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INTERACCIÓN ENTRE EL INSECTO BARRENADOR *Oncideres albomarginata chamela* Y SU PLANTA HOSPEDERA *Spondias purpurea*

TESIS

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PRESENTA

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CONTENIDO

Uribe-Mú Claudia A. 2006. Interacción entre el insecto barrenador *Oncideres albomarginata chamela* y su planta hospedera *Spondias purpurea*. Tesis doctoral. Posgrado en Ciencias Biológicas. Centro de Investigaciones en Ecosistemas. Universidad Nacional Autónoma de México.

RESUMEN

En las plantas dioicas, la variación en las características morfológicas y fisiológicas entre sexos puede afectar la calidad del hospedero y, como consecuencia, las preferencias de los herbívoros. Los patrones de daño entre sexos de plantas dioicas han sido relativamente bien estudiados, sin embargo los estudios en plantas dioicas que han evaluado los efectos del herbívoro sobre el crecimiento y reproducción de las plantas y, a su vez, los efectos que puede tener la planta hospedera sobre el desempeño de los herbívoros han sido escasos. Las consecuencias sobre el crecimiento, reproducción y desempeño de ambas partes de la interacción, están determinadas en gran medida por el tipo de daño que reciben las plantas. Algunos estudios han demostrado que la remoción de ramas puede ocasionar efectos más severos que el consumo de hojas. En este estudio se analiza la relación planta-herbívoro entre el cerambícido *Oncideres albomarginata chamela* y el árbol tropical dioico *Spondias purpurea.* Se describe el patrón de remoción de ramas, y se evalúan las consecuencias de la interacción sobre el crecimiento y la reproducción de las plantas, además de los efectos del sexo de la planta sobre la sobrevivencia y peso de las larvas del insecto bajo condiciones naturales.

Se encontró que la proporción de ramas removidas fue mayor en árboles hembras que en árboles machos. Las preferencias por remover ramas de plantas hembra aparentemente están asociadas a su contenido de nitrógeno. Los efectos de la remoción de ramas fueron evaluados en ramas intactas y ramas atacadas marcadas en 1999; las ramas removidas regeneraron un año después del ataque de *O. a. chamela.* La proporción de la fertilidad (medida como la proporción de ramas reproductivas) fue mayor en las ramas intactas y en los árboles macho, aunque las diferencias en las proporciones de fertilidad entre ramas intactas y regeneradas de ambos sexos disminuyeron con el tiempo. La producción de frutos también fue mayor en las ramas intactas. La producción total de frutos por árbol decreció con el incremento del nivel de daño. El total de ramas removidas acumuladas a través del tiempo por árbol, afectó negativamente la producción total de frutos en las temporadas subsecuentes.

No encontramos efectos del sexo de la planta sobre el número de sitios de oviposición, sobreviencia y masa larval de *O. a. chamela,* aunque detectamos efectos de la variación entre árboles. La composición de nutrientes (fósforo y carbohidratos no estructurales) se analizó en una muestra de ramas colectadas intactas de árboles hembra y árboles macho, pero no hubo diferencias entre sexos. Los resultados sugieren que el sexo de la planta no determina el desempeño de las etapas iniciales de desarrollo de *O. a. chamela* en *S. purpurea*. Otros factores asociados con la variación en la resistencia individual de las plantas o factores externos como la competencia dentro de las ramas, deberian ser analizados para explicar el desempeño de las larvas de *O. a. chamela.*

Uribe-Mú Claudia A. 2006. Interacción entre el insecto barrenador *Oncideres albomarginata chamela* y su planta hospedera *Spondias purpurea*. Tesis doctoral. Posgrado en Ciencias Biológicas. Centro de Investigaciones en Ecosistemas. Universidad Nacional Autónoma de México.

SUMMARY

In dioecious species, the variation in morphological and physiological characteristics between genders might affect the host quality and, in consequence, the preferences of herbivores. Patterns of plant damage between genders have been relatively well studied, but the studies in dioecious plants that have evaluated the effects of herbivores on plant growth and reproduction, and the effects of plant gender on insect performance have been scarce. Consequences on growth, reproduction and performance of both parts of the interaction are strongly determined by the type of plant damage. Some studies have demonstrated that branch removal might cause effects more detrimental to plants than leaf consumption. In this study we analyzed plant-herbivore relationships between the longhorned beetle *O. a. chamela* and the tropical dioecious tree *Spondias purpurea*. *O. a. chamela* is a longhorned beetle that removes whole branches of their host trees for oviposition. We described branch removal patterns and evaluated the consequences of the interaction on growth and reproduction of plants as well as the effects of plant gender on survival and weight of insect larvae under natural conditions.

The proportion of removed branches was greater for female than for male trees. The preferences for remove female branches are apparently associated with their nitrogen content. Effects of branch removal were evaluated in intact and attacked branches marked in 1999; removed branches regenerated a year after the insect borer attacked them. The proportion of fertility (measured as the proportion of reproductive branches) was greater in intact and male trees, but intergender differences decreased over time. Fruit production also was greater in intact branches. Total fruit production per tree decreased as damage level increased. Cumulative branch removal over several years negatively affected total fruit production per tree of the subsequent seasons.

Plant gender did not affect the number of oviposition sites, survival and mass of *O. a. chamela* larvae, but an effect of variation among trees was detected. Some nutritional aspects (phosphorus and total non-structural carbohydrates) of the chemical composition in both plant genders were determined from a sample of intact branches, but P and TNC content were similar between genders.The results suggest that plant gender did not determine the performance of initial larval development of *O. a. chamela* on *S. purpurea*. Therefore, other factors associated to the variation in plant resistance or external factors as competition inside branches might be analyzed to account for larval performance of *O. a. chamela.*

INTRODUCCIÓN GENERAL

Durante las últimas dos décadas se ha enfatizado el interés por evaluar las preferencias intersexuales y las consecuencias del daño sobre la reproducción y el crecimiento vegetativo en las plantas dioicas. Se ha considerado que las diferencias morfológicas y fisiológicas entre sexos detectadas en numerosos estudios (Ågren 1987, Danell et al. 1985, Polhemus 1988, Boecklen et al. 1990, Jing y Coley 1990, Krischik y Denno 1990, Danell et al. 1991, Hjältén 1992, Verdu et al. 2004) influyen en los patrones de herbivoría. El consenso es que existe una mayor inversión de recursos a la reproducción por parte de las hembras por los altos costos para producir frutos y semillas (Lloyd y Webb 1977, Obeso 1997, Nicotra 1999, Obeso 2002). Si los recursos destinados para mantenimiento, crecimiento y reproducción de las plantas son finitos, se originará un compromiso en el que la inversión para una de estas funciones necesariamente reducirá lo invertido en las otras (Cody 1966, Gadgil y Bosert 1970). Además, pueden existir compromisos entre crecimiento, reproducción y defensa (Herms y Mattson 1992) y por tanto el efecto de los herbívoros y patógenos puede por también ser distinto entre plantas hembras y machos. En general, se ha propuesto que las plantas hembras son más defendidas, crecen menos y sufren menos herbivoría que las plantas macho (Ågren et al. 1999). Sin embargo, un metanálisis con 53 estudios de plantas dioicas donde se analizan los efectos del sexo de la planta sobre las características químicas de hojas, tallos y ramas (Cornelissen y Stiling 2005) indica que las plantas macho están más defendidas en términos de metabolitos secundarios, tricomas, resinas y dureza de hojas, por lo que no siempre el sexo aparentemente mejor defendido, es el menos dañado.

La mayoría de la literatura por lo general había considerado que la herbivoría tenía efectos negativos sobre las plantas. Esta idea cambió radicalmente a mediados de la década de 1980 cuando se demuestra que el daño en los tallos incrementaba la adecuación en la especie *Ipomopsis aggregata* (Paige y Whitham 1987). A partir de entonces se han evaluado los efectos de esta interacción en la adecuación y en el crecimiento vegetativo tanto a corto como a largo plazo, y se sugiere que existe un continuo de respuestas al daño que van desde favorables hasta desfavorables (Maschinski y Whitham 1989, Whitham et al. 1991, Bergelson y Crawley 1992, Bergelson et al. 1996)). Las respuestas de las plantas al daño pueden ser influenciadas por factores genéticos y por la variación en los factores bióticos y abióticos a los cuales están expuestas las plantas durante su ciclo de vida (Maschinski y Whitham 1989, Marquis 1992). A su vez, estas respuestas pueden modificar el desempeño de los insectos a través de alteraciones en la calidad nutricional y los compuestos de defensa (Bergelson et al. 1986, Faeth 1986, Thompson 1988, Nykänen y Koricheva 2004).

A pesar de que algunas revisiones concluyen que la calidad nutricional de las plantas no es un factor determinante en las preferencias de los herbívoros comparado con los compuestos de defensa (Ågren et al. 1999, Cornelissen y Stiling 2005), el desempeño de algunos gremios de herbívoros puede estar influenciado por características como tamaño y número de hojas o tallos (Craig et al. 1989, Preszler y Price 1995, hipótesis del vigor en plantas *sensu* Price 1991, Rossi y Strong 1991). Por tanto, algunos autores han sugerido que la variación en la calidad del hospedero está determinada por ambos factores, la calidad nutricional y las defensas de las plantas. Se ha sugerido que la influencia de factores bióticos como la presencia de enemigos modifica los patrones de selección de hospederos, así espacios libres de enemigos en hospederos de menor calidad son preferidos sobre hospederos de buena calidad con depredadores frecuentes (Heisswolf et al. 2005). Además, en las plantas dioicas la calidad de los tejidos podría variar debido a la inversión de recursos para la reproducción, los factores ambientales (calidad nutricional del suelo, clima) y su interacción con el dimorfismo de la planta (Jing y Coley 1990).

Hasta ahora, los estudios que han evaluado los efectos del herbívoro sobre la adecuación de las plantas y a la vez los efectos de la planta hospedera sobre el desempeño de los herbívoros han sido escasos, particularmente en las plantas dioicas. En este estudio se analizan los efectos del sexo de la planta sobre la interacción entre el insecto barrenador *Oncideres albomarginata chamela* y el árbol tropical dioico *Spondias purpurea. O. a. chamela* remueve ramas completas en sus árboles hospederos, este tipo de daño poco estudiado en árboles puede ser más severo para las plantas que la herbivoría foliar porque con la remoción de ramas se pierden hojas, flores, frutos y se dañan los tejidos de conducción y de almacenaje de nutrimentos con posibles efectos negativos a largo plazo sobre la reproducción y el crecimiento vegetativo de las plantas y en consecuencia repercusiones en el desempeño del insecto debido a cambios en la calidad del hospedero.

Área de Estudio

El estudio se realizó en la Reserva de la Biósfera Chamela-Cuixmala dentro de los terrenos de la Estación de Biología Chamela (EBCh) perteneciente al Instituto de Biología de la UNAM (19°39’norte, 105°03’oeste) (Fig. 1), presenta elevaciones de 30 a 150 m cerca de la costa. La temperatura es relativamente constante, pero la precipitación se concentra en un periodo de dos meses (Bullock 1988), con un promedio de anual de 714 mm (1978-1990). Los suelos son poco profundos, arenosos y neutros (pH= 6.9 ± 0.15) con 0.14 ± 0.04% de contenido de N y 5.4 ± 1.2% de contenido de materia orgánica. Las pendientes sobre 20°

son comunes. La vegetación es predominantemente es selva baja caducifolia (Bullock 1988). A nivel mundial es una de las áreas mejor estudiadas en cuanto a diversidad, con numerosas especies endémicas de flora y fauna. La riqueza florística comprende 125 familias con 555 géneros (227 especies de árboles, 216 de arbustos, 187 de lianas y trepadoras, 40 de epífitas y 366 de hierbas). Las familias Leguminosae y Euphorbiaceae son las mejor representadas. Les siguen en importancia las familias Compositae, Graminae, Convolvulaceae, Malvaceae, Solanaceae, Rubiaceae, Acanthaceae Bromeliaceae, Cucurbitaceae, Verbenaceae y Boraginaceae (Lott y Atkinson 2002). La riqueza faunística incluye hasta el momento 1887 especies de artrópodos (Pescador-Rubio et al. 2002), 127 especies de peces (incluyendo la bahía y las aguas continentales) (Espinosa et al. 2002), 19 especies de anfibios y 65 especies de reptiles (Ramírez-Bautista y García 2002), 270 especies de aves (Arizmendi et al. 2002) y 95 especies de mamíferos (Miranda 2002).

