UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

Facultad de Ciencias

EFECTO DEL TAMAÑO DEL HÁBITAT SOBRE LA DIVERSIDAD Y LA LONGITUD DE LA CADENA TRÓFICA DE LA COMUNIDAD DE INVERTEBRADOS ASOCIADOS A *MUHLENBERGIA ROBUSTA* (GRAMINEAE) EN LA RESERVA DEL PEDREGAL DE SAN ÁNGEL, D.F. (MÉXICO)

TESIS

QUE PARA OBTENER EL GRADO ACADÉMICO DE

DOCTOR EN CIENCIAS

PRESENTA

VÍCTOR LÓPEZ GÓMEZ

DIRECTOR DE LA TESIS: DR. ZENÓN CANO SANTANA

MÉXICO, D.F. DICIEMBRE, 2010

A mi querida esposa Susana, que me ha apoyado incondicionalmente en este proceso de aprendizaje. Tú eres lo que más quiero y amaré en esta vida.

A mis padres, los que me fomentaron el gusto por el conocimiento y por la ciencia. Por su apoyo y sus enseñanzas que me han permitido lograr mis metas.

A mis sobrinos (Aida, Liz y Alexito) que me recuerdan que la vida es un juego que se debe de disfrutar.

A mis hermanos (Xóchitl, Rafael y Raúl) y sus familias, por los buenos momentos que hemos pasado y sé que cuento con ellos para todo.

La vida es una manifestación de energía compuesta que busca mejorar su capacidad de aclimatarse a los diferentes ambientes para asegurar su permanencia en el tiempo.

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ASUNTO: Asignación de Sinodales

DR. ZENON CANO SANTANA
Presente.

Por este conducto me permito comunicarle como Director(a) de Tesis del(a) alumno(a) **VÍCTOR LÓPEZ GÓMEZ**, quién desarrolló el Trabajo de Tesis titulado **"Efecto del tamaño del hábitat sobre la diversidad y la longitud de la cadena trófica de la comunidad de invertebrados asociados a *Muhlenbergia robusta* (Gramineae) en la Reserva del Pedregal de San Ángel, D.F. (México)",** que el Comité Académico del Posgrado en Ciencias Biológicas en su sesión celebrada el día 4 de octubre del año en curso, asignó a los siguientes sinodales para dictaminar si el trabajo que ha desarrollado como tesis el(a) alumno(a) antes mencionado tiene los méritos para obtener el grado de **DOCTOR(A) EN CIENCIAS**:

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Asimismo, informo a los miembros del jurado, que el Comité Académico aprobó un plazo de hasta 30 días naturales para recibir la revisión del manuscrito de tesis y, en su caso el voto aprobatorio.

En espera de su pronta respuesta, aprovecho la ocasión para enviarles un cordial saludo.

Atentamente
"POR MI RAZA HABLARÁ EL ESPÍRITU"
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DCRV\ASR\grf*

AGRADECIMIENTOS

Agradezco al Posgrado en Ciencias Biológicas, UNAM, por su apoyo académico, de infraestructura y económico, así como por brindarme la oportunidad de continuar preparándome para mi superación personal y para mi mejor desempeño como mexicano.

Agradezco a CONACYT por la beca que me brindó, la cual sustentó mis estudios de posgrado.

Agradezco al Dr. Santiago Zaragoza Caballero y al Dr. Julio Campo Alves por formar parte de mi Comité Tutoral y por sus aportaciones para enriquecer y mejorar esta tesis.

Agradezco a la Dra. Gabriela Castaño Meneses, al Dr. Efraín Tovar Sánchez, al Dr. Luis Zambrano y al Dr. Denis Pierre Boyer por revisar esta tesis y por sus acertados comentarios y sugerencias para mejorarla.

Agradezco al Dr. Zenón Cano Santana por ser mi mentor y mi amigo, porque siempre tuvo tiempo para resolver mis dudas, por brindarme oportunidades para desarrollar mis habilidades académicas y por contagiarme el gusto por hacer investigación y expresar ideas de manera escrita.

Agradezco al Dr. Santiago Zaragoza Caballero, al Dr. Harry Brailowsky, al M. en C. Rafael Gaviño Rojas, al M. en C. Iván Castellanos Vargas y la M. en C. Cristina Mayorga Martínez por la identificación de los especímenes.

