuviera asociado a factores ecológicos (como la presencia de recursos), los potenciales hídricos de las plantas con y sin néctar serían diferentes, porque las plantas productoras de néctar tendrían un potencial hídrico más negativo por perder agua durante la producción de néctar. La presencia de un presón en el sitio de estudio puede considerarse como un experimento en condiciones naturales que simuló diferentes cantidades del recurso agua. En los tres sitios, no hay desviaciones en las proporciones de productores y no productores de néctar (1:1), aún cuando hay diferencias marcadas en los potenciales hídricos. Adicionalmente, al estudiar la población por más de un año, comprobamos que las diferencias en la precipitación de un año a otro no provocaron cambios dentro del mismo individuo en el atributo de producción de néctar entre un año y otro. Nuestras observaciones muestran que durante los últimos 6 años, y en diferentes poblaciones, la proporción de individuos productores y no productores de néctar no se desvió de 1:1, lo que significa una alta repetitibilidad (100 %). Si el atributo estuviera relacionado con el tamaño esperaríamos una relación con la producción de néctar. La evidencia que tenemos sugiere que la producción de néctar no es un atributo lábil, por lo que podemos descartar el efecto ambiental sobre su producción. En este estudio el efecto ambiental fue muy importante desde el punto de vista demográfico. El efecto del sitio y del año tuvieron importantes efectos en el crecimiento del mesquite mielero (Apéndice 2). Sin embargo, no podemos adjudicar las diferencias de producción de néctar a recursos, ya que los árboles crecieron lo mismo, y especialmente en los ambientes secos en donde se esperaba una diferencia notable, al contrario, el valor de λ fue de manera consistente menor en los no productores que en los productores de néctar, sugiriendo que no es un problema energético. Hay evidencia de que el néctar esta asociado a condiciones ambientales como los niveles de recurso.

2.2. Selección

En este escenario, necesariamente encontraríamos diferencias en la adecuación de las plantas. Podríamos pensar en que los árboles productores de néctar van a desplazar a los no productores, simplemente por los beneficios que ofrece el néctar para atraer polinizadores (si se considera que la adecuación es una función de el número y tipo de visitas). Suponiendo que éste fuera el caso, partimos del supuesto de que para generar proporciones 1:1 se necesitaría un escenario en donde los alelos sean totalmente codominantes, dando un fenotipo de tipo néctar (digamos AA) y un fenotipo de tipo no nectar (digamos aa). Los fenotipos híbridos suponemos que tienen una desventaja selectiva fuerte ya que no hay un fenotipo intermedio de producción de néctar. Del capítulo 2, encontramos diferencias en la función macho. Sabemos que los árboles sin nectar producen alrededor de 25 % más semillas que los no productores de néctar (coeficiente de seleccón sobre los árboles no nectar 1-0.25=0.75 y Fig. 2). Si hacemos esta simulación, encontramos que en pocas generaciones (< 10) los individuos con néctar sustituyen a los no productores de néctar. Si realizamos la misma simulación suponiendo que los no productores de néctar tienen una ventaja al producir 7 % más polen que los productores de néctar (coeficiente de selección sobre los néctar S=1-0.07) también vemos una perdida de los productores de néctar al ser reemplazados. En el tercer caso, tenemos la combinación de los dos coeficientes de selección y aunque tarda unas generaciones más, los productores de néctar reemplazan a los no productores de néctar.

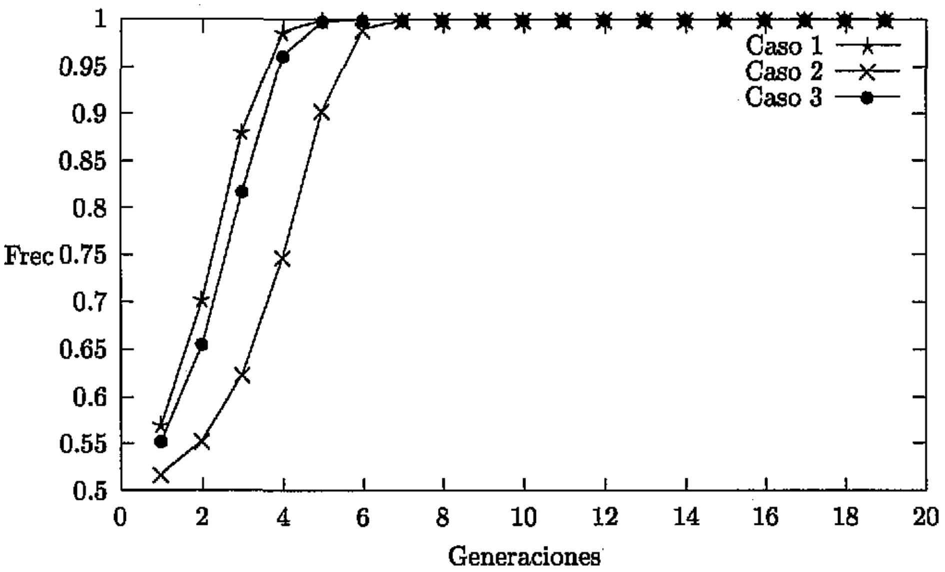


Figura 2: Simulación de diferentes escenarios de selección. En todos los casos, los híbridos son penalizados (W=0). Caso (1): Escenario en donde los productores de néctar tienen una ventaja sobre los no productores de néctar. Caso (2): Los no productores de néctar tienen una ventaja sobre los productores de néctar. Caso (3): Los productores y no productores tienen un coeficiente de selección diferente de 0.

Es claro que en cualquiera de estos escenarios, alguno de los morfos rápidamente desplazaría al otro. Además, podríamos pensar en poblaciones en diferentes estados de divergencia, algunas poblaciones con proporciones similares y algunas poblaciones con proporciones diferentes a las encontradas. No hemos encontrado evidencia que nos haga pensar en este sistema de desplazamiento (ver programa selection.c en los anexos para más detalles del modelo). Solo en el caso en que tuvieramos coeficientes de selección idénticos, podríamos pensar en un sistema estable, sin embargo con una pequeña diferencia en adecuación rápidamente tendríamos un escenario inestable.

2.3. El caracter es selectivamente neutro

En este caso, hay varias consideraciones, como el sistema genético que subyace el dimorfismo y el costo de producción de néctar. Si consideramos un sistema en el cual el caracter néctar es selectivamente neutro y el costo de producir nectar es muy bajo, entonces estaría regido por deriva génica y mutación. Tenemos evidencia de que la producción de néctar no es costosa para *P. glandulosa* (Capítulo 3 y 4). Si consideramos que la mutación es mínima, el caracter estaría regido puramente por deriva génica. Esto nos daría como resultado diferencias en las proporciones de los alelos (que definen la producción de nectar) que resultaría en proporciones diferentes de individuos con producción de néctar entre las poblaciones. En nuestro caso, de las poblaciones muestreadas, tenemos proporciones iguales de productores y no productores de néctar.

3. Escenario Estable

3.1. Selección dependiente de las frecuencias

Dados los costos energéticos de producción de recompensas, en algunas especies han evolucionado sistemas que eliminan los costos de la producción, desarrollando sistemas de engaño de atrayentes. En estos casos, la adecuación de los individuos en una población va a ser determinada por selección dependiente de la frecuencia. Este tipo de selección puede tener dos formas: 1) positiva: un individuo incrementa su adecuación conforme aumenta su frecuencia genotípica en la población y 2) negativa: en donde la adecuación de un individuo incrementa conforme baja su frecuencia genotípica en la población (Fig. 3). Cuando hay selección dependiente de la frecuencia positiva, la adecuación de un fenotipo (que esta determinado por un genotipo dado) incrementa hasta llegar a la fijación. Cualquier desviación de este genotipo daría como consecuencia una disminución en su adecuación y sería rápidamente eliminado de la población. En cambio, con la presencia de selección dependiente de la frecuencia negativa, la selección puede llevar al mantenimiento de polimorfismos (Ridley, 1998) y el mantenimiento del sexo en plantas (Antonovics & Ellstrand, 1984).

3.2. Selección dependiente de las frecuencias

En términos de recursos florales hay varios ejemplos de selección dependiente de la frecuencia (SDF), y los ejemplos son especialmente claros en mimetismos Batesianos en donde miembros dentro de una especie mimetizan a miembros de la misma especie. Por ejemplo, en muchas orquídeas, las flores que no producen nectar (por lo general las femeninas) mimetizan la forma floral a las flores masculinas que tienen recompensas, creando así un sistema en el cual ganan adecuación sin tener el costo de la producción de recompensas. En estos casos, la adecuación de las flores sin recompensa va a incrementar conforme se encuentren en proporciones muy bajas, ya que la probabilidad de ser visitada por insectos es alta. Conforme aumenta la frecuencia de las flores que no tienen recompensa, la tasa de visita va a disminuir al igual que la adecuación de los individuos dentro de la población (Gilbert *et al.*, 1991). Otros ejemplos de selección dependiente de la frecuencia se pueden ver en el color de las flores de *Ipomoea purpurea* (Clegg & Epperson, 1988) en donde los polinizadores prefieren morfos oscuros, pero dentro de la población, los morfos blancos tienen mayores tasas de entrecruzamiento y menores tasas de visita. Conforme aumenta la proporción de flores blancas, las tasas de autofertilización aumentan y las tasas de visita diminuyen. Patrones similares fueron encontrados en relación al tamaño de la flor y la cantidad de néctar producido en *Polemonium* (Cresswell & Galen, 1991). Otros ejemplos en los que la selección dependiente de la frecuencia es importante, incluyen los sistemas de incompatibilidad genética (Richards, 1997) en donde se mantienen varios alelos de incompatibilidad dentro de la población, sistemas heterostílicos en donde los morfos *pin* y *thrum* se mantienen por SDF (Lloyd & Webb, 1993) y habilidad competitiva en poblaciones dioicas (Richards, 1997). En poblaciones ginodioicas, la frecuencia de las plantas femeninas va a estar determinada por la cantidad de plantas masculinas que afectan la cantidad (y a veces la calidad) de polen que puede haber en la población. Pocas plantas hermafroditas y las plantas femeninas van a a estar limitadas por polen, mientras que en poblaciones con muchas plantas hermafroditas, las plantas femeninas van a tener una ventaja sobre las hermafroditas (Charlesworth, 1993).

La función más importante de las flores es la atracción de polinizadores para la importación y exportación de polen. Se ha reportado que un aumento en el número de visitas de los polinizadores lleva a una mayor cantidad de óvulos fecundados (Zimmerman, 1983; Winsor *et al.*, 2000), y una mayor proporción de polen dispersado. Sin embargo, el aumento en el número de visitas no siempre conlleva a ventajas (Klinkhamer *et al.*, 1994). Por lo tanto, esperaríamos una reducción en las ganancias netas de la planta conforme aumentan las visitas. Por ejemplo, si 2 visitas son suficientes para la fertilización del 80 % de los óvulos, cuatro visitas no van a duplicar el número de óvulos fertilizados. En consecuencia, esperaríamos que las plantas evolucionaran para optimizar los recursos invertidos en las flores, maximizando el número de fertilizaciones por unidad de inversión a caracteres secundarios de recompensa (Bell, 1986). Bajo este escenario,

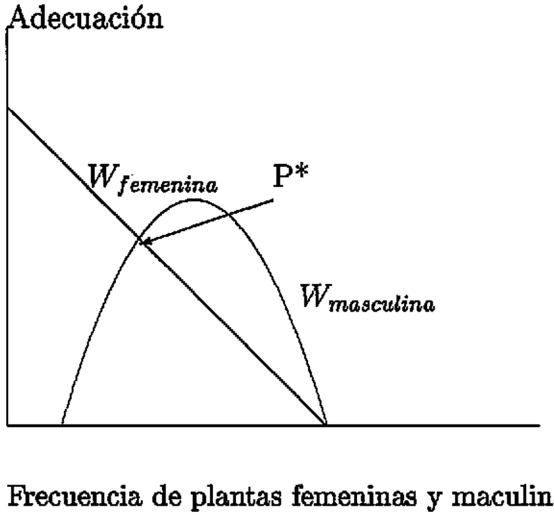


Figura 3: Adecuación de atributos con respecto a la adecuación vía masculina y adecuación vía femenina cuando la función se encuentra bajo selección dependiente de la fecuencia. P* es el punto de equilibrio en donde se maximizan las dos funciones sexuales.

podemos evaluar cuál sería la proporción óptima de plantas con y sin néctar dentro de la población. En poblaciones donde existan plantas con néctar y plantas sin néctar, los visitantes estarían sujetos a encontrar recompensas con cierta probabilidad. Si la proporción de plantas sin néctar aumenta, la población va ha ser menos visitada y por ende disminuiría la adecuación de los individuos que la conforman. En una población de puros productores de néctar, una mutación que no produzca néctar va a ser favorecida o aumentaría en frecuencia, por el simple hecho de que se beneficia por la presencia de las plantas que si producen néctar que están atrayendo a los polinizadores (Gilbert *et al.*, 1991). Esto llevará a tener una estrategia evolutivamente estable (Smith, 1978) que para el mesquite, la producción de néctar y la no producción de néctar son estrategias puras ya que no pueden cambiar de morfo (Ver capítulo 3). Modelamos una estrategia evolutivamente estable (ESS) modificando lo propuesto por Bell (1986). Del capítulo 2 y 3, encontramos que los visitantes a las plantas sin néctar eran hembras y abejas, por lo que suponemos que las abejas son las principales polinizadores del mesquite (López-Portillo *et al.*, 1993).