Sistema de estudio

Oncideres albomarginata chamela Chemsak & Giesbert descrito por Noguera (1993) según se describe a continuación, es una cerambícido perteneciente a la subfamilia Lamiinae, mide de 17.4 a 30.9 mm. de longitud y de 6.5 a 12 mm. de ancho; son ovalados, alargados, semicilíndricos o robustos. El integumento de esta especie es pardo rojizo oscuro a negro, con pubescencia densa y corta, presenta una franja característica de pubescencia blanca a lo largo de los élitros. La distribución actual conocida en México, se restringe a Jalisco, Guerrero y Veracruz. Su período de reproducción abarca de julio a febrero, y hasta ahora las plantas hospederas reportadas para esta especie son *Spondias purpurea, Comocladia engleriana, Bursera* spp.*, Amphypterigium adstringens, Ceiba pentandra, Urera* sp.*, Delonix regia* y *Manguifera indica.* (Noguera, 1993). Las hembras cortan ramas entre 2 y 3 cm. de diámetro en sus plantas hospederas para la oviposición, y sus larvas se alimentan y desarrollan dentro de las ramas cortadas y permanecen ahí hasta transformarse en adultos.

Spondias purpurea L. (Anacardiaceae) es un árbol muy común dentro de la selva baja caducifolia. Alcanza hasta 12 m de altura y hasta 80 cm de dap. Su corteza es de color gris plomizo a gris negruzco, lisa o verrugosa con estrías longitudinales pálidas o fisuradas y con protuberancias irregulares y escamosas, que dan un aspecto verrugoso (Barajas-Morales y León-Gómez 1989). En algunos casos se ramifica desde 1 m de altura, tiene ramas gruesas, retorcidas y frágiles o quebradizas. Presenta hojas compuestas de 9 a 19 foliolos opuestos o alternos de 1.2 x 0.5 a 4 x 1.6 cm elíptico u obovados, en ocasiones asimétricos, con el margen entero o ligeramente aserrado y ligeramente recurvado, ápice acuminado a obtuso, base atenuada, verde brillante en el haz, con indumento escaso en la nervación del envés; pecíolo ligeramente pulvinado en la base y peciólulos de 1 a 2 mm de largo (Martínez 1979). Las hojas son caducas durante la época seca. En Chamela, Jalisco sufre herbivoría foliar intensa en epoca lluviosa particularmente por la mariposa *Rothschildia cinta* y remoción de ramas en época seca por el cerambícido *Oncideres albomarginata chamela* (Bullock 1992). Esta especie es descrita como monoica o hermafrodita (Pennington y Sarukhán 1998), pero en Chamela sólo se ha reportado como dioica (Bullock 1992). Presenta flores en panículas cortas de 1 a 2.5 cm de largo en las axilas de las hojas caídas y glabras; las flores son pequeñas de 6-7 mm de diámetro, rojas y sésiles, las flores estaminadas pesan 1.9 mg y las flores pistiladas 2.7 mg (Bullock 1992). Florece de enero a marzo y es polinizada por insectos (Bullock y Solís-Magallanes 1990, Bullock 1994). Forma infrutescencias erectas de hasta 3 cm de largo y drupas ovoides de 2.5 x 1.5 cm moreno rojizo brillantes con un fuerte sabor agridulce, el endocarpio fibroso contiene una o más semillas aplanadas. Maduran de febrero a junio (Bullock y Solís-Magallanes 1990). El fruto es comestible y constituye uno de los principales recursos alimenticios del bosque seco. Su dispersión es zoocora y entre los principales dispersores están el coyote, el coatí, el venado, la zorra gris, la chachalaca y la iguana (Mandujano 2002). Es originaria de Mesoamérica y se distribuye desde México hasta Brasil y Perú, se puede encontrar desde los 0 a los 1000 m s.n.m. En México, se distribuye desde la costa de Sonora hasta Chiapas, en la cuenca del Balsas, en la depresión central de Chiapas y en el norte de Yucatán y Quintana Roo (Pennington y Sarukhán 1998).

Objetivo de la tesis.

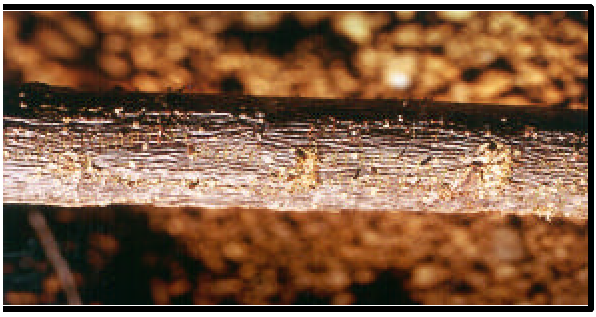
En esta tesis analizo las consecuencias de la remoción de ramas sobre el crecimiento vegetativo y la reproducción de *S. purpurea*, así como los efectos del sexo del hospedero sobre el desempeño de *O. a. chamela*. El documento se compone de cuatro capítulos: en el primero se describen las preferencias y patrones de la remoción de ramas ocasionadas por *O. a. chamela* sobre *S. purpurea*, y se evalúan sus efectos sobre la fertilidad de árboles hembras y árboles machos. En el segundo capítulo se analizan las consecuencias del daño estacional y acumulativo sobre la reproducción de árboles hembra y árboles macho a través de los años.

En el tercer capítulo se examina la relación entre la sobrevivencia y el peso larval de *O.a. chamela* con el contenido de fósforo y carbohidratos no estructurales (CNE) de las ramas de ambos sexos. Finalmente, en el capítulo cuatro se incluye una discusión general sobre aspectos ecológicos de la interacción entre *S. purpurea* y *O. a. chamela*.

Área de Estudio

Spondias purpurea L.

Oncideres albomarginata chamela Chemsak & Giesbert



CAPITULO I

Preferences, patterns and consequences of branch removal on the dioecious tropical tree *Spondias purpurea* (Anacardiaceae) by the insect borer *Oncideres albomarginata chamela* (Cerambycidae)

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Most studies of plant herbivore-interactions in dioecious species have evaluated foliar herbivory. In this research we evaluated preferences of branch removal by the insect borer *Oncideres albomarginata chamela* in the tropical dioecious tree *Spondias purpurea* L. The objectives were to determine the preferences and patterns of the removal of branches, to evaluate the effect of branch removal in the vegetative regeneration of branches, and to evaluate the effect of branch removal on the regeneration of fertile branches of male and female trees of *S. purpurea*. During three consecutive years of study, damage caused to branches by the girdled borer was associated with plant gender. The proportion of branches removed by the insect was greater for female than for male trees. The effects of branch removal were evaluated in attacked regenerated and unattacked branches. Removed branches regenerated a year after the insect borer attacked them. Branch removal affected the probability of producing fertile branches. The preference by *O. a. chamela* is apparently associated with the nutritional quality of the host.

Most studies that have evaluated herbivory in dioecious plants have concentrated on leaves (Ågren 1987, Alliende1989, Jing and Coley 1990, Lovett Doust and Lovett Doust 1985, Polhemus 1988, Oyama and Dirzo 1991), with only a few studies evaluating plant tissue removal on stems (Boecklen et al. 1990, Krischik and Denno 1990, Boecklen and Hoffman 1993), flowers (Bawa and Opler 1978, Wolfe 1997) or other types of plant tissue. A literature review indicates that herbivores prefer male plants (Ågren et al. 1999). Only a few studies have evaluated the consequences of leaf damage on the growth and reproduction of dioecious plants with variable results between genders (Ågren 1987, Elmqvist and Gardfell, 1988, Delph et al. 1993, Mutikainen et al. 1994).

Another type of damage rarely analyzed is stem or branch removal caused by insects or vertebrates (Paige and Whitham 1987, Gadd 2002). Although this type of damage has not been analyzed in dioecious plants, it could be more detrimental to plant fitness than leaf consumption because the removal of stems represents the loss of reproductive structures, groups of leaves and vascular connections with possible lethal consequences to plants (Zangerl and Bazzaz 1992). A few studies have shown that damage to the apical meristems of plants by herbivores alter architecture, decrease light exploitation, limit the tolerance to herbivory, affect the sexual expression and could kill plants with apical dominance (i.e palms) (Whitham and Mopper 1985; Stowe et al. 2000, but see Paige and Whitham 1987, Cobb et al. 2002).

Longhorn beetles (Cerambycidae) have the ability to remove entire twigs or branches (Bosq 1950, Linsley 1959, 1961). Only two studies have documented the patterns and effects of damage by longhorn beetles in plants. These studies show that branch removal alters the architecture and the spatial distribution of *Dicorynia guianensis* (Caraglio et al. 2001) and affect the architecture, growth and flowering patterns of *R. mangle* (Feller 2002).

The patterns and consequences of branch removal have not been studied in dioecious plants. The first objective of this study is to describe the preferences and patterns of branch removal caused by the insect borer *Oncideres albomarginata chamela* (Chemsak and Giesbert) in the tropical dioecious tree *Spondias purpurea* (L.) The second objective is to evaluate the effect of branch removal caused by the insect borer on the vegetative regeneration of branches of *S. purpurea*. The third objective is to evaluate the effect of branch removal on the regeneration of reproductive branches.

Materials and methods

Study site–The study was conducted in the Chamela-Cuixmala Biosphere Reserve at Chamela Biological Station, UNAM (19°30'N, 105°03'W) located on the pacific coast of Jalisco, Mexico from September 1999 to October 2002. The vegetation is tropical dry forest with a mean annual rainfall of 707 mm and a dry season that extends from November to June (Bullock 1988).

Study species–We studied the interaction between the insect borer, *Oncideres albomarginata chamela* (Coleoptera: Cerambycidae) and the tropical tree *Spondias purpurea* (Anacardiaceae). Both species are distributed from México to the northern region of South America (Pennington and Sarukhán 1968, Chemsak et al. 1992, Guillespie 1999). In México, *S. purpurea* is a common dioecious tree of the tropical dry forest (Bullock 1992). This species can reach 15 m in height and almost 80 cm in diameter at the base (Barajas- Morales and León-Gómez 1989). Leaves are compound with 5 to 12 elliptic-acute leaflets of 2 to 4 cm in length (Martínez 1979). Flowers are red, sessile, unisexual and dimorphic between males and females (Bullock 1992). Trees are deciduous with flowering and fruiting occuring from December to May and leaves are maintained from June to November (Bullock and Solís-Magallanes 1990). A previous study showed that there are differences in the amount of total non-structural carbohydrates (TNC) between the reproductive branches of male and female trees. Fertile female branches have more TNC than male branches before the initiation of the reproductive season of *S. purpurea*. Non reproductive branches produce similar amounts of TNC between genders (Bullock 1992).

Oncideres albomarginata chamela is a longhorn beetle that removes branches and oviposits within them. The body length of this species is 17 to 31 mm and 6.5 to 12 mm wide (Noguera 1993). The reproductive period of this species begins in October and finishes in February, just before the flowering of *S. purpurea*. During this period, female beetles girdle and completely remove the branches of *S. purpurea*. These branches either fall to the ground or hang from the trees where the insects oviposit within them and their eggs pupate and develop inside until the adults emerge.

Beetle preference–To determine the preferences of branch removal by the insect borer on *S. purpurea*, we estimated the number of available branches of male and female trees that could be potentially removed by the beetles. To do this we first determined the sex ratio of 105 trees of *S. purpurea* distributed along 7 km of trails within the study site. To estimate the size of attacked branches by *Oncideres*, we measured the diameter at the base of branches removed by the insects. Measurements were conducted with an electronic caliper (Mytutoyo Inc) on 530 branches obtained from 51 trees (26 female and 25 male trees). To control for tree size we measured the diameter at breast height (DBH) of each tree. Data were analyzed using an ANCOVA (GLM, SAS 2000) where the diameter of the branches was the dependent variable; the gender of the tree was the independent variable and the DBH was a covariate.

In a subset of 51 trees located at the study site, we estimated the number of potential branches for removal by the insect borer on each male and female tree in June 1999, 2000 and 2001. We counted unattacked branches of 20 to 30 mm in diameter, which corresponds to the size of branches attacked by *O. a. chamela* under natural conditions. We used a generalized linear model applying the Genmod procedure (SAS 2000) for repeated measurements where tree was the repeated factor in the model for each year. The number of potentially attacked branches was used as the dependent variable. Because the number of potentially attacked branches does not follow a normal distribution, we used a Poisson distribution with a logarithmic link function in the analysis. Tree gender, year, and the interaction of these terms were used as the independent variables. The DBH measured for each tree was used as a covariate. A block effect was also used in the model to control for the variation associated to groups of trees clumped along each trail.

To determine the preferences and patterns of annual removal caused by the insect borer on the branches of male and female trees, we estimated the attack on each tree in the spring of 1999, 2000 and 2001. We counted the number of removed branches in the same 51 trees used in the previous analysis, 26 female and 25 male trees of *S. purpurea*. We used a generalized linear model applying a Genmod procedure for repeated measurements where tree was the repeated factor in the model for each year (SAS 2000). The number of attacked branches was used as the dependent variable. Because the number of branches does not follow a normal distribution, we used a Poisson distribution with a logarithmic link function in the analysis. Tree gender, year, and the interaction of these terms were used as the independent variables. Diameter at breast height measured for each tree was used as a covariate. We also used a block effect in the model to control for variation related to groups of trees clumped along each trail.