Agradezco a Susana Alejandre Grimaldo, a Erick Daniel Villamil, a David Humberto Basilio Hernández, a Isael Victoria Salazar, a Iván Castellanos Vargas y a Carmen Alejandra por su apoyo en el campo. Además a Elsa Valiente Riveros, a Manuel Hernández Quiroz y a Marco Romero Romero por su ayuda técnica en el laboratorio.

Agradezco a Iván, Olivia, Ixchel, Ramiro, Gabriela, Mónica y a todo el grupo de trabajo que me mostró siempre su apoyo y que me contagiaron su entusiasmo.

López-Gómez, V. 2010. Efecto del tamaño del hábitat sobre la diversidad y la longitud de la cadena trófica de la comunidad de invertebrados asociados a *Muhlenbergia robusta* (Gramineae) en la Reserva del Pedregal de San Ángel, D.F. (México). Tesis Doctoral. Facultad de Ciencias, Universidad Nacional Autónoma de México, México. 48 pp.

Resumen

El tamaño del hábitat es uno de los principales factores que modifica la estructura de las comunidades ecológicas. La interacción planta-artrópodo es de gran importancia en los sistemas naturales; además es un sistema que ha ayudado al entendimiento de las comunidades y los ecosistemas. Los objetivos de este trabajo son: (1) determinar el efecto del tamaño del zacatón sobre la estructura de la comunidad de artrópodos asociados a *Muhlenbergia robusta* en la Reserva del Pedregal de San Ángel, bajo el efecto de la sombra, la fenofase de la planta hospedera y su lejanía con plantas conespecíficas, (2) conocer la proporción y la identidad de los artrópodos que especializan en utilizar a *M. robusta* como único hábitat, y (3) determinar las relaciones entre la longitud máxima de la cadena trófica con el tamaño de esta planta hospedera, así como con la riqueza de especies de la comunidad de artrópodos asociada. Se encontró que la estructura de la comunidad de artrópodos (riqueza, abundancia, diversidad y biomasa) está relacionada positivamente con el tamaño de *M. robusta* y más estrechamente con el peso seco de la planta. Se encontró que las comunidades con mayor riqueza de especies se presentan en los sitios sombreados, mientras que la fenofase de la planta y su lejanía con plantas conespecíficas no tuvieron efecto sobre la comunidad de artrópodos. La estructura de la comunidad de artrópodos es constante a lo largo del día, aunque solamente el 4.3% de las especies de artrópodos utilizan al zacatón como único hábitat en todo el día. No se registraron relaciones significativas entre la longitud máxima de la cadena trófica y el tamaño de *M. robusta*, así como con la riqueza de especies. Se concluye que (1) el tamaño de *M. robusta* modifica la estructura de la comunidad de artrópodos asociados, (2) la comunidad asociada tiene un bajo porcentaje de especies que se especializan en el uso de esta planta como hábitat y (3) que el tamaño de esta planta hospedera y la riqueza de especies presentes no afectan a la longitud de la cadena trófica.

López-Gómez, V. 2010. Host-plant size effect in diversity and food-chain length of invertebrate community within *Muhlenbergia robusta* (Gramineae) at the Reserva del Pedregal de San Ángel, D.F. (Mexico). Doctoral thesis. Faculty of Sciences, Universidad Nacional Autónoma de México, Mexico city. 48 pp.

Abstract

Habitat size is one of the most important factors that modify the community structure. Plant-insect relationship is very important in natural systems, besides this system has helped to increase the knowledge of the ecological communities and ecosystems. The goals of this study are (1) to determine plant size effect in community structure of arthropods within *Muhlenbergia robusta* at the Reserva del Pedregal de San Ángel; on different plant foliage (dry and fresh), shade and conspecific distance, (2) to determine the ratio and taxa identity of arthropods with high specialization using *M. robusta* as host-plant, and (3) to determine the relationships between maximum food-chain length and ecosystem size (dry weight of the grass *Muhlenbergia robusta*), as well as, the relationship with the arthropod species richness within the grass. The community structure of arthropods (morphospecies richness, abundance, diversity and biomass) was related directly with the host-plant size, and it was most related with the dry weight of the plant. Communities with the highest richness species of arthropods were presented at grasses in shady sites, while phenophase of plant foliage and conspecific distance did not affect to arthropods attributes. The community structure of arthropods was homogeneous along the day, although only 4.3% of the taxa used *M. robusta* as exclusive habitat in the whole day. There were not relationships between maximum food-chain length and habitat size, neither with arthropod richness. We conclude that (1) *M. robusta* size modify structure of arthropod community associated, (2) arthropod community had a low quantity of species with a high level of specialization using this grass, and (3) the habitat size and arthropod richness do not affect the maximum food-chain length on this system.