3.3. Genes ligados al sexo

La determinación sexual en plantas monoicas se ha concentrado en especies agrícolas principlamente. Aún cuando la determinación sexual no ha sido identificada de manera explícita, se ha demostrado que en ciertas condiciones la determinación sexual de las plantas puede ser modificada de manera muy similar a la herencia sexual en animales. Por ejemplo, en *Vitis vinifera* y *Asparagus officinalis* (especies de origen dioico), la autofecundación de hermafroditas dan como resultado progenie con plantas femeninas y progenie con plantas "masculinas" en una proporción de 1:3 en donde la condición heteróciga (XY), que produce una hermafrodita lleva los genes de masculinidad. De tal forma que cuando hay cruzas de tipo XY x XY se genera una planta ginomonoica (XX), 2 hermafroditas (XY) (que contienen el gene de "masculinidad") y una andromonoica (YY). En estas especies, la evolución hacia el diocismo pudo darse por 3 vías principales: (1) Un gene que confiera la esterilidad masculina en plantas ginomonoicas, (2) un gene que confiera ganancia en la función femenina en plantas andromonoicas, y (3) un incremento en el desequilibrio de ligamiento de los genes que confieren mayor o menor grado de masculinidad o feminidad, llegando a la formación prácticamente idéntica a los sistemas en donde hay genes ligados al sexo (Richards, 1997). Los genes que confieren mayor o menor funcioninalidad sexual se pueden generar por cambios en los tiempos de madurez de los órganos sexuales femeninos y masculinos, cambios en los arreglos morfológicos de la flor y cambios en la cantidad y calidad de polen (Charlesworth & Charlesworth, 1978b).

Se ha sugerido que los atributos florales en las plantas son moldeadas por selección natural, por los efectos que tienen sobre la adecuación. Los atributos florales tienen importantes consecuencias. En primer término, los efectos de producir néctar fueron muy importantes en 2 aspectos principalmente: (1) el número de visitantes florales y (2) los componentes sexuales de cada morfo. La diferencia más marcada en los visitantes florales fue el número y tipo de visitantes. En nuestro caso, los individuos del morfo néctar son 20 veces más visitadas que las del morfo sin néctar (Capítulo 2 y 3). Además, el tipo de visitante es diferente, el morfo néctar es vistado exclusivamente por abejas solitarias hembra. El hecho de ser visitado por abejas hembras es muy importante, ya que son las responsables de la mayor parte del flujo de polen (son las colectoras y acarreadoras). Los demás visitantes (abejas macho, avispas y moscas) pueden tener un papel en el flujo de polen pero su eficiencia es mucho menor. El número de visitantes no cambia entre años, sin embargo, la dominancia específica del los visitantes si. Estos cambios posiblemente hayan tenido efectos sobre las plantas. Sabemos que la cantidad de frutos producidos difiere entre años y entre morfos. Aunque no podemos determinar causalidad entre los visitantes y las diferencias en la producción de frutos, si hay una correlación.

La producción de néctar no tiene efectos sobre la fenología de la población. Desde el punto de vista genético, la producción de néctar no le confiere ventajas al que lo produce, ya que los índices de fijación (F) fueron negativos y las heterocigosis altas (H=0.45), sin diferencias entre los morfos. Aún dadas las diferencias tan grandes en visitas florales (1 vs. 20) entre morfos, las tasas de entrecruzamiento no fueron diferentes de 1 para ambos casos. Si tomamos el componente femenino, tenemos que los productores de néctar producen ligeramente más semillas que las que no producen néctar (25 % más), y no hay diferencia el peso de las semillas entre morfos. Sin embargo, encontramos que las semillas más pesadas son consistentemente más heterócigas. Al hacer cruzas controladas, encontramos que existe cierto grado de autoincompatibilidad pero no dada entre morfos, sino dentro del individuo.

En cuanto al costo de poducir néctar, al evaluarlo desde el punto de vista demográfico, encontramos que producir néctar no le confiere un costo a la planta. En procesos demográficos, son mucho más importantes los factores amientales como la disponibilidad de agua y la combinación de ambientes entre años.

Claramente, la producción de néctar afecta tanto la función macho como la función hembra. En cuanto a la función macho, los resultados sugieren que no hay diferencias en el flujo de polen entre productores y no productores de néctar. El papel de los polinizadores es tan importante que aún cuando no se produce néctar, el flujo de polen es homogéneo en la población.

Prosopis galndulosa es un componente importante de las zonas áridas en América (Apéndice 3). Es un recurso explotado por animales y plantas, y tiene efectos importantes a nivel de ecosistema, modificando la cantidad de nitrógeno, carbono y agua en los suelos donde se encuentra. En muchos casos se han descrito los efectos nocivos del mesquite, porque modifican la homogeneidad de los ambientes de pastizal, concentrando los recursos en "islas de fertilidad". Aún si consideramos estos efectos, las ventajas asociadas al mesquite son mayores.

4. Perspectivas

Como primer acercamiento, un estudio paralelo que se va a realizar es la presencia de un nectario por vías histológicas. La presencia de un nectario en plantas que no producen néctar significaría que se ha perdido la habilidad de producir néctar recientemente, la no existencia del nectario nos sugeriría que la ausencia de producir néctar es un carácter con origen antiguo. Como se dijo en la introducción general, nuestra visión de adaptación en este trabajo ha sido enfocado a una en el cual se ignora la historia evolutiva del atributo, en este caso, el néctar. Realmente para obtener la parte histórica y reforzar el caracter adaptativo de atributos florales como en este caso el néctar, necesitaríamos usar el método comparativo, en el cual sabríamos la relación que existe entre las especies del género *Prosopis*, y además sabriamos la presencia/ausencia de este caracter en las diferentes especies. Si realmente encontramos algun patrón, se podría deber a 2 razones: 1) un componente histórico o arrastre filogenético y 2) realmente el néctar constituye un atributo adaptativo. Para diferenciarlos, se tendría que probar que el néctar es adaptativo en todos las demás especies en donde se encuentra el dimorfismo. Un segundo aspecto mucho más complicado de definir es el origen del dimorfismo. La producción de néctar es un caracter contínuo, por lo tento estaría sujeto al campo de la genética cuantitativa y su control estaría mediado por varios genes. En nuestro caso, al tener un dimorfismo tan claro, suponemos que es un proceso más complicado. Por un lado, pocos genes (1 tal vez 2) median la presencia o ausencia de néctar, y por otro, ya que se define producir néctar, la tasa de producción estaría definida por varios genes. Descubrir los genes responsables de la producción de néctar realmente sería parte central del estudio a futuro, aunque el trabajo de encontrarlo sea inmenso. La descripción de este sistema genético sería realmente innovador.

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Apéndice 1

Flujo de polen en el mesquite mielero

PAGINACIÓN
DESCONTINUA

Male Function of the Honey Mesquite

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Abstract

We evaluated the mating systems of nectarful and nectarless individuals in a natural population of *Prosopis glandulosa* var. *torreyana.* We selected 10 individuals (5 per nectar morph) as potential female parents and randomly selected 40 seeds of different pods from each individual. The surrounding trees were fingerprinted as potential fathers of the selected seeds. We extracted DNA from the tissue of parents and seedlings and all samples were subject to PCR with intsersimple sequence repeats (ISSR) primers that yielded high polimorphism that could be used to identify potential parents. The analysis of paternity was determined using a maximum likelihood approach. We suggest a possible mechanism by which the dimorphic system of nectar production is maintained.

Introduction

Fitness of hermaphrodite plant individuals comes from two routes: male and female functions (Richards, 1997). The female component mainly contemplates the selection of adequate pollen for fertilization and the production of seeds, and related constituents for dispersal (mainly fruit production). The male counterpart consists of the production of pollen and the successful fertilization of ovules of the same genet (autogamy and geitonogamy) or different genets (xenogamy). In natural environments and under experimental treatments, female components are relatively easy to quantify as the production of seeds gives a rough estimate of female fitness. On the other hand, the male component is harder to follow as pollen production is not always a good estimate of male function, while pollen removal is a much better estimate (Ashman, 1998). The importance of studying male function is clear as this component has been considered a major force in the evolution of floral display of some species (Bell, 1985; Bertin, 1988), and is a major evolutionary force shaping genetic diversity within and among populations (Levin & Kerster, 1974). Most theoretical and empirical studies suggest an important male component in the evolution of floral display but only under the assumption of low variability between fruit and pollen quality (Bertin, 1988). Many studies rely on pollen production and some estimates of pollen flow through fluorescent dyes and pollen carryover but these studies are often plagued by assumptions that are not always met (Handel, 1983; Campbell, 1991). However, in some cases, pollen removal has correlated with siring success (Ashman, 1998). Even though one of the most promising approaches to quantitatively assign pollen flow is through paternity assignment (Adams *et al.*, 1992), relatively few studies have used this approach mainly because of two reasons. (1) The theoretical background needed for these studies was developed in the early 1970's, but the molecular techniques needed to assign paternity were limited in the amount of variation that could be obtained. Until recently paternity assignment has had two main developmental routes, paternity exclusion analysis and a maximum likelihood approach (Adams *et al.*, 1992; Milligan & McMurry, 1993). Unfortunately neither approach yields optimum results, the former can only be used in small isolated or controlled populations and only sometimes may this approach be useful (Chakraborty *et al.*, 1988) while the latter may not always assign the correct parentage to some seeds or when the probability of parentage is the same between two individuals the sampled offspring is discarded. In addition, the likelihood approach biases paternity towards homozygotes (Devlin *et al.*, 1988). However, the fractional paternity approach can solve the problem of bias towards homozygotes by assigning paternity fractionally to all nonexcludable males, the fraction being the proportional contribution in the transition probability function (Devlin *et al.*, 1988). (2) In addition, to accurately establish paternity, the studies often require large amounts of information that increase sample sizes dramatically. This has caused studies to be limited by the number of individuals in the population and have often been reduced to laboratory and controlled conditions. With the advent of molecular techniques, the analysis of a large number of variable markers is possible, and the theoretical tools are also well developed for a large number of marker types (Luikart & England, 1999; Lewis & Snow, 1992), that can even include male characters in the analysis (Smouse *et al.*, 1999). Even after the development of an increasing numbers of markers that can be obtained relatively quickly, natural populations are usually difficult to follow, especially as a large proportion (> 60%) of gene flow occurs from individuals outside the studied population (Streiff *et al.*, 1999; Dow & Ashley, 1996; Krauss, 1999), even though in some cases, paternity can be assigned with higher efficiency (Krauss, 1999).

The honey mesquite is a perennial tree found in the the arid environments of the Southwestern USA and in many parts of northern Mexico (Rzedowski, 1988). This species is of particular interest for paternity analysis because of two main observations: (1) nectar production seems to be determined genetically, affecting the number and sex of visiting bee species (Golubov *et al.*, 1999) and (2) the proportion of nectarful to nectarless individuals is not different from 1 (López-Portillo *et al.*, 1993). Given the fact that the dimorphism of nectar production causes a differential behavior of visitors and the condition does not change from year to year, pollen flow within the population of the honey mesquite will likely be experiencing differential pollen flow. Previous studies have shown an increase in pollen production in nectarless individuals and an increase in seeds in the nectarful individuals. In addition, nectarful individuals receive a larger amount of pollen grains (see chapter 1, this thesis). This evidence suggests that nectar production is increasing female function, not expected under Batemans principle. The purpose of this manuscript is to determine the consequences of nectar production on pollen flow within and among nectarful and nectarless individuals under natural conditions. We wanted to answer the following questions: 1) What is the relative contribution of necatrful and nectarless individuas to the pollen pool, 2) what proportion of seeds is sired by each nectar morph and 3) how many parents are responsible for siring all the seeds within a pod.