To make a comparable analysis of the attack levels between genders, we determined the relative attack of each tree. We counted the number of removed branches in relation to the total number of branches of equivalent diameter during years 1999, 2000 and 2001. The total number of branches was obtained by adding the number of removed branches and potential branches for attack each year. We then used a generalized linear model applying the Genmod procedure (SAS 2000) for repeated measurements with tree as the repeated factor in the model. The model used the number of removed branches divided by the total number of branches for each year as the dependent variable. A Poisson distribution and a logarithmic link function were used for the analysis. Tree gender, year and their interaction were used as the independent variables. To control for variation associated with tree size, we used the DBH as a covariate in the model. A block effect was also used to control for the variation associated with groups of trees clumped along each trail.

Because a previous study showed that patterns of nutrient production in branches of *S. purpurea* changed throughout the year (Bullock 1992), we analyzed the seasonal pattern of attack. We conducted a monthly census on the number of attacked branches for two years from 2000 to 2001 in the 51 trees used in the previous section (26 male and 25 female trees).

To determine the effect of nitrogen content between male and female trees in relation to the preference of the insect borer, we collected a sample of 90 branches between 20 and 30 mm of diameter in October 2002. Three branches per tree from 15 male and 15 female trees were used to quantify the total amount of nitrogen. The semi-kjeldhal method for acid digestion was used for each branch and then nitrogen content was determined colorimetrically with an auto-analyzer (Bran-Luebbe Auto Analyzer III, Nordestedt, Germany; method no. 696-82W; Technicon Industrial System 1977). We performed an ANCOVA (GLM; SAS 2000), using tree gender and individual tree nested within gender as independent variables and the total amount of total nitrogen per branch as the dependent variable.

Consequences of attack on vegetative growth–To determine the regeneration of naturally attacked branches of male and female trees, 210 branches were marked in the spring of 1999 (5 unattacked and 5 attacked branches of 10 male and 11 female trees of *S. purpurea*). A year later, we estimated the volume of the branches (unattacked branches and attacked regenerated branches). The volume was obtained by measuring the diameter at the base and at the tip of the meristem; and the length of each branch with the use of an electronic caliper (Mytutoyo Corporation). We obtained the volume of each branch by calculating the volume of a cylinder.

To analyze the regeneration of naturally attacked branches of male and female trees, we compared the volume of unattacked and regenerated branches between tree genders using a generalized linear model (Genmod, SAS 2000). The volume of branches was the dependent variable. Tree gender, branch condition (unattacked vs. attacked regenerated branches), individual tree nested within gender, and the interaction between tree gender and branch condition as the independent variables. We used a Poisson distribution for each analysis and a logarithmic link function.

Consequences of attack on reproductive function–To determine the probability that a regenerated branch reproduced a year after natural damage had occured, we used categorical statistical analysis to compare the proportion of fertile and non reproductive branches on unattacked and regenerated branches. The model used the number of fertile branches divided by the total number of branches of each tree as the response variable. Because the scale and distribution of this variable did not follow a normal distribution, we used a generalized linear model using a binomial distribution for the dependent variable and a logit link function using the GENMOD procedure of SAS (Stokes et al. 2000). We used the same sampled branches used in the previous vegetative section. The model used tree gender (male vs. female plants), branch condition (unattacked branches vs. attacked regenerated branches), individual tree nested within gender, and the interaction between tree gender and branch condition as the independent variables.

Results

Beetle preference

The sex ratio of male and female trees of *S. purpurea* in the population at the study site did not differ significantly from a 1:1 ratio (χ^2 = 0.009, df. = 1, P >0.05; 53 males and 52 females). The measurements of the diameter of 530 branches (obtained from 26 female and 25 male trees) removed by *O. a. chamela* indicated that there were no significant differences by gender ($F_{1,\ 528}$= 0.15, P=0.697 ANCOVA). The insect borer removed branches between 20 to 30 mm in diameter (21.7 ± 3.9), the mean diameter for removed branches in female trees was very similar to the diameter for male branches, (females= 21.8 ± 0.24), (males= 21.6 ± 0.24).

The number of branches that insects could potentially remove was counted for three consecutive years (1999-2001). A generalized linear model showed that number of potential branches for removal by the insect borer was significantly different between genders, female trees had less potential total branches for removal than male trees (χ^2 = 14.37, df = 1, P<0.0001; Genmod Procedure, SAS 2000; Fig. 1). This difference was maintained across years (χ^2= 28.47, df= 2, P<0.0001) with no significant interaction of gender by year (χ^2= 1.77, df = 2, P=0.4136). There was no effect by tree DBH in the number of removed branches (χ^2= 1.45, df =1, P=0.2283) or by block (χ^2= 11.15, df = 6, P =0.0838).

The total number of removed branches was counted for each of three consecutive years (1999-2001). The total number of removed branches did not differ significantly by tree gender (χ^2 = 0.039, df = 1, P =0.5317) though there was a significant difference across years (χ^2= 28.45, df = 2, P<0.0001) and a significant interaction between tree gender and year (χ^2 = 6.1, df = 1, P =0.05). In 1999, female trees were attacked significantly more than male trees (χ^2 = 5.83, df = 1, P <0.05) but there were no differences for 2000 or 2001 (χ^2 = 0.44, df = 1, P =0.5074 and χ^2 = 0.07, df = 1, P =0.7967, respectively) The number of removed branches was significantly affected by the DBH (χ^2 = 8.67, df = 1, P <0.005) but not by block (χ^2 = 7.11, df = 6, P =0.3105; Genmod Procedure; SAS 2000).

The proportion of attacked branches was significantly affected by tree gender (χ^2 = 10.96, df = 1, P <0.0001), by year (χ^2 = 21.33, df = 2, P <0.0001) and by the interaction of gender by year (χ^2 = 9.91, df = 2, P <0.05). In 1999 and 2000, the proportion of attacked branches in female trees was significantly greater than in male trees (χ^2 = 75.42, df = 1, P <0.0005 and χ^2 = 4.29, df = 1, P <0.05, respectively) and marginally significant for 2001 (χ^2 = 3.31, df = 1, P =

.069). The relative attack was not affected by the DBH (χ^2 = 1.82, df = 1, P =0.1777) but there was a significant block effect (χ^2 = 24.49, df = 6, P <0.0005; Genmod Procedure; SAS 2000; Fig. 1).

Oncideres albomarginata chamela girdled reproductive branches only in the dry season. For years 2000 and 2001 the reproduction period of the insect started in October, the maximum activity of attack to branches was in January of the next year and finished in April.

The nitrogen content was significantly different between genders (F= 8.3, gl= 1, P>0.005), with female trees having a greater concentration of total nitrogen than male trees. In addition, there was a significant difference in the effect of individual tree nested within gender (F= 1.71, gl= 28, P <0.05; GLM procedure; SAS 2000).

Consequences of attack on vegetative growth

There was a significant branch condition effect (attacked regenerated vs. unattacked branches) on the volume of branches (χ^2= 117, df = 1, P<0.001), with unattacked branches having more volume than attacked regenerated branches. The volume of branches was not significantly different between genders (χ^2= 2.53, df = 1, P= 0.1120). There was a significant effect of individual tree nested within gender (χ^2= 3.09, df = 19, P<0.0001), but there was not a significant effect in the interaction of tree gender by branch condition (χ^2= 0.05, df = 1, P=0.8208).

Consequences of attack on reproductive function

Figure 2 shows the reproductive response of *S. purpurea* to the removal of branches caused by *O. a. chamela* one year after branch removal occurred in relation to unattacked branches of equivalent size that were not removed. There was a significant branch condition effect (attacked regenerated vs. unattacked branches) on the probability to develop fertile branches (χ^2 = 21.91, df = 1, P<0.0001), the proportion of fertile unattacked branches was greater than the proportion of fertile regenerated branches. The proportion of fertile male branches was greater than the proportion of female branches (χ^2 = 4.01, df = 1, P<0.05). The proportion of fertile branches was not affected by individual trees nested within gender (χ^2= 26.56, df= 19, P<0.1153) and there was no effect of the interaction of gender by branch condition (χ^2= 0.41, df= 1, P=0.5237; Genmod Procedure; SAS, 2000).

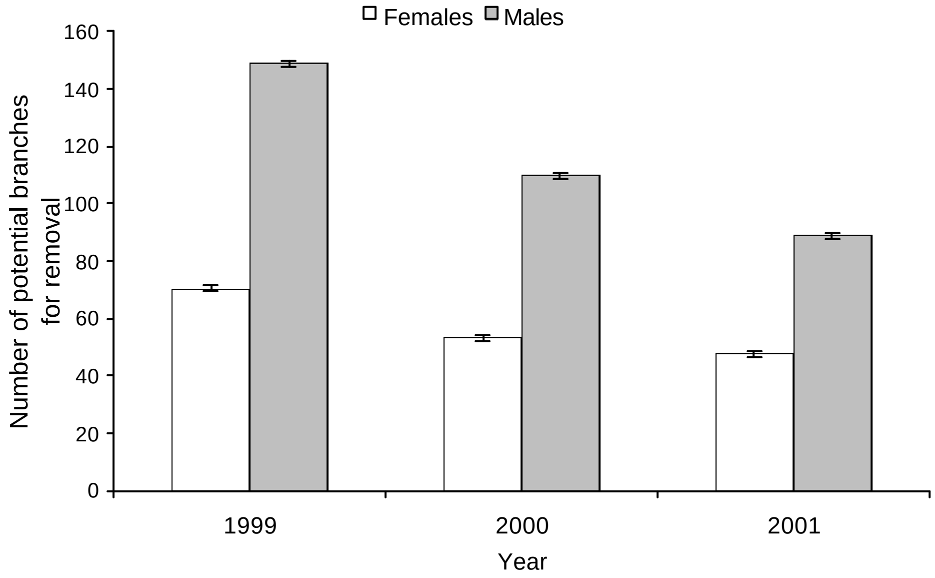

Figure 1a. LSMeans ±SE of the number of potential branches for removal.

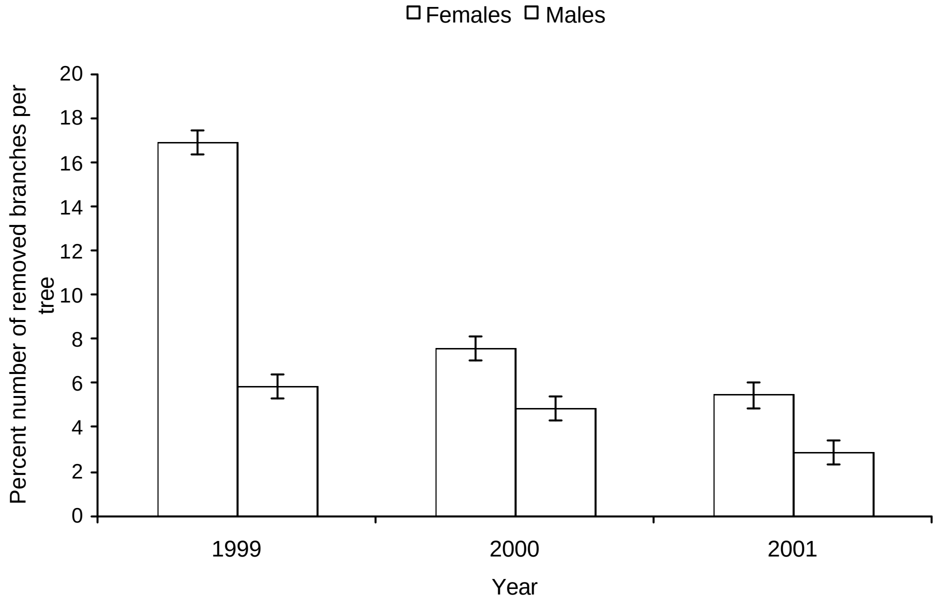

Figure 1b. Percentage of removed branches in relation of the potential branches for removal by gender. Standard errors are shown in the error bars.