ÍNDICE

Presentación

El presente estudio pretende comprobar o rebatir teorías de la interacción planta-artrópodo que en la actualidad requieren de evidencias empíricas para incrementar su entendimiento. Además, se hacen nuevas preguntas que contribuirán al conocimiento y entendimiento de la interacción planta-artrópodo. En la introducción se da un breve panorama de la importancia de la interacción planta-artrópodo. Posteriormente (en el capítulo II) se determina cuál es el mejor atributo de la planta hospedera para determinar la riqueza de artrópodos asociada, además se prueba si la fenofase de la planta, la sombra y la lejanía con fuentes de colonización puede afectar la estructura de la comunidad de artrópodos. Después, en el capítulo III, se describe la variación diurna de la comunidad de artrópodos asociados a este zacatón y el porcentaje de especies que se especializan en el uso de la planta como único hábitat. En el siguiente capítulo (IV) se pone a prueba la teoría del efecto del tamaño del ecosistema sobre la longitud de la cadena trófica en este ecosistema. Por último, en el capítulo V, se hace una discusión que relaciona los resultados de los capítulos II, III y IV, y se comparan con nuevos estudios sobre la comunidad de artrópodos asociados a *M. robusta*. En este capítulo también se señalan las perspectivas de futuros estudios y se formulan las conclusiones generales de este trabajo.

I. INTRODUCCIÓN GENERAL

La relación planta-artrópodo es una de las interacciones más importantes en la ecología moderna, es una interacción fundamental para el conocimiento de la biósfera terrestre (Schoonhoven *et al.*, 2005). La importancia de esta relación se basa en que abarca dos grandes grupos taxonómicos uno que incluye la mayor parte de los taxa de la tierra: la Clase Insecta (Borror *et al.*, 1989) y otro que representa el mayor compartimento de biomasa de la tierra: el reino Vegetal (Pimentel and Andow, 1984).

La relación de estos grupos es muy estrecha porque la vida animal no puede existir sin las plantas ya que éstas constituyen la principal fuente de energía para los organismos heterótrofos (Schoonhoven *et al.*, 2005). Se ha postulado que una de las principales causas de la gran diversidad de las plantas ha sido la prolongada exposición que han tenido a la acción de los animales, ya que la gran variedad de formas de vida e historias de vida de los insectos pudieron haber sido una de las fuerzas más importantes en la evolución de las plantas (ver, p. ej., Ehrlich y Raven, (1964).

La interacción planta-artrópodo también es de crucial importancia para resolver problemas prácticos. Actualmente los insectos son los líderes como plagas de los cultivos y de productos almacenados, a pesar de las medidas de control utilizadas que pueden ser caras y nocivas al ambiente (Pimentel, 1997). Es indispensable entender mejor los factores que modifican las relaciones entre los insectos y las plantas para poder disminuir los efectos negativos de las plagas sobre los recursos alimenticios de la humanidad.

La relación especies-área (SAR, por sus siglas en inglés) predice un incremento en el número de especies conforme aumenta el área del sistema. SAR es uno de los patrones más importantes en la ecología debido a la gran cantidad de evidencias empíricas que la apoyan en una amplia variedad de taxa y tipos de ecosistemas (Schoener, 1976; Connor and McCoy, 1979; Lomolino, 2000; Williamson *et al.*, 2001). La relación SAR ha sido estudiada ampliamente en la interacción planta-artrópodo al relacionar la riqueza de especies de insectos con el tamaño de las plantas hospederas (Strong *et al.*, 1984). Sin embargo, actualmente no se tiene claro cuál es el atributo de la planta hospedera que mejor se ajusta a esta relación. Asimismo no se ha probado si las condiciones micro ambientales o la fenofase de la planta hospedera pueden ayudar a SAR a explicar la variación de la riqueza de insectos asociados a una planta.