Methods

Pollen flow Individuals within the Mapimí Biosphere reserve (MBR) were tagged and nectar condition established with 2 μl micropippetes. Leaf tissue of all reproductive individuals in a 1 ha plot of desert scrubland was collected. Of all individuals, we selected 10 individuals to function as pollen receptors (potential mothers). The potential parents that were relatively isolated were selected in order to reduce the number of parents that had to be sampled for assigning paternity. All reproductive individuals within a 15 meter radius of the potential mother were sampled (Figure 1). Pods of the selected maternal individuals were collected and a single seed per pod was extracted ($N = 40$ seeds per tree) to avoid cosanguineous progeny and a possible bias towards a single parent.

Siring success. To determine the number of parents within a pod, ten randomly selected pods were collected from five nectarful and five nectarless individuals. All the seeds withiin the pod were extracted and seed position within the pod as well as each individual seed weight were recorded. Differences between nectar morphs and individuals in seed traits were analyzed by ANOVA, having nectar morph and individuals as factors and the specific seed trait as the response variable. To determine the number of parents, we partially followed the procedure descibed by Ellstrand (1983). Briefly, the maternal genotype is scored and the genotypes of each offspring within each fruit is compared to the maternal genotype. Those banding patterns that differ from the maternal genotype are therefore the paternal contribution. Scoring and comparing between offspring will also indicate the number of parents that were involved.

DNA extraction and PCR methods Seeds were cleaned with sterile water and a dilute chlorine solution and germinated in petri dishes on 1% bacteriological agar. Seedlings were collected and stored at -70 C until used. Adult plant tissue was collected in the field and dried with silica gel.

DNA of both adults and seedlings was extracted with a 2X CTAB protocol (Milligan, 1998). Samples were then subject to PCR with one of 8 ISSR primers under the following conditions: 1.5 min @ 92°C, 35 cycles of 40' @ 94 °C, 45' @ 44 °C and 1.30 @ 72 °C, followed by 45' @ 94 °C, and 5min @ 72 °C. The following ISSR (intersequence repeats) primers were used (note that some are degenerate Wolfe & Liston, 1998): (CT)8–TG, (CT)8–RG, (CA)6–RY, (GT)6–RG, (GT)6-AY, (GT)6–YR, (CA)6–RG and CAA(GA)5 after PCR optimization. PCR products were then run on 7% Acrylamide–bisacrylamide gels and silver stained Dean & Milligan (1998). Gels were scanned and bands were analyzed using DNA/GUI version 2.0. Individuals were identified by the presence/absence of banding patterns due to the dominant nature of these markers. The resulting data was then used to infer the most likely parents using a maximum likelihood approach (Milligan & McMurry, 1993). We used ISSR primers as they have proven to be useful in genetic studies, especially in detecting clonal diversity and fingerprinting closely related individuals (Wolfe & Liston, 1998; Esselman *et al.*, 1999; Zietkiewicz *et al.*, 1994; Nagaoka & Ogihara, 1997). ISSR bands were scored as present (1) or absent (0) for each DNA sample.

Results

The amount of seeds between pods differed greatly (range = xx – xx). Seed weights did not differ between positions within a pod nor between nectar morphs but significant differences were found between individuals (F=kk) All the primers that were used in the analysis resulted in multiple banding patterns, however optimum resolution was obtained only through an optimization procedure of the buffer solution for PCR. Most primers yielded more than 5 bands that could be easily scored (Figure 2). The selected primers generated bands ranging in size from 220 to 1400 bp.

Discussion

Few studies on pollen flow have been done on natural populations due to the difficulty of assigning paternity. Some studies have been successful in assigning paternity but populations can be considered controlled due to the low frequency of individuals in the population (Kaufman *et al.*, 1998). Others have used specific phenotypic of genetic markers that characterize individuals. We would expect an asymmetric contribution of pollen flow biased towards nectarless individuals, that would be increasing male function, while nectarful individuals produce more fruits. In addition, the number and quality of visitation differes greatly within years and between years (Golubov *et al.*, 2001), which would affect the quality of seeds. Few studies have assessed multiple paternity within fruits, even though multiple paternity has become a widespread issue in breeding systems of animal species. Experimental studies have suggested that increasing the number of pollen donors often increase the seed set of individual fruits (Janzen *et al.*, 1980). Furthermore, multiple paternity is well documented from those studies of pollen flow (Levin, 1981). But relatively few studies have quantitatively described multiple paternity in wild populations. Theoretical predictions vary as to the extent and benefits of multiple paternity in seed plants. On one hand, sexual selection would favour those maternal plants bearing multiple–sired progeny (Janzen, 1977), on the other, pollen competition in multiseeded fruits would strongly favour single–sired fruit (Levin, 1975). ISSR primers have proven to be excellent markers to identify closely related individuals (such as clonal organisms).

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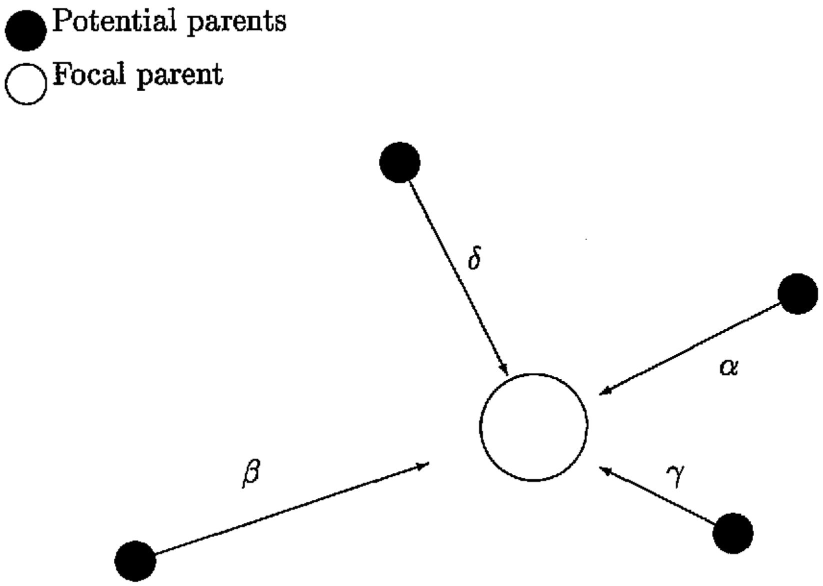
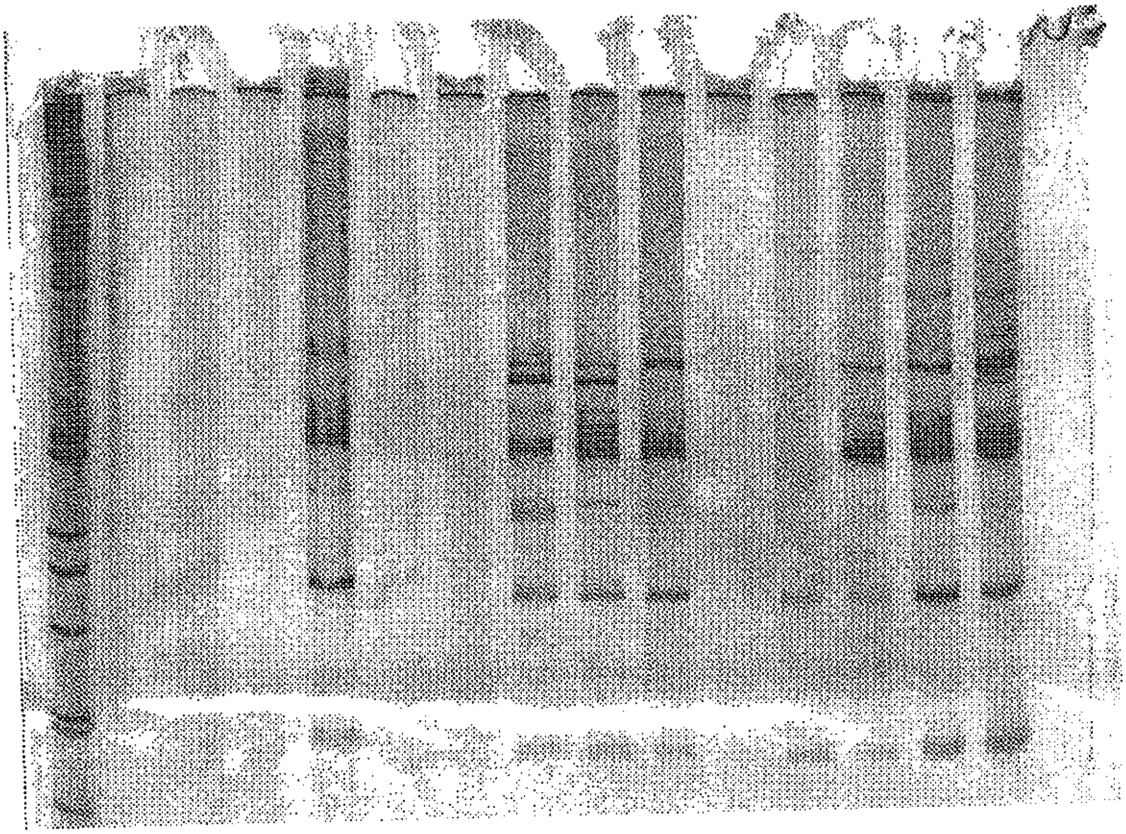
Figure Legends

Figure 1. Representation of sampling procedures. Greek letters indicate the amount of pollen flow between the potential parents and the focal parent.

Figure 2. Acrylamide/bis–acrylamide gel silver stained. The primer used was CG6nn.


● Potential parents
○ Focal parent
δ
α
β
γ



PAGINACIÓN DESCONTINUA

Apéndice 2

Demography of the invasive woody perennial *Prosopis glandulosa* (Honey mesquite)

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Demography of the invasive woody perennial *Prosopis glandulosa* (honey mesquite)

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Summary

1 To assess the effect of annual environmental variability on the long-term population dynamics of the invasive woody perennial *Prosopis glandulosa* var. *torreyana* (honey mesquite), we employed elasticity analyses of annual, mean and periodic matrix models. Growth, survival and reproduction were recorded for 1306 individuals in a 1-ha plot over a 4-year period. The volume of each individual was estimated, and transition matrices with nine size classes were constructed. Standard matrix analysis was performed, and the relative importance of individual life-cycle components to changes in the finite rate of population increase (λ) was determined.

2 Periodic matrix analysis projected a 29% annual increase in population size ($\lambda = 1.29$), while annual projection λ-values varied between 0.99 and 1.44. For both methods, elasticity of seedling recruitment was always very low in all 4 years, and the highest elasticities were generally associated with permanence in the same size class.

3 Periodic and annual projections predicted similar elasticity patterns, with the relative contribution to a change in λ of different demographic processes changing between 'good' and 'bad' years. However, annual matrices identified two bad years, with fecundity and growth elasticity decreasing relative to survival, whereas periodic analysis identified only one such year, and elasticity changes were seen only in fecundity and survival.

Key-words: demographic parameters, demographic triangle, demography, elasticity, invasive species, life history, mesquite, periodic matrices, *Prosopis glandulosa*, sensitivity

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Introduction

Projection of demographic data has provided a tool by which the dynamics of populations can be explored in detail (Piñero *et al.* 1984; van Groenendael & Slim 1988; Svensson *et al.* 1993; Horvitz & Schemske 1995; Caswell 1997). The benefits include allowing the estimation of extinction probabilities, the prediction of the invasiveness of both native and non-native species, and the study of life-history evolution. Sensitivity (Caswell 1978, 1989) and elasticity analyses (de Kroon *et al.* 1986) allow the contribution of different demographic processes to be assessed, and this has improved our understanding of population dynamics as well as allowing comparisons to be made across taxa and populations (Silvertown *et al.* 1993, 1996; Franco & Silvertown 1996).

Projections of population growth must consider the temporal variation of demographic parameters (Tuljapurkar 1985; Nakaoka 1996). For long-lived perennials, the ways in which the effects of such variation over their lifetime influence their dynamics are not readily approximated by short-term demographic analyses (Cain & Damman 1997; Damman & Cain 1998). Environmental heterogeneity may interact with a sequence of intrinsic biological processes that only take place over long periods of time, and it is therefore necessary to assess popula-

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tion dynamics of perennial species over long time periods. This is especially true for species inhabiting extreme environmental conditions where specific demographic processes, such as growth and reproduction, may be limited to occasional 'opportunity windows'(*sensu* Eriksson 1989). Several models have accounted for this variation by including a stochastic environmental component (Tuljapurkar 1985, 1989; Huenneke & Marks 1987; van Groenendael & Slim 1988; Nakaoka 1996; Damman & Cain 1998). We used periodic matrix models (a subset of stochastic models in which the assumption of time-invariance is relaxed; Skellam 1966) and their associated sensitivity and elasticity analyses (Caswell 1989; Caswell & Trevisan 1994). We assumed that the matrices reflect the range of environments encountered and that population growth can be described in a hypothetical habitat that cycles among the environments observed (Caswell & Trevisan 1994). We used a demographic study of *Prosopis glandulosa* var. *torreyana* over a period of 4 years to determine (i) how elasticity analysis of periodic matrix models provides information on the impact of different demographic processes at different stages of the environmental cycle; and (ii) how the use of this method in conjunction with annual and mean matrix models improves our understanding of the natural dynamics of populations.