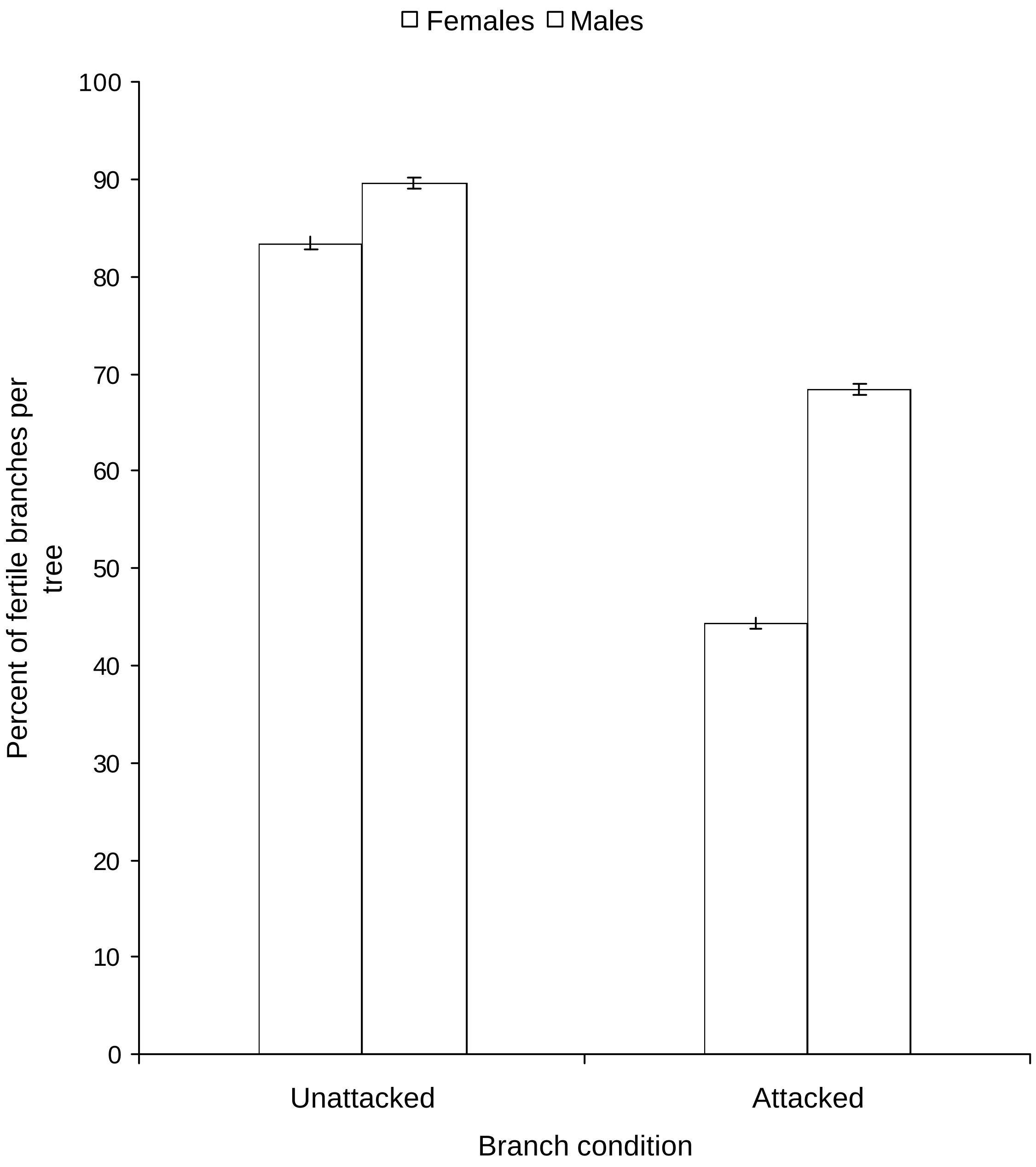

Figure 2. Percentage of fertile branches in male and female trees of *S. purpurea* one year after removal by insects occurred and on branches of equivalent size that were not removed. Standard errors are shown in the error bars.

Discussion

Studies on the patterns of removal of entire branches and its consequences for growth and reproduction of plants are few (Caraglio et al. 2001, Feller 2002). The preference of attack for female trees of *S. purpurea* during some years does not agree with several other studies on dioecious species. A review of the literature indicates that in 15 studies of foliar herbivory, 11 showed more preference for male than female plants (Ågren 1999). Similar evidence has been found for twig damage, where most studies indicate preference for male plants (Danell et al. 1985, Boecklen et al. 1990, Krischik and Denno 1990, Danell et al. 1991, Hjältén 1992, Boecklen and Hoffman 1993). Contrary to expectation, our study shows the proportion of branches removed by the insect borer was greater for female than for male branches in some years, even though the sex ratio of trees in the population is equal and male trees had far more potential branches for removal. Therefore, the possibility that an insect finds and removes a male branch is greater than a female branch. Insects preferentially attack and remove the branches before the reproductive season of *S. purpurea* when fertile branches had accumulated the maximum concentration of TNC (Bullock 1992) and nitrogen. In addition, the fertile branches of female trees had significantly more TNC and nitrogen than male branches (Bullock 1992). The female insect borer cut and oviposited on the branches after removal, the preference for female trees by *Oncideres* could be associated with a greater quality of resources for their progeny, because the period of branch removal, oviposition and initial development of insect larvae, corresponds to the period of time with the greatest amount of nonstructural carbohydrates and nitrogen content in female branches.

An alternative explanation for the preference of female trees by *O. a. chamela* might be related to the defenses of attacked plants. Preferences of herbivores for plants have also been explained by differential concentration of secondary compounds for defense. However, this evidence differs between plant species and gender (Alliende 1989, Boecklen and Hoffman 1993). A review of studies in herbivory on dioeciuos plants have shown that in 13 species the concentrations of secondary compounds was higher in female plants; however in five species the concentration of at least one secondary compound was higher in male plants (Ågren et al. 1999). This type of herbivory isolates the tissue that is used by the insect from the plant, possibly preventing induced compounds from reaching the damaged plant tissue. Even though we did not quantify the production of secondary compounds, induced resistance has been reported in Anacardiaceae (Strauss 1991), so *S. purpurea* could produce induced responses. Plants higher in constitutive compounds are likely to be more defended by secondary compounds, consequently female branches should have more protection than male branches due to higher amounts of TNC and N. However, even if male trees were more defended, the insect borer might avoid these compounds by removing entire branches. Therefore, the preference for female trees by the insect borers could be more related to the nutritional quality than to the avoidance of secondary compounds produced differentially among genders.

Consequences on plant reproduction by leaf damage have shown a continuum of responses from negative to favorable, though most of the evidence has indicated detrimental effects to plant fitness (Marquis 1984, Whitman et al. 1991, Marquis 1992, Quesada et al. 1995, Strauss et al. 1995, Avila-Sakar and Stephenson 2003). In dioecious species, female plants have a greater investment in biomass and energy for reproduction in detriment to vegetative growth (Lloyd and Webb 1977, Delph 1999, Avila-Sakar et al. 2001). In *S. purpurea*, the volume and number of branches in both genders is negatively affected by the damage caused by the insect borer a year after damage had occurred. However, male trees produced a greater proportion of fertile branches than females. Female trees were significantly more attacked and had less number of branches than male trees. Therefore, female plants need to invest more resources to replace the detached vegetative and fertile tissue with greater negative consequences to their fitness than male trees.

In conclusion branch removal is a type of damage scarcely studied that significantly affects growth and reproduction of trees. The pattern of attack by *O. a. chamela* on *S. purpurea* branches indicates a preference for female plants, apparently associated with the greater nutritional quality found in females.

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CAPITULO II

Consequences of branch removal by the insect borer *Oncideres albomarginata chamela* (Cerambycidae) on the male and female reproductive success of the tropical tree *Spondias purpurea* (Anacardiaceae).

ABSTRACT

Few studies of plant herbivore-interactions have evaluated the effects of branch damage in tropical dioecious species. The consequences of branch removal by the girdled borer *Oncideres albomarginata chamela* on fertility and fruit production of wild prune (*Spondias purpurea*) were evaluated over the 1999-2003 reproductive seasons. The goals were (1) to determine the effects of branch removal on female fertility, (2) to determine the effects of branch removal on male fertility, (3) to evaluate the effects on fruit production during three reproductive seasons, and (4) to measure the seasonal and cumulative effects of branch removal on the total production of fruits per tree from two to four reproductive seasons. The consequences on reproduction were evaluated in intact and attacked regenerated branches. The fertility of branches was affected by branch removal in both tree genders; female trees produced less number of fertile branches than male trees. This pattern was maintained between years. The number of fruits produced per branch and the total fruit production per tree also was negatively affected by branch removal; in both cases the fruit production differed between seasons. Cumulative branch removal over several years affected fruit production of the subsequent seasons.

RESUMEN

Pocos estudios de interacciones planta-herbívoro han evaluado los efectos de la remoción de ramas sobre especies tropicales dioicas. Las consecuencias de la remoción de ramas por *Oncideres albomarginata chamela* sobre la fertilidad y la producción de frutos del ciruelo silvestre (*Spondias purpurea*) fueron evaluadas durante las temporadas reproductivas de 1999 a 2003. Los objetivos fueron (1) determinar los efectos de la remoción de ramas sobre la fertilidad femenina, (2) determinar los efectos de la remoción de ramas sobre la fertilidad masculina (3) evaluar los efectos sobre la producción de frutos durante tres temporadas reproductivas y (4) evaluar los efectos estacionales y acumulativos de la remoción de ramas sobre la producción total de frutos por árbol de dos a cuatro temporadas reproductivas. Las consecuencias sobre la reproducción fueron evaluadas en ramas intactas y ramas regeneradas. La fertilidad de las ramas fue afectada por la remoción en árboles de ambos sexos; los árboles femeninos producen menor número de ramas fértiles que los árboles masculinos, manteniendo este patrón entre años. El número de frutos producidos por rama y la producción total de frutos por árbol también fueron negativamente afectados por la remoción de ramas; en ambos casos la producción de frutos fue distinta entre temporadas. El número de ramas removidas acumuladas después de varios años afectó la producción de frutos de las temporadas subsecuentes.

INTRODUCTION

Dioecious plants produce unisexual flowers in different individuals (Lloyd and Webb 1977). Theoretical models generally identify three key factors that have determined the evolution of separate of sexes in dioecious plants: the optimal allocation of resources to genders, a genetic control of sex expression and the fitness consequences that complete outcrossing may have over selfing (Barrett 2002). Recently, other theoretical models suggest biotic factors, such as herbivory, as potential selective forces in the evolution of separate sexes (Ashman 2002).

Studies of leaf herbivory in dioecious plants have established the preferences of herbivores to plant genders, the relation of herbivores to certain morphological and physiological characteristics of leaves between plant genders, and the consequences of herbivory damage on growth and reproduction of plants (Ågren *et al.* 1999, Obeso 2002). Studies of preference patterns by herbivores have reported greater herbivory rates or higher density of herbivores on male plants (Danell *et al.* 1985, Alliende 1989, Jing and Coley 1990, Krischik and Denno 1990, Elmqvist *et al.* 1988, Boecklen and Hoffman 1993, Boecklen *et al.* 1990). A qualitative review of the morphological and physiological differences between genders suggest there are higher concentrations of phenol and terpens in female plants, but higher nutritional quality, amount of secondary compounds, trichoms, resins and hardness in male plants (Danell *et al.* 1985, Ågren, 1987, Allen and Antos 1988, Polhemus 1988, Boecklen *et al.* 1990, Jing and Coley 1990, Krischik and Denno 1990, Danell *et al.* 1991, Hjältén 1992, Cipollini and Whigham 1994, Ågren *et al.* 1999, Verdu *et al.* 2004). However, a more recent meta analysis showed no consistent differences because plant genotype or environmental conditions are more associated to chemical differences (for nutrition or defense) than plant gender (Cornelissen and Stiling 2005).

Only few studies have evaluated the consequences of herbivore damage on growth and reproduction of dioecious plants. These studies showed that in male plants, apex damage decreases branching and that artificial damage to leaves reduces the number of male flowers and vegetative growth (Delph et al. 1993, Mutikainen et al. 1994, Mutikainen and Delph 1996). In female plants, leaf damage decreased the number of flowers, capsule production, seed production, seed size and increased the abortion of inflorescences, although apex damage increased inflorescence dry mass and plant branching (Elmqvist and Gardfell 1988, Mutikainen *et al.* 1994). The consequences of insect damage to dioecious plants have mainly concentrated on herbivory to leaves but the consequences of damage to branches, stems and trunks have been scarcely evaluated on dioecious species, despite the fact that this kind of damage caused by insect borers is common in nature (Strauss 1991, Uribe-Mú and Quesada 2006). Cerambycid beetles are distributed worldwide and about 50% of the species are capable of girdling or remove complete branches of trees, causing severe damage to certain species in natural populations and plantations (Linsley 1961, Morewood et al. 2003). Compared to leaf consumption, branch removal implicates the loss of reproductive and photosintetic tissue, less resource storage in branches and the loss of more biomass (Zangerl and Bazzaz 1992, Feller and Mathis 1997, Feller 2002). Therefore, a decrement of resource storage in branches might negatively affect plant reproduction in subsequent reproductive years.

In this study we analyze seasonal and cumulative consequences of branch removal by the girdler borer *Oncideres albomarginata chamela* on the reproduction of the tropical dioecious tree *Spondias purpurea.* A previous study indicated that *O. a. chamela* removed greater proportions of woody tissue from female trees (Uribe-Mú and Quesada 2006). The first objective of this study was to determine the effects of branch removal on female and male fertility. The second objective was to evaluate the effects of branch removal on fruit production during two reproductive seasons. The third objective was to measure the seasonal and cumulative effects of branch removal on total fruit production per tree for three reproductive years. We predicted that females will show stronger negative effects on reproduction caused by the greater proportion of tissue removed.