Existe una gran cantidad de estudios sobre los invertebrados asociados a su planta hospedera, en los cuales se da el supuesto de que todas las especies tienen el mismo grado de relación con la planta. Actualmente se sabe que los insectos herbívoros tienen un alto grado de especialización alimentaria con su planta hospedera (Strong *et al.*, 1984; Bernays and Graham, 1988; Schoonhoven *et al.*, 2005); sin embargo, no se sabe la proporción de especies de toda la comunidad de invertebrados que tiene un alto grado de especialización con su planta hospedera, así como si estos taxa son sólo herbívoros.

Por otro lado, en los últimos 20 años se ha incrementado el interés por determinar los factores que modifican la longitud de la cadena trófica de los ecosistemas. Una de las hipótesis más importantes es la del tamaño del ecosistema, la cual afirma que los sistemas de gran tamaño pueden soportar una longitud de la cadena trófica más larga porque en este tipo de sistemas existe una mayor cantidad de recursos energéticos y una diversidad de especies (Schoener, 1989; Vander Zanden *et al.*, 1999; Post *et al.*, 2000). Actualmente son pocas las evidencias para corroborar la hipótesis del tamaño del ecosistema en ecosistemas terrestres (Schoener, 1989). Además, no encontramos algún estudio en un sistema basado en la relación planta-artrópodo.

El objetivo general de este trabajo es determinar el efecto del tamaño del zacatón sobre la estructura de la comunidad de artrópodos asociados a *Muhlenbergia robusta* en la Reserva del Pedregal de San Ángel.

Los objetivos particulares derivados del anterior son los siguientes:

1. Determinar el atributo de *M. robusta* que se relaciona mejor con la riqueza de especies de artrópodos asociados; así como el efecto de la sombra, la fenofase de la planta

hospedera y su lejanía con fuentes de colonización a la estructura de la comunidad de artrópodos.

2. Conocer la proporción y la identidad de artrópodos que se especializan en utilizar a *M. robusta* como único hábitat.

3. Determinar las relaciones entre el tamaño de la planta hospedera y la riqueza de especies de la comunidad de artrópodos asociado a *M. robusta* con la longitud máxima de la cadena trófica.

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Entomological Science

Entomological Science (2010) **13**, 174–182 doi:10.1111/j.1479-8298.2010.00381.x

ORIGINAL ARTICLE

Best host-plant attribute for species–area relationship, and effects of shade, conspecific distance and plant phenophase in an arthropod community within the grass *Muhlenbergia robusta*

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Abstract

Increased understanding of the species–area relationship (SAR) can improve its usefulness as a tool for prediction of species loss for biodiversity conservation targets. This study was conducted: (i) to determine the best plant attribute for the SAR in the community of arthropods living within the grass *Muhlenbergia robusta*; (ii) to determine the contribution of phenophases of plant foliage (dry and fresh), shade and conspecific distance to the variation in arthropod richness within the plant; (iii) to determine the best functional model of changes in the abundance, diversity and biomass in communities of arthropods in response to increases in plant size; (iv) to determine the best host-plant attribute for prediction of these community attributes; and (v) to determine the effect of the plant phenophase, shade and *M. robusta* isolation on the abundance, diversity and biomass of the arthropod community. The above-ground dry weight of grass was found to be the best host-plant attribute for the SAR, while the light environment explained the arthropod richness within the grass, with higher richness observed in shaded environments. This study also showed that the best functional mathematical models for estimation of changes in the abundance, dry weight and diversity of arthropods in response to increases in grass size (dry weight) are the power model, exponential model and logarithmic model, respectively. Furthermore, the host-plant foliage phenophase, shade and the isolation of *M. robusta* with other conspecifics had no effect on the abundance, biomass or diversity per basal area of the grass.

Key words: abundance, biomass, diversity, Insecta, Mexico, Poaceae, xerophilous scrub.

INTRODUCTION

Single host plants and their arthropods form interesting systems for the evaluation of ecological factors that can modify a community structure (Ehrlich & Raven 1964; Janzen 1968; Hartley & Jones 2003; Schoonhoven *et al.* 2005). The habitat size, fresh tissue plant phenology, distance to potential sources of colonization and variations in the environment can all modify the arthropod community of a plant.

The effect of habitat size on arthropods in a plant has been studied based on the species–area relationship (SAR), which predicts a greater quantity of resident species in larger host plants than in smaller ones (Strong *et al.* 1984). The SAR, which is one of the most studied and robust patterns in ecology, has generally been described by the power function $S = cA^z$, where S is the number of species, A is the area, c is a fitted constant and z represents the slope or the rate of accumulation of richness within an area.