Materials and methods

Prosopis glandulosa var. *torreyana* (Benson) Johnston (honey mesquite), a woody perennial, has a wide distribution in the south-western United States and northern Mexico (Burkart 1976; Rzedowski 1988). Mesquites are a common, often dominant, species of arid and semi-arid ecosystems and typically bloom in spring before the main rainy season (Simpson & Solbrig 1977). They are considered to be aggressive invaders (Glendening 1952), although prior to livestock introductions they had been confined to mesic drainages and upland slopes and have only recently expanded into grasslands (Polley *et al.* 1994). A population of honey mesquite in a 1-ha plot of desert scrubland surrounding a water catchment in the southern Chihuahuan desert, Mexico (26°29′ to 26°52′ N and 103°32′ to 103°58′ W; 264 mm mean annual rainfall; 20.8 °C mean temperature; Montaña 1990), was censused annually from March 1994 to March 1998. Rainfall was below average throughout the study period (138.5 mm, 198.4 mm, 234.7 mm and 210.4 mm, in 1994–97, respectively; data from Mapimi Biosphere Reserve climatic station). In March 1994 the 1-ha plot contained 1306 individuals, of which 418 were reproductive adults. Because of its relatively round crown, the size of each mesquite can be estimated as the volume of a sphere the radius of which is half the average of three plant measurements: height and two orthogonal horizontal widths. For each reproductive individual we calculated the yearly fruit set by averaging the number of pods recorded on three tagged branches of known volume per plant and extrapolating to the total volume of the plant. Fecundity per size class j at time t was calculated as the total number of seedlings recruited between times t and $t + 1$, weighted by the proportional contribution of an average individual in that size class to the total fruit set at time t.

Use of Moloney's (1986) algorithm suggested that the population should be divided into nine size classes. Seedlings and small plants (volume = $vol \leq 0.8\,\mathrm{m}^3$) were considered to be size 0, with size 1 representing volumes (in m^3) $0.8 < vol \leq 1.7$; size 2, $1.7 < vol \leq 2.2$; size 3, $2.2 < vol \leq 3.7$; size 4, $3.7 < vol \leq 4.7$; size 5, $4.7 < vol \leq 5.4$; size 6, $5.4 < vol \leq 6.5$; size 7, $6.5 < vol \leq 8$; and size 8, $vol > 8$. With this classification we constructed four annual transition matrices to derive three kinds of models. First, the four annual matrices *per se*. These contained the transition probabilities and contributions of an average individual at each of the different stages of the life cycle for each of the four yearly intervals of study ($\mathbf{A} = \{a_{ij}\}$, where $i, j = 0, 1, \ldots, 8$; Caswell 1989) and were used to describe the population growth in individual years, which could be classed as 'favourable' ($\lambda > 1$) or 'unfavourable' ($\lambda < 1$). Secondly, the mean matrix was obtained by averaging each entry in the four annual transition matrices, and thirdly, a periodic matrix was produced by multiplying all four annual matrices sequentially (Caswell 1989; Caswell & Trevisan 1994).

In the deterministic analyses (for annual and mean matrices), population growth was projected by multiplying each annual matrix (A), or the mean matrix, by a column vector ($\mathbf{n}$) that incorporated the number of individuals in each of the nine size classes. Thus $\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$ or, assuming matrix A remains constant for a length of time t, $\mathbf{n}_t = \mathbf{A}^t\mathbf{n}_0$, where $\mathbf{n}_0$ is the initial population. The properties of this model are well known (Caswell 1989) and they include the facts that the dominant eigenvalue of the matrix is equivalent to the finite rate of population increase (λ), i.e. $\mathbf{n}_{t+1} = \lambda\mathbf{n}_t$, and that there exist a right eigenvector and a left eigenvector associated with λ, which describe the stable size distribution ($\mathbf{w}$) and the reproductive value distribution ($\mathbf{v}$), respectively. We then calculated the sensitivity of λ to small changes in each matrix element, a_{ij} ($s_{ij} = \partial\lambda/\partial a_{ij} = v_i\,w_j/\mathbf{vw}$, where v_i is the ith element in the reproductive value eigenvector $\mathbf{v}$, w_j is the jth element in the stable size distribution vector $\mathbf{w}$, and $\mathbf{vw}$ is the product of the two vectors, a scalar; Caswell 1989). We also calculated the elasticity matrix ($e_{ij} = s_{ij}\,(a_{ij}/\lambda)$; de Kroon *et al.* 1986) the elements of which are the proportional change in λ that results from a proportional change in each a_{ij}.

In the periodic analysis, product transition matrices could be used to represent the effect of annual demographic variation assuming a cyclic environment. The dynamics of the population over a cycle can be described by the periodic matrix product (Caswell & Trevisan 1994):

$$\mathbf{n}_{(t\ +\ m)} = [\mathbf{B}^{(m)}\,\mathbf{B}^{(m-1)}\ \ldots\ \mathbf{B}^{(h)}]\,\mathbf{n}_{(t)}$$

$$\mathbf{n}_{(t\ +\ m)} = \mathbf{A}^{(h)}\,\mathbf{n}_{(t)}$$

where each matrix **B** corresponds to one phase of the cycle. The cycle has a duration of m time units and $\mathbf{A}^{(h)}$ is the matrix product that projects the population through the whole cycle, starting at phase h. In our case, each phase lasted 1 year and we assumed the cycle had a duration of 4 years ($m = 4$), the duration of the study. The product matrix that projects the population through the whole cycle, starting in phase 1 (1994–95), is therefore:

$$\mathbf{n}_{(t\ +\ 4)} = [\mathbf{B}^{(4)}\,\mathbf{B}^{(3)}\,\mathbf{B}^{(2)}\,\mathbf{B}^{(1)}]\,\mathbf{n}_{(t)}$$

$$\mathbf{n}_{(t\ +\ 4)} = \mathbf{A}^{(1)}\,\mathbf{n}_{(t)}$$

with $\mathbf{A}^{(1)}$ indicating that the projection starts in phase 1, and $\mathbf{B}^{(1)}$ to $\mathbf{B}^{(4)}$ indicating the four annual projections (1 = 1994–95, 2 = 1995–96, 3 = 1996–97, and 4 = 1997–98). The long-term growth rate over the cycle is given by the dominant root of the product of the periodic matrices and can be written as λ^h. Due to the cyclic arrangement λ^h is the same for all hs and its value can be represented simply as λ. This value can be used to give an annual λ by either taking its m-root or by converting it first to r ($r = \ln \lambda/m$, where m scales it to the time step considered, in our case 1 year) and then taking its antilogarithm.

Our study comprised 4 years (we had four annual $\mathbf{B}^{(h)}$ transition matrices) and the elasticity values of each phase of the cycle could therefore be estimated by calculating four periodic $\mathbf{A}^{(h)}$ matrices, and their corresponding four sensitivity matrices ($\mathbf{S}_{\mathbf{A}}^{(h)}$), for cycles 'beginning' in years 1994–97 (i.e. $h = 1, 2, 3, 4$). The sensitivity of λ to changes in each entry of one of the matrices in the cycle ($\mathbf{B}^{(h)}$) was calculated as (Caswell & Trevisan 1994):

$$\mathbf{S}_{\mathbf{B}}^{(h)} = [\mathbf{B}^{(h-1)}\quad \mathbf{B}^{(h-2)}\quad \ldots\quad \mathbf{B}^{(1)}\quad \mathbf{B}^{(m)}\quad \mathbf{B}^{(m-1)}\quad \ldots\ \mathbf{B}^{(h+1)}]^T\mathbf{S}_{\mathbf{A}}^{(h)}$$

(notice the formula excludes $\mathbf{B}^{(h)}$, and T is the transpose of the matrix product). For example, to calculate the sensitivity of λ to changes in each element of $\mathbf{B}^{(3)}$, cyclically permute the individual matrices $\mathbf{B}^{(2)}$ to $\mathbf{B}^{(1)}$. When the latter appears at the right-hand end of the product matrix continue with $\mathbf{B}^{(m)}$ (in this case $m = 4$) and carry on until you reach $\mathbf{B}^{(h\ +\ 1)}$ (i.e. in this case stop at $\mathbf{B}^{(4)}$ because $m = h + 1$). That is:

$$\mathbf{S}_{\mathbf{B}}^{(3)} = \mathbf{B}^{(2)}\mathbf{B}^{(1)}\,\mathbf{B}^{(4)}]^T\mathbf{S}_{\mathbf{A}}^{(3)}$$

The corresponding elasticity values were finally calculated as (Caswell & Trevisan 1994):

$$e_{ij}^{(h)} = (b_{ij}^{(h)}/\lambda)s_{ij}^{(h)}$$

where $b_{ij}^{(h)}$ is each entry of matrix $\mathbf{B}^{(h)}$. All matrix analyses were performed with MATLAB©(The MathWorks 1995).

Because there was no reason to suspect our study period repeated itself indefinitely, we relaxed the assumption of a strict sequence of matrices and simulated all possible permutations of the four matrices in the cycle (${}_n\mathrm{P}_n = n!/n = (n - 1)!$; Zar 1996). The projections that resulted from this process generated the distribution of possible outcomes given our 4-year data set and provided a confidence interval for the rate of population growth. The elasticities of different demographic processes for each product matrix were calculated and their confidence intervals were obtained with the percentile method (Meyer *et al.* 1986; Caswell 1989). To test the assumption of the first-order Markov process of the matrix models, we fitted a log-linear model (Bierzychudek 1982; Caswell 1989; Horvitz & Schemske 1995) using GLIM (Royal Statistical Society 1993). The models tested whether the transition probabilities during the time interval (t to $t + 1$) depend only on the state at the beginning of the time interval and not on any other point in time ($t - 1$, $t - 2$, etc., i.e. serial correlation; Tuljapurkar 1997).

Matrix elements were classified into four demographic processes: (i) positive growth, or simply growth (lower diagonals); (ii) permanence in the same size class, or stasis (main diagonal); (iii) decrease in size, or retrogression (upper diagonals except elements on the first row); and (iv) fecundity (first row, except the first element, which belongs to the main diagonal). From the resulting elasticity matrices (annual, mean and periodic), we summed elasticities by size class and by each of these four demographic processes (Gotelli 1991; Silvertown *et al.* 1993). Finally, we investigated the variation in the relative contribution of different demographic processes to relative changes in λ according to the demographic interpretation of Grime's triangle proposed by Silvertown *et al.* (1992). This was done by adding the elements of the main diagonal (stasis) to those of the upper diagonals (retrogression) to give a class called survival (L), and taking the values on the first row (but excluding stasis in the seedling category) into fecundity (F), and all subdiagonal elements into growth (G) (Silvertown *et al.* 1993; Franco & Silvertown 1996).

Table 1 Values of the finite rate of increase (λ) calculated for *Prosopis glandulosa* using three different methods of matrix projection. The demographic information was obtained from a 1-ha permanent plot of scrubland in the southern Chihuahuan desert

Year	λ	Total annual precipitation (mm)*
1994–95†	1.13	138.5
1995–96†	0.99	198.4
1996–97†	1.44	234.7
1997–98†	1.39	210.4
1994–98‡	1.29	195.5¶
1994–98§	1.29 (± 0.004)	

*January–December of the year beginning the interval.
†Annual transition matrix.
‡Mean of four annual transition matrices.
§Periodic matrix product. Value in parentheses shows the 95% confidence interval.
¶Mean annual precipitation during the study period.

Results

Each annual matrix provided an independent prediction of demographic fitness (λ) for the population, with values for 3 out of 4 years indicating population increase ($\lambda > 1$). Both mean and periodic matrices indicated a 29% annual population increase overall (Table 1). Elasticity values for all types of matrix projections showed that stasis (main diagonal) and growth (lower diagonals) contributed proportionately the most to population growth throughout the study (Table 2). Stasis was the most important demographic process in the mean matrix analysis (elasticity = 0.47), followed by growth, fecundity and retrogression (Table 2a). In the annual matrices for 1994–95 and 1995–96 (Table 2a), when λ was close to 1 (Table 1), stasis represented close to 60% of the total elasticity, and elasticities for fecundity were very low ($\ll 0.01$). When λ predicted a significant yearly population increase (> 35% in 1996–97 and 1997–98; Table 1), growth contributed more than 40% to the total elasticities and the elasticity of fecundity was far more important than in the previous 2 years (Table 2a). When total elasticities were analysed for each size class, using annual projections, the 1995–96 interval gave very different results to all other annual time intervals (Fig. 1a). The class with the highest contribution to a change in λ in this period was class 7, while in the other years the highest contributions were given by seedlings and class 3, and class 7 made the lowest contribution to changes in λ.