METHODS

The study was conducted in the Chamela-Cuixmala Biosphere Reserve at Chamela Biological Station, UNAM (19°30'N, 105°03'W) located on the pacific coast of Jalisco, Mexico from March 1999 to March 2004. The vegetation is tropical dry forest with a mean annual rainfall of 707 mm and a dry season that extends from November to June (Bullock 1988).

We studied the interaction between the insect borer, *O. a. chamela* (Chemsak and Giesbert) (Coleoptera: Cerambicidae) and the tropical tree *S. purpurea* L. (Anacardiaceae). *S. purpurea* is a common dioecious tree of the tropical dry forests of México. This species can reach to 15 m in height and almost 80 cm in diameter at the base (Barajas-Morales and León-Gómez 1989). Leaves are compound with 5 to 12 eliptic-acute leaflets of 2 to 4 cm in length (Martínez 1979). Flowers are red, sessile and unisexual (Bullock 1992). Trees are deciduous; flowering and fruiting occurs from December to May and leaves are maintained from June to November (Bullock and Solís -Magallanes 1990).). Bullock (1992) has shown tha fertile female branches had more TNC than male branches before the reproductive season of *S. purpurea*, but that such difference was not significant when comparing sterile branches between genders.

Oncideres albomarginata chamela is a longhorn beetle that removes and oviposits branches of plants. The body length of this species is 17 to 31 mm and 6.5 to 12 mm wide (Noguera 1993). The reproductive period of this species ranges from October to January, during these months female beetles use their mandibles to completely detach branches of 20 to 30 mm in diameter. Detached branches of unknown fertility may fall to the ground or hang from the trees or shrubs below the affected *S. purpurea* tree. Female insects oviposit on the removed branches were offspring remain until they emerge as adults.

FEMALE AND MALE FERTILITY IN S. PURPUREA— The proportion of fertile (i.e reproductive) and unfertile branches were registered in 106 (53 intact and 53 regenerated branches) from 10 trees at one, two and five years after *O. a. chamela* attack occurred. The DBH was measured for each tree. To analyze the probability that a regenerated branch reproduces at one, two or five years, we used a categorical statistical analysis to compare the proportion of fertile and unfertile branches on intact and regenerated branches. In order to control the influence of plant age for fertility and fruit production, the DBH was measured for each tree. We conducted a Genmod procedure (SAS 2000) for repeated measurements, with tree as the repeated factor in the model for each year. The model used branch condition (intact branches vs. attacked regenerated branches), year and their interaction as main effects; the categorical dependent variable was branch fertility and the DBH was a covariate. A binomial distribution with a logit link function was used in the analysis (Stokes et al. 2000).

To determine the effects of branch removal on male function of *S. purpurea*, the proportion of fertile (*i.e* reproductive branches) and unfertile branches was evaluated in 86 (43 intact and 43 regenerated branches after attack) from 8 male trees. We registered branch fertility one, two and five years after branch removal occurred. In order to control the influence of plant age on male fertility we measured the DBH for each tree. We used a Genmod procedure for repeated measurements (SAS 2000), where individual tree was the repeated factor in the model for each year. The model used branch condition (intact branches vs. attacked regenerated branches), year and their interaction as main effects; branch fertility as the categorical dependent variable and the DBH as a covariate. A binomial distribution with a logit link function was used in the analysis (Stokes et al. 2000).

NUMBER OF FRUITS PER BRANCH. — The number of fruits produced per branch was counted one, two and five years after damaged had occurred on the same branches used in the fertility analysis. To determine the relationship between the number of fruits produced with respect to branch condition we conducted a generalized linear model using a Genmod procedure for repeated measurements (SAS 2000) where tree was the repeated factor in the model for each year. The model used branch condition, year and their interaction as independent variables; the number of fruits per branch was the dependent variable. We used a Poisson distribution for the analysis with a logarithmic link function.

BRANCH REMOVAL EFFECTS ON TOTAL FRUIT PRODUCTION. — To determine the effect of branch removal on the total production of fruits per tree into the same reproductive season, we first determined the proportion of removed branches by *O. a. chamela*. This proportion was the total number of branches damaged by the cerambycid in relation to the total number of branches of equivalent diameter for each tree. We obtained the total number of branches by adding the number of removed branches and potential branches corresponds to the size of branches attacked by *O. a. chamela* under natural conditions (20 to 30 mm in diameter; Uribe-Mú and Quesada 2006). Branch removal was divided into three categories: 0-10% (low), 10-20% (medium) or more than 20 %(high). The total number of fruits produced per tree was counted in 37 female trees distributed along 7 km of trails in the study site from 2000-2003. DBH was measured for each tree and used as a covariate. We used a generalized linear model applying the Genmod procedure (SAS 2000). Branch removal category, year and their interaction were the independent variables and total fruit production was the dependent variable. A Poisson distribution with a logarithmic link function was used for the analysis.

To determine the cumulative effects of branch removal by *O. a. chamela* on the total production of fruits per tree we used a subsample of 18 female trees from the section of total fruit production per year; we first obtained the cumulative proportion of removed branches during two years of reproductive periods (2000-2001). Cumulative proportions of damage for years 2002 and 2003 were also obtained, adding the data for the subsequent reproductive periods. The total number of fruits produced in the 18 female trees for years 2001, 2002 and 2003 were counted. We performed regression analyses: the dependent variable was the logtransformed number of fruits (in years 2001, 2002 and 2003) and the independent variable were the cumulative proportion of branch removal (arcsin transformed).

RESULTS

FEMALE AND MALE FERTILITY IN S. PURPUREA— Branch condition (intact vs. regenerated) had a significant effect on the fertility of branches ($\chi^2 = 3.87$, df = 1, $P < 0.05$). Intact branches had higher proportion of reproductive branches. The proportion of fertile branches was not significantly different among years ($\chi^2 = 4.85$, df = 2, P = 0.08). There was no year by branch interaction on the proportion of fertile branches ($\chi^2 = 0.2$, df = 2, P = 0.90), and DBH had no effect on the fertility of branches ($\chi^2 = 0.05$, df = 1, P = 0.82). (Fig. 1)

Branch condition (intact vs. regenerated) had a significant effect on the fertility of branches ($\chi^2 = 4.6$, df = 1, P < 0.05) Intact branches produced more fertile branches than regenerated ones. There were significant differences in the fertility of branches among years ($\chi^2 = 6.17$, df = 2, P < 0.05). However, there was no effect of the interaction of branch condition by year ($\chi^2 = 1.36$, df = 2, P = 0.51), and no effect of the DBH in the proportion of fertile branches ($\chi^2 = 0.02$, df = 1, P = 0.90) (Fig. 2).

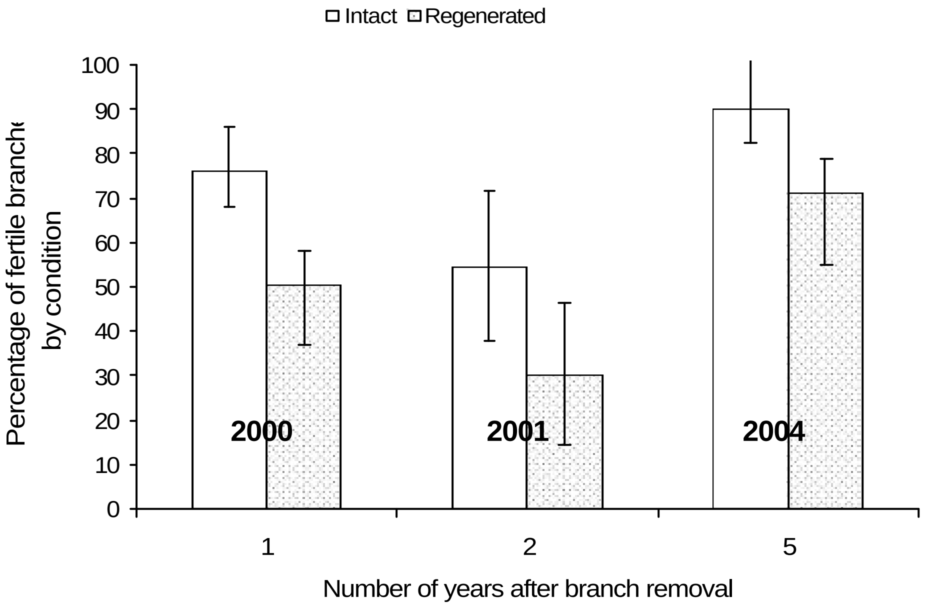

Figure 1. Percentage of fertility from intact and regenerated branches in female trees. Confidence limits are shown in the error bars.

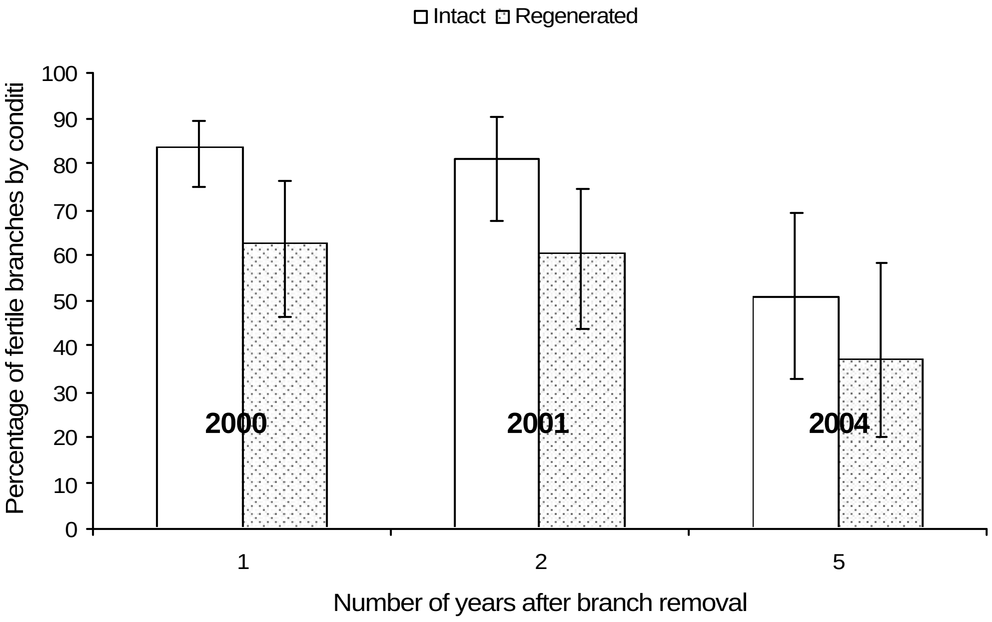

Figure 2. Percentage of fertility from intact and regenerated branches in male trees. Confidence limits are shown in the error bars.

NUMBER OF FRUITS PER BRANCH. —There was a a significant effect of branch condition on the number of fruits produced (χ^2 =3.69, df = 1, P = 0.05), and intact branches produced more fruits than regenerated branches. The number of fruits produced per branch was significantly different between years (χ^2 = 3.68, df = 2, P = 0.05). Female trees produced more fruits in both branch types one year after damage than two years later. There was no effect of branch condition by year (χ^2 = 0.38, df = 1, P = 0.54) (Fig. 3).

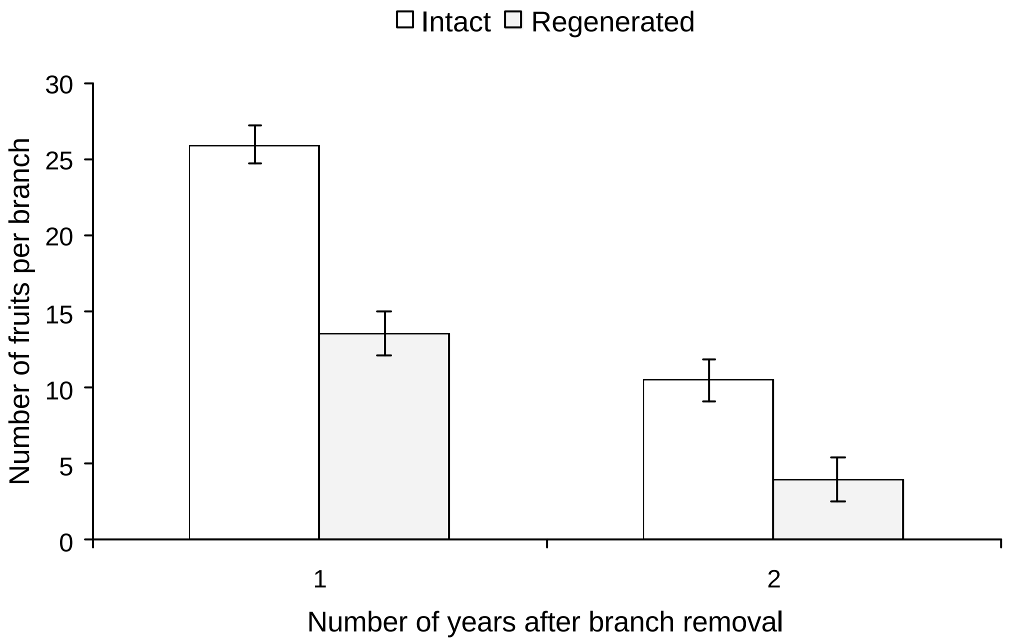

Figure 3. Mean number of fruits from intact and attacked regenerated branches. Standard errors are shown in the error bars.