SAR studies of insect–plant interactions have used various plant attributes such as height, foliage cover and volume. However, these studies have provided contradictory results (e.g. Southwood *et al.* 1982; Strong *et al.* 1984; Richardson 1999; Anglade & Bigot 2001; Sanchez & Parmenter 2002). Consequently, it is not clear which plant attribute best explains the variation in

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Received 5 November 2008; accepted 8 December 2009.

arthropod richness in the host-plant. Moreover, it is unclear if other parameters such as environmental conditions or resource availability contribute to the variation of arthropod richness within a plant. However, an increase in the accuracy with which the SAR is predicted may help enhance its usefulness as a tool for forecasting the future loss of species.

Studies have been conducted to evaluate the effects of plant size on other arthropod community attributes such as abundance, diversity and biomass (e.g. Marques *et al.* 2000; Hodkinson *et al.* 2001; Araújo *et al.* 2003; Izzo & Vasconcelos 2005; Veldtman *et al.* 2007). However, none of the studies conducted to date has provided the best functional relationship model for these community attributes; hence, the best plant attribute to estimate these community attributes is not known. Accordingly, it would be helpful to identify a functional model and determine the plant attribute that best predicts the arthropod community attributes.

The host–plant distance to potential sources of colonization can reduce the richness of the arthropod community of the plant (Sanchez & Parmenter 2002). This phenomenon is related to the dispersal abilities of the fauna, which may limit the colonization of isolated habitats because isolated plants are more difficult for dispersers to find (Wiens 1997). For example, in a study conducted by Gripenberg and Roslin (2005), mines made by *Tischeria ekebladella* Bjerkander larvae (Lepidoptera) were more likely to be present on less-isolated *Quercus robur* L. plants. Both the seasonal growth of plants and the length of their growing season may also influence the composition of insects on the plant, as well as their richness and abundance. This is because these factors can modify plant exposure and the availability of food sources for herbivores (e.g. Lawton 1978). Accordingly, many herbivores are seasonal specialists on a particular plant tissue or during a particular period of plant phenology (Strong *et al.* 1984).

Variations in temperature and humidity directly affect arthropod physiology, mainly through changes in their body temperature and water balance (Willmer 1982). In addition, environmental variations are related to foraging and the activity of seeking mates because arthropods choose the portion of the day at which the conditions for these activities are most favorable (Juniper & Southwood 1986). Plants provide important habitats for arthropods because they provide a favorable microclimate that can differ remarkably from the standard climate to which the vegetation, as a whole, is exposed (Schoonhoven *et al.* 2005). Vegetation produces microclimate gradients from the top of the vegetation to the ground level. Specifically, plants reduce the amount of radiation, limit wind speed, lower temperatures and cause an increase in humidity (Cox *et al.* 1973). The microclimate variation surrounding the entire plant is related to the position of the sun and the type of vegetation. Arboreal strata reduce air temperature to a greater degree than other plant growth forms (Stoutjesdijk & Barkman 1992); therefore, the presence of an arboreal stratum provides a more stable and suitable habitat for arthropods, which could prove to be a decisive factor in their community structure.

Based on the currently available information regarding plant–arthropod relationships, this study was conducted to identify factors that modify the structure of arthropod communities within an area of abundant *Muhlenbergia robusta* (Fourn.) Hitchc. (Poaceae) grass in an ecological reserve. The specific goals of this study were: (i) to determine the best host-plant attribute (height, foliage cover, basal area at ground level, volume, above-ground dry weight) for the SAR; (ii) to determine the contribution of plant phenophase, shade and conspecific isolation of the plant to the variance of arthropod richness within a plant; (iii) to find the best functional model that determines the abundance, diversity and biomass of an arthropod community with increased plant size by testing linear, exponential, logarithmic and power models for each case; (iv) to determine the host-plant attribute that best predicts these community attributes; and (v) to determine the effect of plant phenophase, shade and isolation of *M. robusta* from other conspecific grasses on the abundance, diversity and biomass of the arthropod community.