The periodic matrix analyses could be decomposed into four annual periods that each corresponded to one of the annual transition matrices. Elasticities of stasis were consistently higher than those for growth in all four years. Elasticity of fecundity was lower for 1995–96 than for any other year (Table 2b). The summed elasticity values per size class gave different results to those given by the annual projections. Periodic matrix analysis predicted relatively fixed elasticities in all years for all size classes, and the most important stage in all but one year was the seedling class (Fig. 1b). Finally, the log-linear analyses showed that successive matrices in the sequence were non-independent ($\chi^2 = 1948$, d.f. = 64).

Discussion

By incorporating variation in demographic processes through several growing seasons, periodic matrix models provide a picture of mesquite population dynamics in changing environments that cannot readily be approximated by the average-year approach. This is because periodic matrix models allow investigation of the effect that differences in the order of occurrence of demographic events may have on the dynamics of the population. In the case of *Prosopis*, although the projected λ from individual annual matrices showed little variation (CV = 14%), such matrices could predict either

Table 2 (a) Elasticity of annual and mean projection matrices of *Prosopis glandulosa*; and (b) elasticity (± 95% confidence interval) of periodic projection matrices of *P. glandulosa* in the southern Chihuahuan Desert

Demographic process	1994–95	1995–96	1996–97	1997–98	Mean matrix 1994–98
(a) Elasticity of annual and mean projection matrices					
Fecundity	9.22×10^{-05}	1.01×10^{-06}	0.12	0.13	0.07
Stasis	0.62	0.58	0.41	0.40	0.47
Growth	0.26	0.25	0.44	0.43	0.39
Retrogression	0.12	0.17	0.03	0.04	0.07
(b) Elasticity (± 95% confidence interval) of periodic projection matrices					
Fecundity	0.10 (± 0.02)	1.5×10^{-4} ($\pm 4 \times 10^{-5}$)	0.09 (± 0.03)	0.09 (± 0.03)	
Stasis	0.48 (± 0.04)	0.48 (± 0.04)	0.47 (± 0.04)	0.47 (± 0.03)	
Growth	0.37 (± 0.03)	0.37 (± 0.03)	0.39 (± 0.03)	0.39 (± 0.02)	
Retrogression	0.05 (± 0.01)	0.15 (± 0.03)	0.05 (± 0.01)	0.05 (± 0.01)	

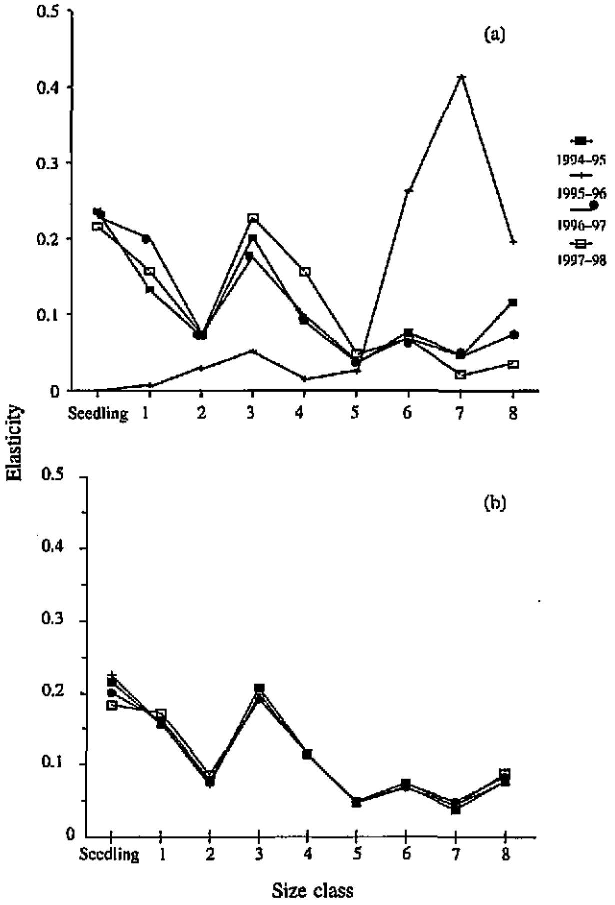

Fig. 1 Variation in elasticity among life-cycle stages of *Prosopis glandulosa* var. *torreyana* in the southern Chihuahuan desert, as calculated from (a) projection of annual matrices, and (b) projection of the periodic matrix model. The seedling class (class 0) includes seedlings and small plants (volume = $vol \leq 0.8\,m^3$), and the remaining eight classes are defined by the following limits (in m^3): (1) $0.8 < vol \leq 1.7$; (2) $1.7 < vol \leq 2.2$; (3) $2.2 < vol \leq 3.7$; (4) $3.7 < vol \leq 4.7$; (5) $4.7 < vol \leq 5.4$; (6) $5.4 < vol \leq 6.5$; (7) $6.5 < vol \leq 8$; (8) $vol > 8$.

growth or decline depending on the year studied. Although the mean matrix, as well as the periodic matrix, can be used to estimate the annual population growth rate over the study period (Huenneke & Marks 1987; McFadden 1991), the average-year approach misses the correct estimation of the influence that different years and processes have on the population's long-term growth (Caswell & Trevisan 1994). This is especially important when specific demographic processes are sensitive to between-year environmental variation or when processes respond in opposite directions to environmental change (M. del C. Mandujano *et al.*, unpublished data). Thus, periodic elasticity analysis provides a means of evaluating the varying influence that different demographic processes have over time periods longer than 1 year. Furthermore, sensitivity and elasticity of periodic matrices can measure the influence of temporally correlated demographic events on population growth. Not surprisingly, such analyses give different results to those obtained with discrete, independent annual matrices. In *P. glandulosa*, although both annual and periodic analyses indicated that the different demographic processes switched in importance from year to year, the detailed patterns predicted were rather different.

The mean, periodic, and three out of four annual projections predicted positive population growth, even though all years had below-average rainfall (Table 1). For annual matrices, the highest λ corresponded to the year with the highest precipitation, in which growth was found to be the most important demographic process (Table 2a). In a study of mesquite clustering from aerial photographs in southern Texas, Archer *et al.* (1988) also found an apparent correlation between growth rate of clusters and precipitation over two time periods longer than 1 year (1941–60 and 1960–83). Because current year growth in *P. glandulosa* depends to a large extent on the previous year's rain, the correlation with precipitation is in reality likely to be more complicated. Annual matrices project the population close to equilibrium ($\lambda = 0.99$) in the period following the driest year (1995–96), but project population growth in all other time intervals, including the driest (1994–95). Our analyses suggest demographic factors that may enable woody species such as mesquites to be aggressive invaders of grasslands (as considered by Scholes & Archer 1997). First, annual matrices show that this mesquite population could grow even in drier-than-average years, and this characteristic will be especially important in variable habitats such as those found in arid environments. Secondly, elasticity analysis of both annual and periodic matrices shows that, overall, stasis is the predominant factor (contribution towards changes in λ > 40%) followed by growth (> 25%). This pattern is typically found in shrubs inhabiting frequently perturbed habitats (Silvertown *et al.* 1993; Franco & Silvertown 1996) and can be interpreted as a measure of adaptability to changing interannual environmental conditions in species where, once established, death of individuals is rare. Thirdly, however, while annual matrices indicate that growth and fecundity become increasingly important (with stasis and retrogression elasticities decreasing) as rainfall increases, the changes predicted by the elasticity analysis of periodic matrices are more subtle. In these analyses, the elasticity values are rather constant in 3 out of 4 years and only in 1 year (1995–96, the one following the driest) do they show substantial differences (i.e. higher than the 95% confidence limits) in the elasticity values of fecundity (decreasing) and retrogression (increasing). This is in agreement with mesquites performing rather poorly after particularly bad years.

Although in annual projections there is an apparent correlation between fecundity and growth, this disappears in periodic analysis, as might be expected if several demographic processes are involved. While annual matrices assume independence among demographic events over time, periodic matrices take into account the sequence in which these events occur. Thus, while the elasticity of annual matrices segregates into two distinct groups (94–95 and 95–96, vs. 96–97 and 97–98; Table 2), which can be seen clearly when plotted on the demographic triangle (after Silvertown *et al.* 1992, 1993) (Fig. 2), values for periodic matrices are more clustered and all but one fall close to the position of the average matrix (Fig. 2). This difference may have important consequences for the way we perceive the life history of mesquites. Following the classification introduced by Silvertown *et al.* (1993), annual matrices would suggest that mesquites 'switch' strategies from one characteristic of shrubs in good years to one more

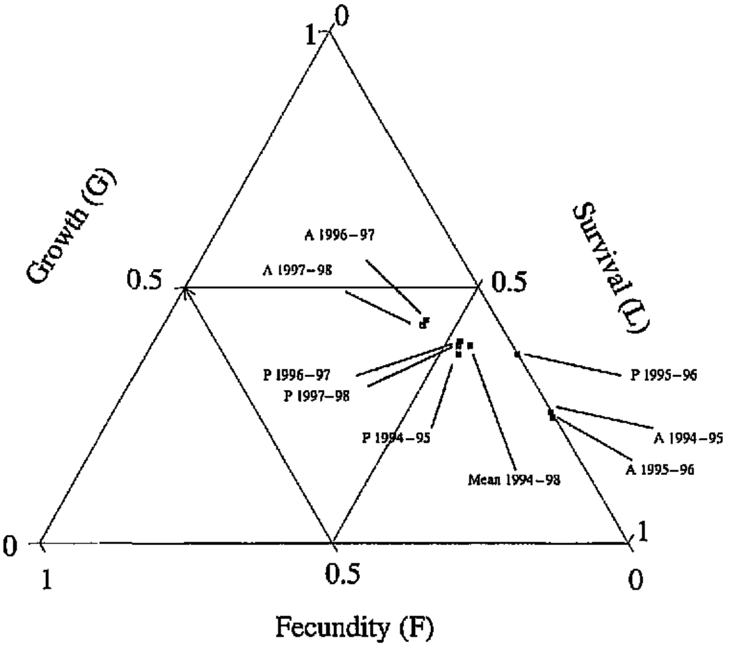

Fig. 2 The position in the 'demographic triangle' of the elasticities of *Prosopis glandulosa* var. *torreyana* in the southern Chihuahuan desert, as calculated from the projection of four annual matrices (A), the average of these four matrices (Mean) and the projections of a periodic matrix model (P).

typical of longer-living trees in bad years (compare Fig. 2 with fig. 1d in Franco & Silvertown 1996). The periodic analyses, on the other hand, point out the response of mesquites to extremely poor environmental conditions within their invasive habit (Fig. 2).

In conclusion, while periodic elasticity analysis allows investigation of the way that different demographic parameters affect the long-term dynamics of the mesquite population, the analysis of annual matrices for perennial organisms can at best give a number of snapshots that are difficult to interpret in terms of the long-term dynamic picture. The use of annual and periodic matrix models for perennial species in changing environments can indeed produce contradicting results. For example, the size class that contributed most towards λ in our study changed between annual, but not between periodic, projections (for a similar pattern see Lesica & Shelly 1995). By incorporating at least some of the inter-annual demographic variation, periodic matrix models provide a more realistic and interpretable picture of population dynamics, thus adding to the explanatory power of the matrix method.

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Apéndice 3

The paradox of mesquites (*Prosopis* spp.): invading nightmare or biodiversity enhancers

PAGINACIÓN DESCONTINUA

The paradox of mesquites (Prosopis spp.): Invading species or biodiversity enhancers?

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Abstract

Arid and semi-arid lands cover a significant portion of terrestrial surface, they have a large species diversity, and are also heavily used by human populations (i.e. livestock grazing). In particular, semi-arid grasslands and savannas of North America have recently undergone considerable change in structure and species composition often associated to losses in species diversity. The expansion of woody species towards grasslands, with a concomitant decrease in land value towards livestock grazing has caused many "brush control" methods that often lead to unsuccessful long term results. In this paper we highlight the importance and ecological roles of the genus *Prosopis* (mesquite). Toward this end, we compile information on species that are associated with *Prosopis* spp. and propose its conservation as a means of maintaining species diversity. In addition, we point out the importance of mesquites in the Nitrogen and

Carbon balance of arid and semi-arid environments. We conclude that the conservation of mesquites in these environments should be considered, especially in areas depleted through conversion. Adequate management should be applied in areas of livestock grazing and alternative uses should be considered (i.e. Integrated Brush Management Systems, IBMS). This would provide a compromise between livestock productivity on the one hand, and conservation of species diversity and maintenance of ecosystem structure on the other.