EFFECT OF BRANCH REMOVAL ON TOTAL FRUIT PRODUCTION PER TREE. — There was a significant effect of branch removal on the total fruit production per tree into the same season (χ^2 = 5.86, df = 2, P < 0.05). The number of fruits per tree decreased as damage level increased. There were non-significant differences between years on total fruit production (χ^2 = 2.99, df = 2, P = 0.22). There was no damage level by year interaction (χ^2 = 4.32, df = 4, P = 0.36). The DBH had a significant effect in the total number of fruits per tree (χ^2 = 5.93, df = 1, P < 0.01) (Fig. 4)

A regression analysis showed that there was no significant effect of cumulative branch removal for years 2000-2001 on total fruit production per tree (R^2 =0.095, P=0.22) (Fig. 5a). For years 2000-2002 there was a significant effect of cumulative branch removal on total fruit production per tree (R^2=0.232, P < 0.05) (Fig. 5b). For years 2000-2003, there was a significantly negative effect of cumulative branch removal on total fruit production per tree (R^2=0.245, P< 0.05) (Fig. 5c).

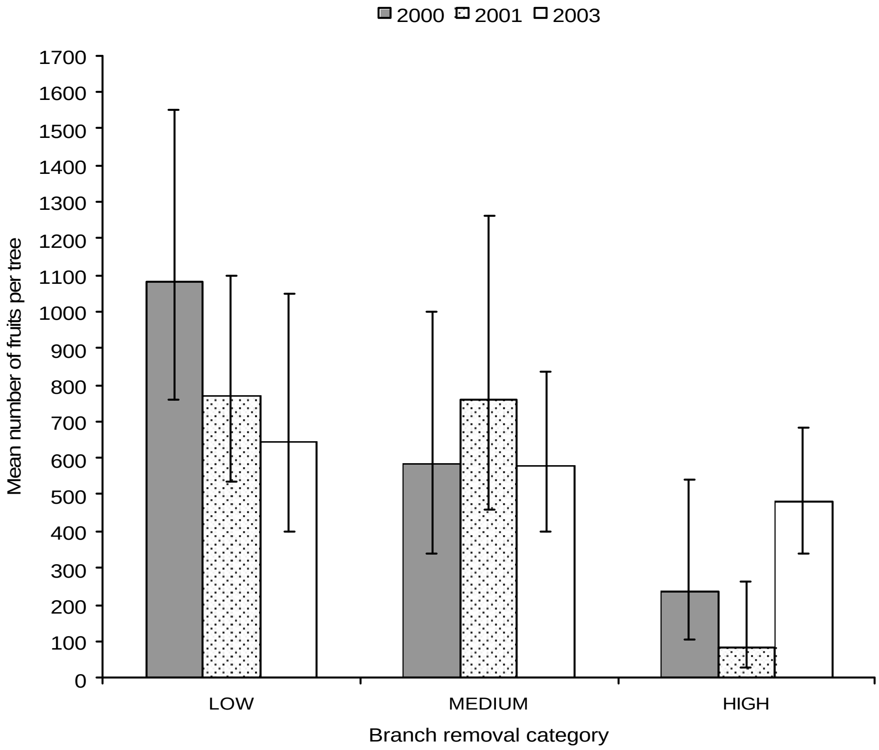

Figure 4. Relationship between total fruit production and branch removal on female trees of *S. purpurea*. Confidence limits are shown in the error bars.

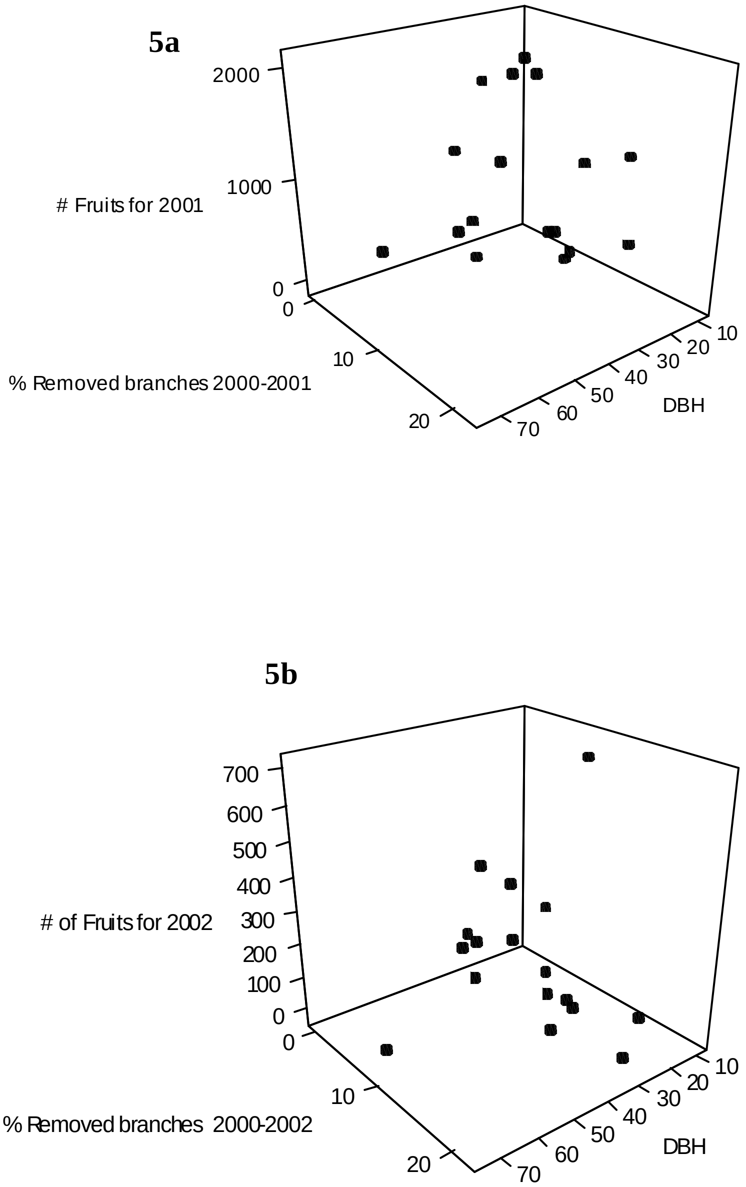

Figure 5. Relationship between total fruit production per tree, DBH and percentage of cumulative branch removal during subsequent years, a) 2000 -2001, b)2000-2002

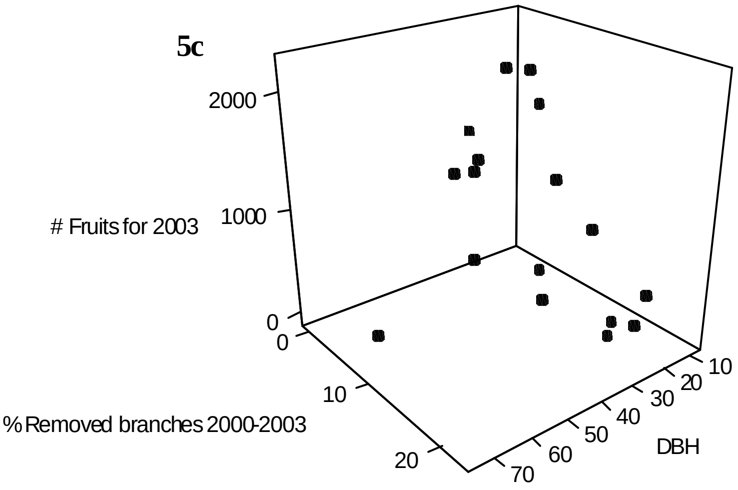

Figure 5. Relationship between total fruit production per tree, DBH and percentage of cumulative branch removal during subsequent years, c) 2000-2003.

Discussion.

Similar to the studies of leaf damage (Elmqvist and Gardfell 1988, Delph *et al.* 1993, Mutikainen *et al.* 1994, Cornelissen and Stiling 2005), we found that branch removal by *O. a. chamela* negatively affected the reproduction of *S. purpurea*. First, we found that in both female and male plants, the proportion of fertility was greater in intact branches compared to regenerated branches one, two and five years after damaged had occurred. Second, in male trees, the proportion of fertile branches was greater in intact than in regenerated branches, but the difference in fertility between branch types decreased over time. Third, the number of fruits produced per branch was greater in intact than in regenerated branches. Fourth, at the individual tree level, total fruit production decreased as the percentage of branch removal increased every year.

The first two results indicated that female and male trees of *S. purpurea* always maintained a greater proportion of fertility in intact branches and that difference between branch conditions were similar across years. Allocation of resources for growth of vegetative tissue rather than reproduction occurred in recently damaged branches (Uribe-Mú and Quesada 2006). Some regenerated branches reproduced one, two and five years after damage occurred but their output was always lower than in intact branches. Also, there were differences in the number of fertile branches across years, whith the lowest year for females is 2001 and for males is 2004. Therefore, differences in fertility across years might be due to internal resource allocation between genders rather than to external environmental conditions. In general, damage caused by insect borers was likely to reduce the number of fertile branches which, in turn, reduced the production of flowers and fruits over several years, thus potentially affecting the fitness of *Spondias purpurea*. Our results support other studies with long lived species that have indicated negative effects of herbivory on female reproduction (Rockwood 1973, Stephenson 1980, Heichel and Turner 1984, Marquis 1984, Louda 1984, Elmqvist and Gardfell 1988, Tuomi *et al.* 1988, Sacchi and Connor 1999) and male function (Mutikainen *et al.* 1994, Quesada et al. 1995, Mutikainen and Delph 1996, but see Strauss et al. 2001)

Our third result showed that intact branches produced more fruits per branch compared to regenerated branches, and that female plants could not compensate in the fruits produced per branch two years after damage occurred. Differences between years in fruit production possibly might be caused by the decrement in fertility of year 2001, and by the low resource assigned to reproduction in 2001 compared to year 2000. Branch removal might be more severe than leaf damage (Zangerl and Bazzaz 1992, Feller 2002) because plants must regenerate the lost vegetative tissue. In the european tree *Ilex aquifolium,* artificial damage of girdled and 50% of defoliation reduced 30% of fruit production compared to ungirdled branches with the same defoliation treatment, but there were no effects of girdling treatment alone. The results of this study suggest that most assimilates in girdled branches were imported from other branches and used to fruit production (Obeso 1998). In *S. purpurea* the distribution of resources in recently damaged branches affects the production of fruits because most assimilates must be used to produce vegetative and reproductive new tissue.

The fourth result showed strong effects of branch removal on total fruit production over several years. The reduction of fruit production in *S. purpurea* depended of the proportion of removed branches with the exception of year 2001. Similar results have been found in most of the studies that have evaluated the effects of leaf removal in woody plants: in general, higher fruit abortion or fewer fruits per branch or whole individuals have resulted in several species of tropical trees after leaf damage occurred (Rockwood 1973, Obeso 1993).

Four years of cumulative branch removal by *O. a. chamela* caused a significantly negative effect on total fruit production of *S. purpurea*. Few studies have analyzed cummulative damage on plant performance over several consecutive years. Our study coincides with the results found in *Piper arieianum,* where seed production of large plants was still reduced after 2 years of defoliation (Marquis 1984). Cumulative defoliations also affected vegetative growth (Kaitaniemi et al. 1999). In *Cornus florida* trees maintained their leaf biomass and apparently was not affected by defoliations of one previous year, but two years of cumulative events of leaf removal affected the number of long shoots (Sacchi and Connor 1999). Similarly, in *S. purpurea* branch removal through years also might affect the resources for growth of new tissue. The removal of vegetative structures implicates the loss of potential resources for growth obtained during the previous rainy season via photosynthetic tissue and/ or stored in woody tissue (Bullock 1992). Therefore, through loss of vegetative tissue, cumulative damage through subsequent years does affect plant reproduction.

In conclusion, our data suggest that branch removal by *O. a. chamela* had seasonal and cumulative negative consequences on the reproduction of *S. purpurea*. The loss of whole branches also might affect the storage and allocation of resources. Finally, the absence of compensation in male fertility even five years after branches were removed, and the decrement on total fruit production through consecutive years suggest that this kind of damage might be more severe than other types of herbivory.