MATERIALS AND METHODS

Study area

This study was conducted in the Pedregal de San Ángel Ecological Reserve (19°19′N, 99°11′W, elevation 2300 m), which encompasses 237 ha of the main campus of the National Autonomous University of Mexico, south-west of Mexico City. Vegetation at the reserve is composed of a xerophilous scrubland, and the area has a sub-humid, temperate climate. This site has an annual mean temperature of 16.1°C and its annual mean rainfall is 835 mm (César-García 2002). The reserve has a wet season between June and October (Rzedowski 1954). The area is located over a basaltic substratum that was deposited 1670 years ago during the eruption of the Xitle volcano (Siebe 2000). Most plant species are herbaceous or shrub-like; however, there are a few small trees with heights of 3–7 m.

The reserve has patches of two noticeably different microclimates: sunny and shady. The shady sites have a lower sun radiation at ground level, higher density of trees (10.4 ± 2.1 ind/25 m^2; mean ± standard error

(SE)) (Cano-Santana 1994) and smaller temperature variation than the sunny sites, which show the opposite conditions (4.3 ± 0.9 ind/25 m^2).

Study system

Muhlenbergia robusta is a perennial grass 1–2 m tall. This plant contributes about 15% of the above-ground net primary productivity in the study area (Cano-Santana 1994). Flowering occurs between June and August and fruiting occurs between September and June (César-García 2002). In the ecological reserve, *M. robusta* shows two contrasting foliage phenophases: fresh foliage and dry foliage. The fresh foliage phenophase is seen when *M. robusta* has the highest quantity of the fresh standing crop during the year (74.5 ± 18.7 g/m^2), which occurs between October and November (Cano-Santana 1994). The dry foliage phenophase occurs when most foliage is senescent and the fresh standing crop has the lowest quantity (18.2 ± 6.0 g/m^2), which occurs between April and May (Cano-Santana 1994). This grass occurs in association with other grasses and shrubs, as well as within pine and oak forests at elevations ranging from 2250 to 3200 m (Rzedowski & Rzedowski 2001).

Methods

Muhlenbergia robusta was sampled twice, once in November 2003 when the foliage was fresh, and once in May 2004 when the foliage was dry (Cano-Santana 1994). Ten random sites were chosen for each sampling event. At each site, circular plots with a diameter of 20 m were drawn in both a sunny site and a shady site. Three individual grass plants of different sizes were then selected in each plot. A factorial design of two plant phenophases (fresh and dry) × two luminosity levels (sunny and shady) was used and 30 plants were sampled for each treatment. The selected grass plants were then cut at ground level using a garden saw, after which they were wrapped carefully in plastic bags. Field sampling was conducted between 07.00 and 10.00 hours.

Prior to wrapping, the following were determined for each grass sample: foliage height (h), perimeter at ground level (Pe), largest diameter of foliage cover (d_1), perpendicular diameter of d_1 (d_2) and distance to its ten nearest *M. robusta* neighbors. Next, the foliage cover, basal area at ground level and volume of each plant were calculated.

Because the foliage cover of *M. robusta* shows a similar circle form, the grass cover (C) was calculated using the method described by Mueller-Dombois and Ellenberg (1974):

$$C = \pi\left(\frac{d_1 + d_2}{4}\right)^2$$

The basal area of the plant (A) was determined using the circle perimeter (Pe) and the circle area equation:

$$A = \frac{Pe^2}{4\pi}$$

The volume of the plant was given using the equation for a truncated cone:

$$V = 1/3\pi h\left((Pe/2\pi)^2 + \left(\frac{d_1 + d_2}{4}\right)^2 + (Pe/2\pi)\left(\frac{d_1 + d_2}{4}\right)\right)$$

The average distance of ten conspecific grasses for each selected *M. robusta* was used as an isolation measure with the assumption that the rate with which the arthropod species colonized *M. robusta* depended on the nearest conspecific grass as well as the surrounding conspecific plants.

The above-ground dry weight of each plant was obtained by drying the plant in an electric oven at 50°C to constant weight. The samples were then weighed using an analytical balance (Ohaus AV812, ±0.005 g).

The fauna were extracted in the laboratory immediately following collection by direct exploration and examination of the leaves of the grass. Only organisms with a body length ≥3 mm were collected. The species were initially sorted into morphospecies by one author (VLG), which is a common practice in biodiversity studies that does not compromise scientific accuracy (Oliver & Beattie 1996) and has clear advantages when expertise in all taxonomic groups is not available (Gaston 1996). The morphospecies were then sent to several taxonomists for species identification.