Palabras Claves /Arid land biodiversity / mesquites / range management / wildlife habitat / woody-plant increase /

Arid and semi-arid environments contain relatively high species diversity (Redford *et al.*, 1990) that decreases with increasing aridity (Huenneke and Noble, 1996). For example, the richest apifauna in the world is along the Mexico-USA border, with close to 900 species of solitary bees (Ayala *et al.*, 1993). Mexican xerophilous scrub and grasslands contain *ca.* 6,000 plant species (20% of total Mexican flora Rzedowski, 1988) and Mexican desert scrub alone contains *ca.* 206 bird species (Escalante *et al.*, 1979). Biotic and abiotic resources in these environments are scarce and patchily distributed during most of the year, largely depending on highly variable rainy periods (Noy-Meir, 1973). Spatial and temporal variation in rainfall, coupled with high average temperatures and differing soil textures, give rise to high environmental heterogeneity which influences species diversity (Pianka, 1967; Rosenzweig and Winakur, 1969). Since conditions are highly variable, net primary productivities are low (6,000-40,000 kg ha^{-1}) and the distribution and abundance of higher trophic levels are limited (Noy-Meir, 1973; Huenneke and Noble, 1996). Because of this relatively high species diversity, there is increasing concern on the conversion of the arid environments that, for instance, may lead to desertification with a consequent loss of species diversity (Huenneke and Noble, 1996).

In particular, semi-arid grasslands and savannas of North America have recently undergone considerable change in structure and species composition (Buffington and Herbel, 1965). Especially, mesquite (*Prosopis* spp.) and juniper (*Juniperus occidentalis* Hook.) increase into southwestern savannas have had consequences on rangeland management. As a result, a wide array of research into the ecological impacts and control of encroaching species is being done. The increasing expansion of invading species has been attributed to a set of factors that range from drought, fire suppression, livestock grazing, and elevated atmospheric CO_2 concentrations (Archer *et al.*, 1988). Habitat fragmentation and livestock grazing of arid environments have had high ecological costs, including disruption of ecosystem function, alteration of ecosystem structure and loss of species diversity (Aizen and Feinsinger, 1994a,b; Fleischner, 1994) but see (Brown and McDonald, 1995).Thus, we must assess the relative importance of species interactions in these environments in order to quantify the ecological costs of fragmentation and conversion in order to propose management ad conservation strategies. In this sense, we compile information on species that are associated with *Prosopis* spp. (mesquite) and point out its role in ecosystem functioning. We highlight the importance of mesquite for many species, and propose its conservation as a means of maintaining species diversity in arid environments.

Mesquite Biology

All species of mesquite (the genus *Prosopis*), comprising 10 species in North America (Rzedowski, 1988) and 28 species in South America (Burkhart, 1976), should be regarded as important ecologically for arid environments in the Americas. Mesquite are aggressive invaders (Glendening, 1952), due to the production of long-lived seeds that germinate in a wide range of edaphic conditions, rapid root growth and a high potential for N_2 fixation (Glendening, 1952; Polley *et al.*, 1994). However, mesquites have only recently expanded into grasslands from their characteristic mesic drainages and upland slopes, where they had been confined prior to livestock introductions during the Holocene (Polley *et al.*, 1994). Mesquites are common and often the dominant species of these arid and semiarid ecosystems, providing abundant resources at very specific times of the year (Simpson and Solbrig, 1977; Nilsen *et al.*, 1991). In South America and western USA, mesquites always bloom in spring before the main rainy season (Simpson and Solbrig, 1977). In the southern Chihuahuan desert, during a three year period with widely varying precipitation (1994-1996; 138, 198.4 and 204.3 mm total annual rainfall, respectively), peak flowering periods in *Prosopis glandulosa* var. *torreyana* differed by less than ten days (Golubov, unpub. data). The phenological constancy of *Prosopis* species is in part due to a variety of adaptations to avoid water stress (Nilsen *et al.*, 1983) which allow an escape from temporal and spatial unpredictability of rainfall. This buffers mesquites against environmental stochasticity, allowing them to grow and to reproduce in the driest seasons, providing resources for organisms that feed on their nectar, pollen, leaves, bark and fruits (Simpson *et al.*, 1977).

Prosopis **as a Resource for animal and plant populations.**

Mesquites are used by a large number of invertebrate and vertebrate species (Table 1) having specific mutualistic interactions, such as those with solitary bees (e.g. *Perdita* spp. Simpson *et al.*, 1977). In the southern Chihuahuan desert in March, *Prosopis glandulosa* and *Opuntia* spp. are the only dominant plants producing abundant flowers, pollen and nectar. While only 7 bee genera visit *Opuntia* spp. flowers (Mandujano *et al.*, 1996, mostly oligolectic bees), at least 20 genera visit *P. glandulosa* flowers (López-Portillo *et al.*, 1993; Golubov *et al.*, 1999). Bird diversity has been shown to be higher in a *Prosopis juliflora* scrubland than in oak forests in western Mexico (Corcuera and Butterfield, 1999) and over 70 bird species are associated with mesquite scrublands in Mexico (Escalante *et al.*, 1979). Few examples have addressed the change in avian communities after mesquite removal (Soutiere and Boulen, 1976; Reitzel, 1982; Smith *et al.*, 1996; Nolte and Fulbright, 1997), but they all showed higher species diversity when mesquites were present when compared to grassland with no mesquites present. Reptile diversity and abundance has also shown to be higher in mesquite scrublands than in grasslands (Germano and Hungerford, 1981). Furthermore, mesquites are known to be visited by at least 200 species of herbivorous invertebrates (Cates and Rhoades, 1977; Wisdom, 1991) and by over 150 species of solitary bees (Simpson *et al.*, 1977). The habitat structure provided by areas with mesquites has been shown to influence arthropod diversity, mainly by providing architectural diversity (Gardner *et al.*, 1995). In addition, mesquites have important and often overlooked associations with nematodes (Freckman and Virginia, 1989) and symbiotic bacteria (Jenkins *et al.*, 1987).

Besides the animals that feed directly or indirectly on mesquites, a diverse flora can be found growing beneath them, including many cacti and grasses (Cornejo-Oviedo *et al.*, 1992; Suzán *et al.*, 1994). Thus, mesquites, as other perennial species of arid and semi-arid environments, may function as potential nurse plants by passive facilitation, providing nutrients such as C and N, lower temperatures, higher humidity, and different microtopographies under their canopies (Tiedemann and Klemmedson, 1973; Steenbergh and Lowe, 1977; Fulbright *et al.*, 1995). All of the above mentioned characteristics are pivotal in successional processes from savannas to mesquite thorn woodlands (Archer *et al.*, 1988). Given the high amount of interactions associated with *Prosopis* species, mesquites become ecologically important, especially providing a large amount of resources for a large range of species.

Prosopis as a key element in Ecosystems

At an ecosystem level, mesquites have been shown to have high net primary productivities (3,650 kg h^{-1} Sharifi *et al.*, 1982) and, as other Leguminosae, are able to fix atmospheric nitrogen. This N fixation is by means of nodulating rhizobia, that improve soil fertility at different depths (Jenkins *et al.*, 1987) and increases microbial biodiversity. Large amounts of N (2,500 kg NO_3-N ha^{-1}) associated to litter decomposition outweighs denitrification processes under mesquite canopies (0.5 kg N ha^{-1} Virginia *et al.*, 1982, 1983). Given the scarcity of N in arid and semi-arid environments, the large amount of N fixed by *Prosopis* (45-150 kg N ha^{-1} yr^{-1}) makes it a large contributor to the N budget of these environments (Johnson and Mayeux, 1990). The large amount of N found in mesquite "fertility islands" would suggest increases in shrub species growth associated to them. Barnes and Archer (1996) did not find a significant effect of a *Prosopis glandulosa* Torr. overstory on physiological characteristics and growth of 7 associated shrub species. In contrast, Tiedemann and

Klemmedson (1973) showed that the Arizona cottontop (*Trichachne californica*) had 15 times greater N yield in mesquite soil although there was only a 3 fold difference in N between soils. Furthermore, there seems to exist some passive facilitation of *Prosopis* species towards other shrubs such as *Celtis* (Franco-Pizaña *et al.*, 1995). Apparently conditions for conversion of organic N to available forms are more favorable in soil under mesquite than in adjacent soil. Even compared to other leguminous shrubs of arid and semi-arid environments such as ironwood (*Olneya tesota*) N_2 fixation was higher under mesquite individuals (Shearer *et al.*, 1983).

In general, soil properties beneath mesquites have been shown to favor water infiltration, avoiding soil sealing after heavy rainfall (Virginia *et al.*, 1983) and their association with nematodes seems to be an important component of deep soil nutrient cycling (Freckman and Virginia, 1989). In addition, high annual litter to soil coupled with subsequent decomposition and a low leaching environment found under mesquite canopies provides an accumulation of CA^+ and Mg^+ (Virginia *et al.*, 1983). Shrub communities such as those associated to mesquite enhance spatial heterogeneity of soil resources and biomass (Connin *et al.*, in press) creating "islands of fertility". The change from surface to deep C storage by shrubs leads to a greater long-term C storage in soils. However not all shrubs act similarly, in particular, mesquite communities maintain total C levels while other shrubs such as the creosote bush (*Larrea tridentata*) have a net loss of soil C (Connin *et al.*, in press). The increase of atmospheric CO_2 concentration since the early 1800's has been said to have favored C_3 over C_4 plants, however, the loss of productive grasslands to shrublands appears to be unrelated to climatic fluctuations, and the conversion of grasslands to scrublands is largely attributed to anthropogenic disturbances (Connin *et al.*, in press). At an ecosystem level mesquite dominated communities, by creating "islands of fertility" and enhancing environmental heterogeneity, provides an increase in species richness.

Management Practices

Mesquite encroachment to desert grasslands is partially due to inadequate management of arid environments and rangelands. Historically, the Sonoran and Chihuahuan Deserts were covered by a dry tropical forest in the late Eocene that has experienced a drying trend, especially in the last 8,000 years (Smeins, 1983). The expansion of shrublands has thus created an "impoverished" system for livestock grazing, which in turn has reduced the income of many rangelands. Mesquite is often associated to impoverished ranges as it gradually replaces desirable grasses, it increases soil erosion and higher water runoff, while it decreases soil nutrients, and increases environmental heterogeneity. The vast prairies observed by European settlers may in fact be remnants from previous favorable conditions for grasslands. These persisting grasslands in the already deteriorating environment have surely been accelerated with the intensity of livestock grazing. In relation to native Holocene fauna (rodents, peccary and coyote) livestock have become a much more effective disperser (Janzen, 1986; Brown and Archer, 1987), coupled with prolonged livestock grazing and high grazing intensities have caused the doubling of mesquite cover in grasslands (Glendening, 1952; Buffington and Herbel, 1965). These rangelands have frequently been cleared in favor of introduced grass species that often affect ecosystem structure and functioning (Fleischner, 1994; Pierson and McAuliffe, 1994). Furthermore, clearing of mesquites does not result in long-term favorable responses of forage grasses (Holecheck *et al.*, 1994) and does not seem to decrease water evaporation (Dugas and

Mayeux, 1991). Studies on how mesquite influences vegetation, show little effects on perennial grasses and non-poisonous forbs at mesquite cover levels below 17% (Warren *et al.*, 1996). Besides supporting a large number of animals, *Prosopis* spp. provide resources for a large variety of income producing game such as mule deer (*Odocoileus hemionus*), bobwhite quail (*Collinus virginianus*), collared peccary (*Tayassu tajacu*), mourning dove (*Zenaida macroura*) and wild turkey (*Meleagris gallopavo*) (Mares *et al.*, 1977; Germano *et al.*, 1983; Scifres *et al.*, 1988). Mesquites also provide favorable conditions for native herbaceous, ephemeral and perennial plants under their canopies that are palatable for both livestock and wildlife (such as the Texas wintergrass *Setaria texana* Heitschmidt *et al.* (1986) and *Panicum mexicanum* Cornejo-Oviedo *et al.* (1992); Nolte and Fulbright (1997)). In addition, mesquites are often used as multipurpose agroforestry species as they provide fodder, food, fuel, nitrogen fixation, dune stabilization, soil conservation and honey production (Nair *et al.*, 1984; Fagg and Stewart, 1994), as well as for the recovery of salt lands (Singh, 1995). It is therefore important to take into account the way brush management is seen, from brush ”eradication” to brush ”management”.