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CAPÍTULO III

Effects of plant gender on larval survival and larval weight of *Oncideres albomarginata chamela* (Coleoptera: Cerambycidae)

Abstract

Differential investment of resources in reproduction and defense between male and female plants might influence the quality of insect herbivore hosts. *Oncideres albomarginata chamela* Chemsak & Giesbert is a longhorned beetle that removes complete branches of their host plants for reproduction. We evaluated larval survival and mass of *O. a.chamela* in the wild prune, *Spondias purpurea*. The goals were to compare larval survival and mass in relation to genders of *S. purpurea,* in order to establish a relationship between the nutrional quality of the gender from which the hosts feed and the performance of insect larvae. Insect performance of this xylophagous species was evaluated on the larvae developed on the branches killed by adult females of *O. a. chamela.* Some nutritional aspects of the chemical composition between plant genders were determined from a sample of potential branches for removal from male and female trees.We found no effects of plant gender on the number of oviposition sites, survival and mass of the larvae, but we found effects of variation at individual tree level. Phosphorus content and Total Non-Structural Carbohydrates (TNC) were similar between plant genders. Our results suggest that plant gender did not determine the larvae performance

Resumen

La diferencias en la asignación de recursos para reproducción y defensa entre sexos de plantas dioicas, puede afectar su calidad como hospederos y a su vez influir el desempeño de los insectos que se alimentan y desarrollan en ellas. Evaluamos la sobrevivencia y peso de las larvas de *Oncideres albomarginata chamela* Chemsak & Giesbert en ciruelo silvestre. Los objetivos fueron determinar la sobrevivencia y el peso larval entre los sexos de *S. purpurea,* y establecer la relación entre la calidad nutricional del sexo del hospedero y el desempeño de las larvas de insectos. El desempeño del insecto se evaluó en las larvas que se desarrollaron dentro de las ramas removidas por los insectos adultos de *O. a. chamela*. La sobrevivencia y el peso de las larvas se asociaron con el sexo de la planta. No detectamos efectos del sexo de la planta sobre el número de sitios de oviposición, sobreviencia de larvas y peso larval de *O. a. chamela,* pero encontramos un efecto de árbol anidado dentro de sexo. Algunos aspectos nutricionales de la composición química entre sexos de la planta se analizaron en una muestra de ramas potenciales para remoción provenientes de árboles hembras y árboles machos. El contenido de fósforo y CNE fue similar entre árboles machos y hembras de *S. purpurea*. Los resultados sugieren que el sexo de la planta no determina el desempeño de las etapas iniciales de desarrollo de *O. a. chamela* en *S. purpurea*. Otros factores asociados con la variación en la resistencia de las plantas o factores externos como la competencia dentro de las ramas podrían estar afectando más el desempeño de las etapas iniciales de las larvas que el sexo de los árboles de *S. purpurea*.

Introduction

The choice of plant hosts by adult insects and the subsequent development and performance of its progeny is a central issue in understanding the evolution of plant-herbivore interactions (Thompson 1988). Larval performance and fecundity of insect herbivores are affected by several factors associated to host plant quality such as secondary compounds, physical characteristics, nutrient availability, plant genotype and plant gender (Price et al. 1980, Scriber and Slanski 1981, Thompson 1983, 1988, Dirzo 1984, Haukioja et al. 1985, Krischik and Denno 1990, De Bruyn et al. 2002, Fritz et al. 2003, Hendricks and Collier 2003, Espinosa and Fornoni 2006).

Most of the studies that have analyzed the effects of secondary compounds of plants on insect performance have shown strong negative effects on larval survival, larval growth and developmental time (Hwang and Lindroth 1997, Foss and Rieske 2003, 2004; Donaldson and Lindroth 2004). Some studies that have analyzed physical characteristics of plants have also shown negative effects on insect digestibility, relative growth rate, and larval and pupal mass (Krischik and Denno 1990, Wheeler and Center 1997, Catta-Preta and Zucoloto 2003, but see Foss and Rieske 2003).

Nutrient availability and water content of vegetative tissue affect mainly the performance of larval and immature insect stages (Scriber and Slansky 1981, Haukioja et al. 1985, De Bruyn et al. 2002). For example, nitrogen content can positively affect larval survival (Forcella 1981, Berner et al. 2005), larval mass (Osier and Lindroth 2001 but see Fernandes et al. 2000); pupal mass (Wheeler and Center 1997, Catta-Preta and Zucoloto 2003, Lower and Orians 2003), developmental time (Wheeler and Center 1997, Lower and Orians 2003), and fecundity (Fortin and Mauffette 2002). Other nutrients such as soluble sugars and starch concentration can also increase the relative growth rate of insect larvae (Osier and Lindroth 2001, Caldeira et al. 2002). Water stress in plants may also enlarge the developmental time of herbivores, increasing the risk to predation (Hanks and Denno 1993, Lower and Orians 2003) and decreasing the larval survival (Scheirs and De Bruyn 2005, Agele et al. 2006; but see, Caldeira et al. 2002, Wang et al. 2002).

Effects associated to plant genotype, also influence insect performance (Strauss 1990, Glynn and Larsson 1994, Cronin and Abrahamson 1999, Lindroth et al. 2002, Brodbeck et al. 2004, Osier and Lindroth 2004). For example, the gypsy moth *Limantrya dispar* increase its developmental time, and decreases its growth rate, pupal mass and fecundity in plants with higher phenolic glycosides (Hemming and Lindroth 1999, Hemming and Lindroth 2000, Osier et al. 2000, Osier and Lindroth 2001, Lower et al. 2003, Lower and Orians 2003).

Plant gender can potentially affect the performance of insects that feed on them due to differential investment of resources in plant reproduction and defense (Jing y Coley 1990). However, some studies have shown no difference in insect survival, larval weight and daily fecundity between plant genders (Krischik and Denno 1990, Strauss 1990), while others have shown higher larval survival on female plants under natural conditions (Fritz et al. 2003, Hendricks and Collier 2003) or have reported higher fecundity when female insects feed from leaves of male plants (Krischik and Denno 1990).

In this study we evaluated if larval survival and mass of the girdler borer *O. a. chamela* differed in with male and female tree hosts of the dioecious tropical tree *S. purpurea. O. a chamela* is a cerambycid beetle that removes complete branches of their host plant species for reproduction. A previous study indicates that the number of removed branches by *O. a. chamela* is equal or higher for female trees despite the fact that male trees of *S. purpurea* had significantly more branches than females. In addition, female branches contained greater nitrogen concentrations compared to male branches suggesting that insect selection might be affected by the nutritional quality of the host (Uribe-Mú and Quesada 2006). The objectives of the study were (1) to determine if larval survival and mass differ between genders of *S. purpurea* and (2) to establish if there is a relation between the phosphorus and total nonstructural carbohydrates content of host plant gender, with the performance of insect larvae. We predict that *O. a. chamela* will increase the number of oviposition sites, larval survival and larval mass on female branches if female trees have higher nutritional quality than males.

Materials and Methods

Study site. The study was conducted at Chamela Biological Station, Universidad Nacional Autónoma de México inside the Chamela-Cuixmala Biosphere Reserve (19°30'N, 105°03'W) located on the pacific coast of Jalisco, Mexico from September 1999 to March 2004. The vegetation is tropical dry forest with a mean annual rainfall of 707 mm and a dry season that extends from November to June (Bullock 1988).

Study species. *Oncideres albomarginata chamela* Chemsak & Giesbert is a longhorned beetle that removes completely the branches of the host plants for oviposition. This beetle uses the mandibles to remove branches from 20 to 30 mm in diameter from October to January (Uribe-Mú and Quesada 2006). The branches removed fall to the ground, or hang from the trees and over the shrubs. Female insects make numerous incisions on the bark along the branch, prepare the oviposition sites and oviposits the branches where the larvae develop and pupate until the adults appear. Several species of beetles use the branches removed by girdled borers for reproduction (Linsley 1959, 1961, Hovore and Penrose 1982) and this also is the case for our study system.

The body length of this species is 17 to 31 mm and 6.5 to 12 mm wide, oval, elongated, semicylinder and their color vary from brown reddish to black. The species name is attributed to a characteristic fringe of white pubescence along the elytra (Noguera 1993). *O. albomarginata chamela* is located in Mexico in the states of Jalisco, Guerrero and Veracruz, but the presence in other tropical countries is at present unknown.

Spondias purpurea L. (Anacardiaceae) is a common dioecious tree of the tropical dry forest in Mexico (Rzedowski 1978) that can reach up to 15 m in height and almost 80 cm in diameter at the base (Barajas- Morales and León-Gómez 1989). Leaves are compound with five to 12 eliptic-acute leaflets of two to four cm in length (Martínez 1979). Flowers are red, sessile, unisexual and dimorphic between males and females (Bullock 1992). Trees are deciduous; flowering and fruiting occurs from December to May and leaves are maintained from June to November (Bullock & Solís-Magallanes 1990). A previous study (Bullock 1992) showed that fertile female branches had more TNC than male branches before the reproductive season, but that unfertile branches produced similar amounts of TNC regrdless of gender (Bullock 1992).

Larval performance. We determined the number of ovipositions by *O. a. chamela* on male and female branches of *S. purpurea* on a sample of 56 branches from 21 female and 20 male trees of *S. purpurea* during years 2003 and 2004. Because *O. a. chamela* is the unique lamiinae of big size in the study site and the oviposition marks made by this tribe are very characteristics, we could safely assume that females of this species made the oviposition marks on the branches. The branches were collected, weighted and the number of oviposition sites were registered. We performed a generalized linear model applying the Genmod procedure (SAS 2000). The number of oviposition sites per branch was the dependent variable, the gender of the branch, the year and the individual tree nested within gender were the independent variables. In order to control the variation associated with branch size we used the dry mass of branches as covariate in the model.

To determine larval survival we used a sample of 48 branches from 14 females and 19 male trees of *S. purpurea* that were oviposited by *O. a. chamela*. The branches collected were weighted and the number of oviposition sites were registered. Two months after collections were made, the branches were dissected and the larvae found inside were extracted and preserved in 70% ethylic alcohol. Larvae of *O. a. chamela* were separated using literature of Böving and Craighead (1931), and Duffy (1960). The survival proportion of *O. a. chamela* larvae was obtained as the number of individual larvae divided by the number of oviposition sites. We performed an ANCOVA (GLM procedure; SAS 2000) with the survival proportion as the dependent variable; tree gender, year, and individual tree nested within gender as the independent variables; dry mass of branches was used as a covariate. The survival proportion was arcsin transformed to achieve normality.

To determine any possible effects of host gender on larval performance, we measured the mass of each *O. a. chamela* larvae, 140 individuals (56 larvae from 29 branches of 10 female trees and 82 larvae from 29 branches of 18 male trees of *S. purpurea)*. The larvae of *O. a. chamela* were dried and weighted using an electronic scale. We performed an ANCOVA (GLM procedure; SAS 2000) with the dry mass of larvae as the dependent variable; year, plant gender and individual tree nested within gender as the independent variables. The dry mass of each branch and the number of ovipositions per branch were used as covariates.

Chemical analysis. To determine the effect of phosphorous content on the preference of the insect borer, we collected a sample of 90 branches from 20 to 30 mm of diameter in October 2002, before the reproductive period of *S. purpurea*. Three branches per tree from 15 male and 15 female trees were used to quantify the total amount of phosphorous. Semi-Kjeldhal method for acid digestion was used for each branch and then phosphorous content was determined colorimetrically with an auto-analyzer (Bran-Luebbe Auto Analyzer III, Nordestedt, Germany; method no. 696-82W; Technicon Industrial System 1977). We performed an ANCOVA (GLM; SAS 2000), using tree gender and individual tree nested within gender as independent variables and the total amount of total phosphorous per branch as the dependent variable.

To determine the amount of total nonstructural carbohydrates (TNC) and its difference between male and female trees in relation to the preference of the insect borer, we used the same set of samples of the analysis of phosphorous content. We performed the phenol-sulphuric method for TNC extraction from plant tissues (Marquis et al. 1997, Boege 2005). Soluble sugars and starch concentrations were determined colorimetrically with an UV-visible spectrophotometer (M230 Spectrophotometer, Cam spec Inc). We performed an ANCOVA (GLM procedure; SAS 2000), using tree gender and individual tree nested within gender as independent variables and the total amount of non-structural carbohydrates per branch as the dependent variable.

Results

Larval performance. Plant gender had non significant effect on the number of ovipositions per branch (F= 1.08, df=1, P= 0.31), also there were no significant differences in the number of oviposition sites by year (F= 0.53, df=1, P= 0.18). We detected no significant effects of the individual tree nested within gender (F= 1.62, df=39, P= 0.18) but the dry mass of the branches affected the number of oviposition sites per branch (F=24.08, df=1, P< 0.0005).

In relation to larvae survival the analysis showed no differences related to tree gender (F=2.98, df=1, P= 0.10). Also there was no significant effect of the sampling year (F= 0.06, df=1, P= 0.81). Similar results were found for individual trees nested within gender (F= 1.53, DF=31, P=0.19) and for dry mass of branches (F=0.01, df=1, P=0.90).

In relation to the dry mass of larvae, the analysis showed no differences related to tree gender (F=3.14, df=1, P= 0.079). There was a significant effect of year (F= 4.86, DF=1, P<0.05), and the larvae obtained in 2004 had higher mass than larvae of 2003 (75.71 ± 12.26 vs 126.87 ±13.24). We found significant effects of individual tree nested within gender (F= 2.30, df=26, P<0.001). The dry weight of branches (F=0.00, df=1, P= 0.601), and the number of oviposition sites (F= 0.01, df=1, P=0.902) had no effects on dry larval mass.

Chemical analysis. There were no significant differences between male and female trees in the total amount of phosphorous (F= 0.00, df=1, P= 0.97), though a significant effect of individual tree nested within gender was detected (F=2.82, df=28, P< 0.0005). Similarly there was no difference in the TNC concentration between genders (F = 0.38, df = 1, P = 0.54), although we again found a significant effect of individual tree nested within gender (F = 2.02, df = 28, P < 0.05).

Discussion

Our results indicate no differences in larval survival and larval mass caused by plant gender. Chemical analyses indicated similar amounts of phosphorus and TNC between genders, but detected differences among individual trees that might influence larval survival and larval mass. These results suggest that insect performance is more affected by the variation between individual plants that might be related to plant genotype or environmental factors rather than plant gender.

Host plant quality defined as a combination of nutritional and defensive characteristics, can influence the preference and performance of insect herbivores (Scriber and Slanski 1981). Larval survival, larval growth rate and insect size have been reported to be strongly affected by nitrogen (Mattson 1980, Wheeler and Center 1997, Osier and Lindroth 2001, Catta-Preta and Zucoloto 2003, Lower and Orians 2003) and by soluble sugars (Osier and Lindroth 2001, Caldeira et al. 2002). However, our results showed no effects of plant gender and nutrients in larval initial development. Similar results to our findings, larval survival of the leaf feeding insects *Trirhabda bacharidis, Blepharida rhois* and with the gall maker *Neopelma baccharidis* were similar between genders of dioecious plants (Krischik and Denno 1990, Strauss 1990, Faria and Fernandes 2001). However, Hendricks and Collier (2003) found in the sucker insect, *Murgantia varicolor,* higher larval survival on female plants but this was linked to the consumption of fruits rather than plant gender in itself. In addition, as shown in our study, larval mass did not differ between genders in the chrysomelid beetle

Blepharida rhois (Strauss 1990). In sum, individual variation, plant genotype and environmental conditions may be more important for larval or adult herbivore performance than plant gender.

Variation in plant resistance caused by factors such as plant genotype and the environment where plants occur might act against the preference or performance of herbivore insects (Thompson 1988, Karban and Baldwin 1997, Osier and Lindroth 2001). A recent meta-analysis indicated that variation in resistance might be more important than nutrient concentration for the preference and performance of herbivores (Cornelissen and Stiling 2005). Therefore, the effect of individual nested within gender on the variation in larval performance of *O. a. chamela* might be related to the resistance of individuals or tree genotypes of *S. purpurea*.

Other external factors such as insect competition within branches might influence larval survival and larval mass. Uribe-Mú and Quesada (2006) showed that the adult females of *O. a. chamela* are the only insect borers that remove the branches of *S. pupurea* in the study site and they oviposit them immediately after removal. Larvae of *O. a. chamela* are the first to initiate the exploitation of woody resources inside the removed branches. After a certain time period, other species of woodborer beetles uncapable of removing branches but require dead wood for the development of their offspring, take advantage of the removed branches of *S. purpurea* and oviposit in them as well. Their larvae exploit the same resources under use by the larvae of *O. a. chamela*. Therefore, removed branches may constitute a limited resource that offers protection and nutrients to the larvae of several insect borers where *O. a. chamela* larvae could compete with other beetles. Similarly, studies on other insect borers have proposed intra-specific competition at larval stage (Hovore and Penrose 1982, Hanks et al. 1991, 1993). A decrease in larval survival in other insect borers has been reported under similar conditions of competition (Hanks et al., 2005). Our results in the number of oviposition sites, larval survival and larval mass suggest that competition might be more important than plant gender in determining initial larval performance of *O. a. chamela*. Although the effects of competition are unknown for *O. a. chamela*, the few studies that have evaluated interspecific competition in woodborer species have reported negative effects on the survival of cerambycid larvae and the survival of the larvae of other phytophagous species that co-ocurr inside the branches that both feed upon (Dodds et al. 2001, Hanks et al. 2005).

Finally, our prediction of greater larval performance on female branches was not supported by the results. Other factors associated to the variation in plant resistance or competition should be analyzed to account for larval performance of *O. a. chamela* and to explain why this cerambicyd seems to selects female over male individuals *S. purpurea.*

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CAPITULO IV

Discusión general

El objetivo principal de este trabajo fue analizar la importancia del sexo de la planta sobre la interacción del cerambícido *O. a. chamela* y el arbol dioico *S. purpurea.* Encontramos que *O. a. chamela* prefiere remover mayor número de ramas provenientes de árboles hembras en algunos años, las proporciones de remoción son mayores si se considera la disponibilidad de ramas potenciales para remoción (Uribe- Mú y Quesada 2006; Cap. I). Los resultados sugieren que existen factores relacionados con el sexo de la planta que influyen las preferencias de los cerambícidos. A a su vez, las consecuencias de la remoción pueden ser mas severas para las plantas hembras debido a que proporcionalmente pierden mas tejido que las plantas macho. Los análisis químicos realizados a las ramas de árboles machos y árboles hembras relacionados con la calidad nutricional del hospedero indican que no hay diferencias en las concentraciones de carbohidratos no estructurales y fósforo entre sexos; sin embargo, se detectaron mayores concentraciones de nitrógeno en las ramas provenientes de árboles hembras lo que sugirió que las preferencias estaban relacionadas con la calidad nutricional de los hospederos (Cap. I y III).

En algunos grupos de insectos se ha comprobado que el crecimiento y el peso de las larvas, la masa larval, la masa pupal, la sobrevivencia y el tiempo de desarrollo están fuertemente influenciados por la presencia de nitrógeno en los tejidos vegetales (Forcella 1981, Scriber y Slansky 1981, Wheeler y Center 1997, Osier y Lindroth 2001, Catta-Preta y Zucolotto 2003, Lower y Orians 2003, Berner et al. 2005). En nuestro estudio encontramos que la sobrevivencia de las larvas de *O. a. chamela* fue similar entre sexos a pesar de que la concentración de nitrógeno en las ramas femeninas fue mayor (Cap. I y III). El peso de las larvas también fue similar entre sexos, aunque detectamos efectos de la variación individual de los árboles (Cap. III). Una revisión reciente sobre los efectos del sexo en las interacciones planta-herbívoro indicó que la variación en la resistencia puede ser mas importante que la concentración de nutrientes para el desempeño de los insectos herbívoros (Cornelissen y Stiling 2005), por tanto las variaciones en la resistencia entre sexos de *S. purpurea* podría ser más determinantes que la calidad nutricional para el desempeño de *O. a. chamela.* La variación en los compuestos, concentraciones y mezclas de metabolitos en una planta determina los niveles de defensa contra herbívoros y patógenos, afectando en forma variable a los diferentes gremios de herbívoros (Espinosa-García 2001). Las estimaciones de los niveles de defensa a través de concentraciones de algunos metabolitos secundarios en ocasiones pueden no ser muy eficientes para la evaluación de la defensa en plantas debido a que se pueden estar midiendo metabolitos que no afectan ese herbívoro en particular o que la defensa este dada por efectos sinérgicos de dos o más compuestos. En las plantas dioicas, los niveles de resistencia podrian estar influenciados por las diferencias en los costos de la reproducción y la asignación de recursos entre sexos (Lloyd y Webb 1977, Obeso 1997, 2002; Nicotra 1999), en tal caso las diferencias en las variaciones en el perfil químico de las plantas deberían ser mayores entre sexos que entre individuos de un mismo sexo. A pesar que en nuestro estudio no evaluamos los niveles de defensa, una estimación indirecta de estos puede ser el porcentaje de sobrevivencia o mortalidad de herbívoros, el cual se han utilizado en numerosos estudios sobre preferencias de herbivoría por insectos (Fryxell y Lukefahr 1967, Polhemus 1988, Krischik y Denno 1990, Fox 1993, Hanks et al. 1993, Briese 1996). Los resultados obtenidos en nuestro estudio con relación a la sobrevivencia de las larvas de *O.a chamela* sugieren que posiblemente no hay diferencias en los niveles de resistencia entre árboles hembras y machos de *Spondias purpurea* (Cap. III). Por tanto, la variación en la resistencia de los árboles individuales aparentemente es mas determinante para la sobrevivencia y el peso de las larvas de *O. a. chamela* que el sexo de la planta.

Las consecuencias que la herbivoría ocasiona en las plantas están determinadas en gran medida por el tipo y localización del daño (Crawley 1983, Marquis 1992). Aparentemente la remoción de ramas por insectos es un tipo de daño más severo que la herbivoría foliar particularmente en especies leñosas (Obeso 1993, Feller 2002, Stowe et al. 2000). Estudios previos con *Rhizophora mangle* indican que el porcentaje de dosel removido por insectos defoliadores en esta especie fue menor al 6%, en tanto que la remoción por cerambícidos cortadores de ramas fue alrededor del 50% (Feller 2002). Las consecuencias de este tipo de daño no sólo implican la pérdida de gran cantidad de biomasa proveniente de estructuras vegetativas para las plantas como ramas y hojas, también se pueden perder estructuras reproductivas como flores y frutos, se altera la arquitectura de la planta, su expresión sexual, se pueden modificar algunas interacciones como la polinización, y en ocasiones puede causar la muerte de las plantas (Whitham y Mopper 1985, Zangerl y Bazzaz 1992, Stowe et al. 2000, Cobb et al. 2002). Algunos estudios con plantas dioicas han mostrado que la herbivoría intensa sobre uno u otro sexo de plantas tiene consecuencias sobre su crecimiento vegetativo, reproducción y proporción sexual en las poblaciones (Elmqvist and Gardfell 1988, Elmqvist et al. 1988, Krischik y Denno 1990, Delph et al. 1993, Boecklen y Hoffman 1993, Mutikainen et al. 1994, Obeso 1998). En nuestro estudio no detectamos diferencias en la biomasa de las ramas entre sexos tanto en ramas intactas como en ramas regeneradas, lo que sugiere que la tasa de crecimiento es similar entre árboles hembras y árboles machos, sin embargo el menor número de ramas totales en los árboles hembras es un indicativo de que la inversión de recursos al crecimiento es diferente entre sexos probablemente por algún conflicto de asignación con la reproducción o defensa (Cap. I). La respuesta de recuperación al daño en cuanto a la fertilidad de las ramas fue más afectada a corto plazo en los árboles hembras, considerando que un año después de la remoción la diferencia en las proporciones de fertilidad entre sexos fue de 25% en las ramas regeneradas y sólo 5% en las ramas intactas (Cap. I). A pesar de que no hubo recuperación en la fertilidad de las ramas regeneradas en ninguno de los sexos del árbol a largo plazo, aparentemente la inversión de recursos a la reproducción fue distinta entre sexos, en los árboles machos hubo una disminución en la fertilidad tanto en ramas intactas como ramas regeneradas respecto a los años anteriores posiblemente por un decremento en la inversión de recursos (Cap. II). La remoción de ramas por *O. a. chamela* también redujo la producción de frutos de *S. purpurea* dentro de la misma temporada reproductiva. El daño acumulado a través del tiempo disminuyó la producción total de frutos, además potencialmente puede modificar la distribución y almacenamiento de recursos lo que a su vez altera el crecimiento y defensa de la planta (Cap. II).

S. purpurea podría verse favorecida en caso de desarrollar estrategias mixtas de defensa debido a que los insectos adultos de *O. a. chamela* podrían estar evadiendo en parte, la resistencia de la planta por la forma en que se remueve la rama (sólo consumen pequeñas porciones de madera) y las defensas químicas estarían afectando principalmente a la progenie del insecto. Sin embargo, el daño acumulado y los efectos a largo plazo requieren que la planta invierta recursos en mecanismos de recuperación (Cap. II).

En los últimos años, se ha sugerido que la herbivoría sobre algún sexo en particular dentro de poblaciones de plantas hermafroditas o monoicas, constituye un factor de selección que puede modificar la proporción sexual de flores, favoreciendo algunos mecanismos de transición al dioicismo (Ashman 2002). *S. purpurea* es una especie que ha sido reportada como monoica o hermafrodita (Pennington y Sarukhán 1998), sin embargo la población de Chamela, Jalisco presenta individuos dioicos (Bullock 1992). La reducción en la fertilidad de las ramas regeneradas debido a la remoción por *O. a. chamela* disminuye el número de flores (Cap. II), alterando la proporción sexual de las flores en la población. La escasa coincidencia en la distribución de las especies de estudio, además de las diferencias en los sistemas reproductivos entre la población de Chamela y las poblaciones que se localizadas hacia el sur, sugieren que la interacción de ambas especies probablemente pudiera haber favorecido la transición de un sistema monoico a un sistema dioico en el área de estudio. Es necesario realizar estudios posteriores para comprobar los efectos de este tipo de herbivoría como posible factor de selección que favorezca los mecanismos de evolución al dioicismo.

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