The question arises as to the proper balance between conservation and exploitation of rangelands. Studies in the South American Chaco have shown a negative effect of fragmentation on bee pollinators and on reproduction of several arid and semi-arid zone plant species (Aizen and Feinsinger, 1994a,b). Bock *et al.* (1993) suggested the exclusion of livestock from 20% of current federal grazing lands and Scifres *et al.* (1983) suggested creating mosaics of mesquite infested fields, which could enhance diversity (Whittaker *et al.*, 1979), however, mesquite stands will eventually coalesce into larger thorn woodlands (Archer *et al.*, 1988). There is no clear-cut management practice. Some evidence points towards grazing intensities that do not exceed one third of current year annual growth on key forage species (Holecheck *et al.*, 1994). This may, under favorable climatic conditions, actually improve ecological and perennial grass cover in short time periods (Holecheck *et al.*, 1994). In addition, reduced light levels and competition with a herbaceous layer essentially stops growth of mesquite seedlings (Bush and Auken, 1990). Combined management practices could be the solution to land encroachment if they prove to be cost-effective (e.g. Integrated Brush Management Systems, IBMS Scifres *et al.*, 1983, 1988).

The Rangeland Paradox

The mesquite controversy does not stand alone, as similar management practices are affecting other community structures such as juniper forests in Oregon and the American southwest (Belsky, 1996). The controversies surrounding these species vary greatly, however a common denominator is the expansion of woody species towards grasslands, with a concomitant decrease in land value towards livestock grazing. However, given the characteristics outlined above, conservation and management programs in arid and semi-arid environments should place a priority on the management of mesquite populations in areas depleted through conversion and its control in areas of livestock grazing. This would provide a compromise between livestock productivity on the one hand, and conservation of species diversity and maintenance of ecosystem structure on the other.

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Table 1: Order, number of families, genera and species (in parenthesis) that use different resources of *Prosopis* spp. in arid environments. B = branches, BA = bark, F = fruits, L = leaves, N = nectar, P = pollen, M = microenvironment.

Taxa	fam	gen	Resource	Source
Acari	3	24(?)	L	Wallwork *et al.* (1985)
Angiosperms	24	48(69)	B, M	Mares *et al.* (1977); McPherson *et al.* (1988); Suzán *et al.* (1994); Nabhan and Suzán (1994); Franco-Pizaña *et al.* (1995)
Artiodactyla	2	3(4)	F, L	Mares *et al.* (1977); Arnold and Dawe (1979); Goyal *et al.* (1988)
Coleoptera	8	44(72)	L, S, BA, S	Wallwork *et al.* (1985); Wisdom (1991)
Diptera	1	1(1)	N, F	Keys *et al.* (1995)
Hemiptera	8	31(40)	L	Wallwork *et al.* (1985); Wisdom (1991)
Homoptera	11	42(46)	L	Wisdom (1991)
Hymenoptera	6	20(79)	P, N	Golubov *et al.* (1999)
Hymenoptera	?	?(160)	P, N	Simpson and Solbrig (1977)
Lagomorpha	1	2(2)	B, F	Glendening (1952); Mares *et al.* (1977); Alipayou *et al.* (1993)
Lepidoptera	10	18(20)	L, N	Wisdom (1991); Rivera-Garcia and Equihua-Zamora (1997)
Nematoda	?	5(?)	R	Freckman and Virginia (1989)
Orthoptera	3	16(21)	L	Wisdom (1991)
Reptilia	1	4(4)	M	Germano and Hungerford (1981)
Rodentia	7	16(28)	S, B	Glendening (1952); Rogovin and Surov (1992); Rosati and Bucher (1995)
Thysanoptera	2	2(2)	L, P, N	Wisdom (1991)

PAGINACIÓN DESCONTINUA

Apéndice 4

Códigos de los programas utilizados

Programa para generar matrices de transición y remuestreos

Este es el código para un programa que realiza remuestreos al azar a partir de tres vectores. En sentido estricto si se le elimina la parte correspondiente al muestreo, funciona como un generador de las matrices de transición anuales usadas en dinámica de poblaciones, sin necesidad de hacer cálculos complicados. Por desgracia es un programa que se encuentra en fases muy iniciales y esta lejos de ser comprensible para un usuario normal, ya que el código no es portátil y es poco amigable. Este fué el programa que utilicé para la generación de las matrices anuales para las dos partes de la tesis que tienen análisis matriciales. Las salidas que se generan son fácilmente importadas a Matlab, para generar los parámetros poblacionales. El código para el análisis en Matlab es mucho más sencillo que este por lo que no creo necesario incluirlo.

Para que funcione el progarama se necesitan tener cuatro vectores. El primero es simmplemente el número consecutivo de la planta como identificador (). El segundo vector es del tamaño de la planta o animal en el tiempo 0 (int const time0[SIZE]=38, 45,...,43). El tercero es el tamaño en el tiempo 1 (int const time1[SIZE]=16, 42,...,32; /*individual time 1*/) y el cuarto es el valor de fecundidad asociada a ese individuo (int const reproduction[SIZE]=0, 7,...,0; /*reproduction of individual in time0*/). Se deben de asignar de manera previa el tamaño de los vectores (#define SIZE), el número de individuos que van a ser remuestrados (#define SAMPLE), el número de celdas de la matriz de salida (#define MATRIZ) y el número de clases (#define CLASS).

El formato de salida (ver abajo) esta en formato de texto para que pueda ser importado a Matlab. Si es necesario, el fomrato puede ser cabiado para que funcione como entrada a otros programas (e.g. Mathematica).

Formato de salida de las primeras 3 matrices de 5 x 5 tomadando individuos al azar:

```
[ 0.00000 2.0 1.7 1.9 1.3; 0.00000000 0.68944097 0.06403941 0.04651163 0.05555556;
0.00000000 0.21118012 0.64039409 0.36046511 0.06481481; 0.00000000 0.06832298
0.21182266 0.46511629 0.15740740; 0.00000000 0.01863354 0.07389162 0.08139535
0.72222221]
[ 0.00000 1.9 1.7 2.8 1.8; 0.00000000 0.62345678 0.12264151 0.02531646 0.03809524;
0.00000000 0.21604939 0.59905660 0.36708862 0.03809524; 0.00000000 0.08641975
0.21226415 0.35443038 0.20000000; 0.00000000 0.05555556 0.02358491 0.22784810
0.70476192]
[ 0.00000 2.4 2.2 2.8 1.9; 0.00000000 0.64137930 0.08490566 0.02197802 0.03636364;
0.00000000 0.23448277 0.61792451 0.30769232 0.05454545; 0.00000000 0.06896552
0.21226415 0.37362638 0.17272727; 0.00000000 0.04137931 0.08018868 0.27472529
0.71818179]
```

Principio del programa

```
/*De tres vectores de tamanio SIZE, sacar SAMPLE al azar, clasifica el
individuo en los dos tiempos una cierta clase, determina la
diferencia entyre clases y le asigna una nueva clase del tamanio de
la matriz en donde cae el individuo, cuenta el numero de
individuos que caen en cada clase, saca la transicion y determina la
fecundidad por individuo en cada clase*/
```

```
#include <stdio.h>
#include <stdlib.h>
#define SIZE 654
#define SAMPLE 654
#define MATRIZ 25
#define CLASS 5


int main()
{
  int const individual[SIZE]={0, 1,...,653}; /*individual number*/
  int const time0[SIZE]={38, 45,...,43}; /*individual time 0*/
  int const time1[SIZE]={16, 42,...,32};  /*individual time 1*/
  int const reproduction[SIZE]={0, 7,...,0}; /*reproduction of individual in time0*/
  int i, j, k, l, num_of_clases, p, m, q, r, s, t, u, v, w, x, y, yy, z, aa; /*counter for diff. things*/
  int ii;
  int random[SAMPLE]={};  /*matrix of random samples*/
  int boot[SAMPLE]={};    /*matrix of randomly selected individuals*/
  int class0[SIZE]={}, class1[SIZE]={}; /*class each individual belongs to*/
  int frequency_time_1[SAMPLE]={0}, frequency_time_0[SAMPLE]={0};/*frequency of occurence of each size class*/
  int trans[SAMPLE]={};  /*array of transitions*/
  int transu[SAMPLE]={};
  int sum_repr_per_class[CLASS]={0};
  int frequency_of_ind_in_class[SAMPLE]={};
  float repr_per_ind[CLASS]={};
  double transition_matrix[MATRIZ]={0};
  float casilla1, casilla2, casilla3, casilla4, casilla5;
  float casilla6, casilla7, casilla8, casilla9, casilla10;
  float casilla11, casilla12, casilla13, casilla14, casilla15;
  float casilla16, casilla17, casilla18, casilla19, casilla20;
  float casilla21, casilla22, casilla23, casilla24, casilla25;
  srand(time(NULL)); /*automatic seed number for random numbers*/


  /*prints the matrix individual number*/

  {
   /*  for (i=0; i<=SIZE-1; i++)   */
/*       { */
/*    printf("%d%6d%6d%6d\n",individual[i], time0[i], time1[i], reproduction[i]); */
/*       } */
      /*   printf("%\n"); */
    /*generates a matrix of random numbers that will be the indices of
    the individuals, and assignes the value to a boot matrix with the individuals*/
  }
 /*   { */
/*     printf("%s\n", "Individuals Sampled"); */
/*    } */
 {
    for (k=0; k<=SAMPLE-1;k++)
     {
       boot[k]= individual[random[k]=0+(rand()%SIZE)]; /* [k]; */
      /*   printf("%d\n", boot[k]); */
     }
 }


/*clasifies the individuals in size clases, the ouput is an array that is
 the class of each individual in time 0*/

 /*   { */
/*     printf("%s%8s%10s%10s%12s%10s\n", "Individual", "Class 0", "Class 1", "Size T0", "Size T1", "Rep"); */
/*    } */
{
     {
       for (p=0; p<=SAMPLE-1; p++)
```

```
      {
       if (time0[boot[p]]==0)
 class0[p]=0;
       else if (time0[boot[p]]<=20)
         class0[p]=1;
       else if (time0[boot[p]]<=40)
         class0[p]=2;
       else if (time0[boot[p]]<=60)
         class0[p]=3;
       else if (time0[boot[p]]>=61)
 class0[p]=4;
      }
     }
/*same as above but for time 1*/
     {
       for (p=0; p<=SAMPLE-1; p++)
      {
       if (time1[boot[p]]==0)
 class1[p]=0;
       else if (time1[boot[p]]<=20)
         class1[p]=1;
       else if (time1[boot[p]]<=40)
         class1[p]=2;
       else if (time1[boot[p]]<=60)
         class1[p]=3;
       else if (time1[boot[p]]>=61)
         class1[p]=4;
      }
     }
     /*  { */
/*          for (p=0; p<=SAMPLE-1; p++) */
/*        printf("%d%12d%12d%12d%12d%12d\n", boot[p], class0[p],
 %class1[p], time0[boot[p]],  time1[boot[p]], reproduction[boot[p]]); */
/*        } */

   }

   /*   { */
 /*    printf("%\n"); */
/*      } */
/*quantifies the frequency of individuals of different size
  clases and puts them in an array*/
 {
  for (m=0; m<=SAMPLE-1; m++)
   {
    if (class0[m]==0)
    ++frequency_time_0[class0[m]];
    else if (class0[m]==1)
    ++frequency_time_0[class0[m]];
    else if (class0[m]==2)
    ++frequency_time_0[class0[m]];
    else if (class0[m]==3)
    ++frequency_time_0[class0[m]];
    else if (class0[m]==4)
    ++frequency_time_0[class0[m]];
   }
  for (m=0; m<=SAMPLE-1; m++)
   {
    if (class1[m]==0)
    ++frequency_time_1[class1[m]];
    else if (class1[m]==1)
    ++frequency_time_1[class1[m]];
    else if (class1[m]==2)
    ++frequency_time_1[class1[m]];
    else if (class1[m]==3)
    ++frequency_time_1[class1[m]];
    else if (class1[m]==4)
    ++frequency_time_1[class1[m]];
```

```
   }
 /*    printf("%s%8s%8s\n", "Class", "Freq T0", "Freq T1"); */
/*   { */
/*    for (l=0; l<=CLASS-1; l++) */
/*    printf("%d%8d%8d\n", l, frequency_time_0[l], frequency_time_1[l]); */
/*   } */
 }
 /*   printf("\n"); */
/*generates an array with counts of the number of individuals in each class*/
/*  { */
/*   printf("%s\n", "Individual transitions in aij: "); */
/*  } */

 {
  for (q=0; q<=SAMPLE-1; q++)
    if (time0[boot[q]]==0)
      {
       if (time1[boot[q]]==0)
         trans[boot[q]]=1;
       else if (time1[boot[q]]<=20)
         trans[boot[q]]=2;
       else if (time1[boot[q]]<=40)
         trans[boot[q]]=3;
       else if (time1[boot[q]]<=60)
         trans[boot[q]]=4;
       else if (time1[boot[q]]>=61)
         trans[boot[q]]=5;
      }
    else if (time0[boot[q]]<=20)
      {
       if (time1[boot[q]]==0)
         trans[boot[q]]=6;
       else if (time1[boot[q]]<=20)
         trans[boot[q]]=7;
       else if (time1[boot[q]]<=40)
         trans[boot[q]]=8;
       else if (time1[boot[q]]<=60)
         trans[boot[q]]=9;
       else if (time1[boot[q]]>=61)
         trans[boot[q]]=10;
      }
    else if (time0[boot[q]]<=40)
      {
       if (time1[boot[q]]==0)
         trans[boot[q]]=11;
       else if (time1[boot[q]]<=20)
         trans[boot[q]]=12;
       else if (time1[boot[q]]<=40)
         trans[boot[q]]=13;
       else if (time1[boot[q]]<=60)
         trans[boot[q]]=14;
       else if (time1[boot[q]]>=61)
         trans[boot[q]]=15;
      }

    else if (time0[boot[q]]<=60)
      {
       if (time1[boot[q]]==0)
         trans[boot[q]]=16;
       else if (time1[boot[q]]<=20)
         trans[boot[q]]=17;
       else if (time1[boot[q]]<=40)
         trans[boot[q]]=18;
       else if (time1[boot[q]]<=60)
         trans[boot[q]]=19;
       else if (time1[boot[q]]>=61)
         trans[boot[q]]=20;
      }
```

```
    else if (time0[boot[q]]>=61)
      {
       if (time1[boot[q]]==0)
         trans[boot[q]]=21;
       else if (time1[boot[q]]<=20)
         trans[boot[q]]=22;
       else if (time1[boot[q]]<=40)
         trans[boot[q]]=23;
       else if (time1[boot[q]]<=60)
         trans[boot[q]]=24;
       else if (time1[boot[q]]>=61)
         trans[boot[q]]=25;
     }
}

/*  for (r=0; r<=SAMPLE-1; r++) */
/*      { */
/*      printf("%d\n", trans[boot[r]]); */
/*      } */
{
/*   printf("\n"); */
}
 /*  printf("%s%12s\n", "Class", "Frequency"); */
 {
  for (s=0; s<=SAMPLE-1; s++)
    {
      if (trans[boot[s]]==1)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==2)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==3)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==4)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==5)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==6)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==7)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==8)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==9)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==10)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==11)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==12)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==13)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==14)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==15)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==16)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==17)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==18)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==19)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==20)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==21)
      ++frequency_of_ind_in_class[trans[boot[s]]];
```

```
      else if (trans[boot[s]]==22)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==23)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==24)
      ++frequency_of_ind_in_class[trans[boot[s]]];
      else if (trans[boot[s]]==25)
      ++frequency_of_ind_in_class[trans[boot[s]]];
    }

  /*   printf("\n"); */
   /*  for (t=1; t<=MATRIZ; t++) */
/*    { */
/*     printf("%d%12d\n", t, frequency_of_ind_in_class[t]); */
/*    } */
 }
   printf("\n");
 {
   for (v=1; v<=5; v++)
    {
    if (freqnency_of_ind_in_class[v]>=1)
      transition_matrix[v]=(float)frequency_of_ind_in_class[v]/(float)frequency_time_0[0];
    }
  for (v=6; v<=10; v++)
    {
    if (frequency_of_ind_in_class[v]>=1)
      transition_matrix[v]=(float)frequency_of_ind_in_class[v]/(float)frequency_time_0[1];
    }
  for (v=11; v<=15; v++)
    {
    if (frequency_of_ind_in_class[v]>=1)
      transition_matrix[v]=(float)frequency_of_ind_in_class[v]/(float)frequency_time_0[2];
    }
  for (v=16; v<=20; v++)
    {
    if (frequency_of_ind_in_class[v]>=1)
      transition_matrix[v]=(float)frequency_of_ind_in_class[v]/(float)frequency_time_0[3];
    }
  for (v=21; v<=25; v++)
    {
    if (frequency_of_ind_in_class[v]>=1)
      transition_matrix[v]=(float)frequency_of_ind_in_class[v]/(float)frequency_time_0[4];
    }
 }
      /*  { */
/*      for (w=1; w<=MATRIZ; w++) */
/*        { */
/*        printf("%d%14.8f\n", w, transition_matrix[w]); */
/*        } */
/*      printf("\n"); */
/*      for (ii=0; ii<=CLASS-1; ii++) */
/*        { */
/*     printf("%d\n", frequency_time_0[ii]); */
/*        } */
/*         } */
/*      printf("\n"); */

{
    casilla2=transition_matrix[2];
    casilla3=transition_matrix[3];
    casilla4=transition_matrix[4];
    casilla5=transition_matrix[5];
    casilla7=transition_matrix[7];
    casilla8=transition_matrix[8];
    casilla9=transition_matrix[9];
    casilla10=transition_matrix[10];
    casilla12=transition_matrix[12];
    casilla13=transition_matrix[13];
```

```
    casilla14=transition_matrix[14];
    casilla15=transition_matrix[15];
    casilla17=transition_matrix[17];
    casilla18=transition_matrix[18];
    casilla19=transition_matrix[19];
    casilla20=transition_matrix[20];
    casilla22=transition_matrix[22];
    casilla23=transition_matrix[23];
    casilla24=transition_matrix[24];
    casilla25=transition_matrix[25];
}

/* This generates the array for reproduction*/

 {
  for (x=0; x<=SAMPLE-1; x++)
    {
    if (time0[boot[x]]==0)
     sum_repr_per_class[0] += reproduction[boot[x]];
    else if (time0[boot[x]]<=20)
     sum_repr_per_class[1] += reproduction[boot[x]];
    else if (time0[boot[x]]<=40)
     sum_repr_per_class[2] += reproduction[boot[x]];
    else if (time0[boot[x]]<=60)
     sum_repr_per_class[3] += reproduction[boot[x]];
    else if (time0[boot[x]]>=61)
     sum_repr_per_class[4] += reproduction[boot[x]];
    }
 /*  { */
/*     for (y=1; y<=CLASS; y++) */
/*      { */
/*      printf("%d%9d\n", y, sum_repr_per_class[y]); */
/*      } */
/*   } */

  for (yy=1; yy<=CLASS; yy++)
    {
      if (frequency_time_0[yy]==0)
repr_per_ind[yy]=0;
      else if (frequency_time_0[yy]!=0)
repr_per_ind[yy]=(float)sum_repr_per_class[yy]/(float)frequency_time_0[yy];
       /*  printf("%1d%16.0f%14d%4d\n", yy, repr_per_ind[yy],sum_repr_per_class[yy], frequency_time_0[yy]); */
    }
  {
     casilla1=0;
     casilla6=repr_per_ind[1];
     casilla11=repr_per_ind[2];
     casilla16=repr_per_ind[3];
     casilla21=repr_per_ind[4];
  }

 }

/*  { */
/*     printf("\n"); */
/*  } */

{
    printf("%s%14.5f%14.1f%14.1f%14.1f%14.1f%s\n","[", casilla1, casilla6, casilla11, casilla16, casilla21,";");
    printf("%14.8f%14.8f%14.8f%14.8f%14.8f%s\n", casilla2, casilla7, casilla12, casilla17, casilla22, ";");
    printf("%14.8f%14.8f%14.8f%14.8f%14.8f%s\n", casilla3, casilla8, casilla13, casilla18, casilla23, ";");
    printf("%14.8f%14.8f%14.8f%14.8f%14.8f%s\n", casilla4, casilla9, casilla14, casilla19, casilla24, ";");
    printf("%14.8f%14.8f%14.8f%14.8f%14.8f%s\n", casilla5, casilla10, casilla15, casilla20, casilla25, "]");
}
return 0;
}
```

Programa para calcular frecuencias alélicas

Este programa calcula las frecuencias alélicas y genotípicas bajo diferentes modelos de selección. El usuario define las frecuenicas inciales ya sea de genotipo o alelos, los coeficientes de selección asociados a cada genotipo y el número de generaciones de la simulación. Aunque los cálculos son relativamente sencillos de hacerse en otros programas más amigables, la ventaja de este es que no tiene límite. Pueden asignarse cientos de generaciones con coeficientes de selección muy bajos. Como todos los parámteros son definidos por el usuario, en realidad hace que sea muy flexible. Como es un programa que puede compilarse en cualquier máquina que tenga un sistema UN*X que por lo general tienen un compilador de C (gcc en Linux y cc en NetBSD), es muy portátil. Al compilarlo por lo general se genera un ejecutable llamado a.out que de ejecutarse (con el comando ./a.out) genera las preguntas iniciales y corre iterativamente cada modelo hasta llegar al número especificado de generaciones.

Inicio del programa

```
/* This is a program to calculate the frequency of alleles and
individuals under different models of selection. The user defines the
initial frequencies of the adults the seleccion coefficients associaed
to each genotype, and  the number of generations in the simulation*/



#include <stdio.h>

    float freq_allele_A, freq_allele_a;
    float freq_gen_AA, freq_gen_Aa, freq_gen_aa;
    int data_type, n_of_individuals, generations, i;
    float selection_coefficient_AA, selection_coefficient_Aa, selection_coefficient_aa;
    float selection_coefficient_AA1, selection_coefficient_Aa1, selection_coefficient_aa1;
    float selection_coefficient_Aa2, selection_coefficient_aa3, mean_fitness, delta_A;
    int allele;

main()
{

  printf("Do you have allele frequencies (1) of genotype frequencies (2)?: ");
  scanf("%d", &data_type);
  printf("How many individuals?: ");
  scanf("%d", &n_of_individuals);
  printf("How many Generations?:  ");
  scanf("%d", &generations);
  printf("Selection coefficient for Individuals of type AA?: ");
  scanf("%f", &selection_coefficient_AA1);
  printf("Selection coefficient for Individuals of type Aa?: ");
  scanf("%f", &selection_coefficient_Aa2);
  printf("Selection coefficient for Individuals of type aa?: ");
  scanf("%f", &selection_coefficient_aa3);

  {
  selection_coefficient_AA=(1-selection_coefficient_AA1);
  selection_coefficient_Aa=(1-selection_coefficient_Aa2);
  selection_coefficient_aa=(1-selection_coefficient_aa3);
  printf("%14.8f%14.8f%14.8f\n", selection_coefficient_AA, selection_coefficient_Aa, selection_coefficient_aa);
  }

  {
  if (data_type==1)
    {
```

```
     printf("Frequency of allele A: ");
     scanf("%f", &freq_allele_A);
     printf("Frequency of allele a: ");
     scanf("%f", &freq_allele_a);
     {
       freq_gen_AA=(freq_allele_A)*(freq_allele_A);
       freq_gen_Aa=2*((freq_allele_A)*(freq_allele_a));
       freq_gen_aa=(freq_allele_a)*(freq_allele_a);
       printf("%8.4f%8.4f%8.4f\n", freq_gen_AA, freq_gen_Aa, freq_gen_aa);
     }
    }
  else if (data_type==2)
    {
     printf("Starting frequency of genotype 'AA': ");
     scanf("%f", &freq_gen_AA);
     printf("Starting frequency of genotype 'Aa': ");
     scanf("%f", &freq_gen_Aa);
     printf("Starting frequency of gennotype 'aa': ");
     scanf("%f", &freq_gen_aa);
     {
       freq_allele_A=((freq_gen_AA)+((freq_gen_Aa)/2));
       freq_allele_a=((freq_gen_aa)+((freq_gen_Aa)/2));
       printf("%8.8f%8.8f\n\n", freq_allele_A, freq_allele_a);
     }
    }
 }
printf("%3s%8s%8s%8s%8s%8s%8s\n", "Gen", "Wavg", "FreQA", "Freqa", "FreqAA", "FreqAa", "Freqaa");
{
   for (i=1; i<=generations-1; i++)
     {
     mean_fitness=(1-(((freq_allele_A*freq_allele_A)*(selection_coefficient_AA1))+(2*(freq_allele_A*freq_allele_a)*
(selection_coefficient_Aa2))+((freq_allele_a*freq_allele_a)*selection_coefficient_aa3)));
     delta_A=(((((freq_allele_A)*(selection_coefficient_AA-selection_coefficient_Aa))+((freq_allele_a)*
(selection_coefficient_Aa-selection_coefficient_aa))*(freq_allele_A*freq_allele_a))/mean_fitness);
     freq_allele_A=freq_allele_A+delta_A;
     freq_allele_a=1-freq_allele_A;
     freq_gen_AA=(freq_allele_A*freq_allele_A);
     freq_gen_Aa=(freq_allele_a*freq_allele_A)*(2);
     freq_gen_aa=(freq_allele_a*freq_allele_a);
     printf("%3d%8.4f%8.4f%8.4f%8.4f%8.4f%8.4f\n", i, mean_fitness,
   freq_allele_A, freq_allele_a, freq_gen_AA, freq_gen_Aa, freq_gen_aa);
    }
}
return 0;
}
```