The arthropod community for each plant was described based on the richness, abundance, dry weight and the Shannon–Wiener diversity index (H') using the natural logarithm (Magurran 1988). A zero value was assigned to the Shannon–Wiener diversity index for grasses with one or zero arthropod morphospecies. The faunal dry weight was determined using a power regression between the arthropod body length and the dry weight obtained from previous sampling (October 2003, $n = 76$) using the same method. Organisms were dried in an electric oven at 40°C and weighed using an analytical balance (Sartorius BP105, ±0.00005 g).

The resulting equation was:

$$W = (2.84 \times 10^{-5}) l_c^{\,2.48},\ r^2 = 0.71$$

where W is the organism dry weight (g) and l_c its body length (mm).

Statistical analyses

To identify the plant attribute that best explained arthropod species richness in the SAR, the arthropod morphospecies and plant-size attributes (height, cover, basal area, above-ground dry weight, volume) were fitted to power models. For each attribute, the ANOVA significance test and the coefficient of determination were used (Zar 1999). The best plant attribute for the SAR was then determined by significant regression using the highest determination coefficient.

To determine if shade, plant phenology and plant isolation help the SAR to explain the variance of arthropod richness within *M. robusta*, multiple regression analysis was conducted. The arthropod richness and above-ground dry weight of grass values were log-transformed prior to the analysis.

ANOVA was then used to determine the significance of the multiple regression analysis (Zar 1999). A Student's *t*-test was used to evaluate each partial regression coefficient. To estimate the multiple regression model that best explained the arthropod richness within the grass, the backward elimination procedure was used for selection of the independent variables (Zar 1999). For these analyses, the light environment and plant phenophase variables were transformed to dummy variables, and the richness data were transformed as $\sqrt{(x + 0.5)}$ because the richness data were discrete variables (Zar 1999).

To develop a functional mathematical model and identify the plant attributes (height, cover, basal area, above-ground dry weight, volume) that best explained the community attributes (abundance, diversity index, dry weight), data were evaluated using linear, exponential, logarithmic and power mathematical models, except for the Shannon–Wiener diversity index, which was only calculated using the linear and logarithmic models because the formula for the Shannon–Wiener index is logarithmic (Magurran 1988). To determine the best fit model for each case, ANOVA significance tests for regression analysis were used (Zar 1999). The abundance and dry weight of arthropods were added +1 because there were zero values in the records (Zar 1999).

To determine the effects of shade, plant phenophases and the mean distance to the nearest ten conspecific neighbors on the abundance, diversity index and dry weight of the arthropod community, as well as the interactive effects of these variables (plant phenophase × shade, plant phenophase × plant isolation, shade × plant isolation, plant phenophase × shade × plant isolation), a three-factor ANCOVA was used to evaluate each community attribute. In these analyses, the community attributes per basal area of *M. robusta* (cm^2) were used to avoid the habitat-size effect (individuals/cm^2, g/cm^2, H'/cm^2). The abundance data were transformed as $\sqrt{(x + 0.5)}$ because the abundance data were discrete variables. Additionally, non-normal dependent variables were transformed as $\log_{10}(x + 1)$ (Zar 1999).

All statistical analyses were conducted using Statistica software (StatSoft 2004) at a significance level of 0.05.

RESULTS

Arthropod community of *Muhlenbergia robusta*

In this study, 2061 organisms on 120 collected grasses were found and 151 morphospecies recorded. Specifically, there were 18.37 ± 22.72 individuals/plant, 7.63 ± 6.77 morphospecies/plant, and the organisms contributed 0.01 ± 0.13 mg dry weight/plant. The most abundant taxonomic groups were Formicidae (20%), Araneae (20%), Hemiptera (14%), Blattoidea (12%) and Coleoptera (12%), whereas the arthropods that made the greatest contribution of dry weight were Lepidoptera (34%), Orthoptera (19%), Hemiptera (14%), Blattoidea (7%), Araneae (5%) and Formicidae (5%).

Species-area relationship

The dry weight of *M. robusta* was found to be the plant attribute that best explained the variance of arthropod richness within the grass ($r^2 = 0.57, P < 0.001$), followed by the basal area ($r^2 = 0.47, P < 0.001$), volume ($r^2 = 0.40, P < 0.001$), foliage cover ($r^2 = 0.27, P < 0.001$) and height ($r^2 = 0.16, P < 0.001$) of the grass.

Multiple regression revealed that the influence of shade, plant phenology, plant isolation and plant size on arthropod richness within the grass was significant ($F_{4,115} = 43.53, P < 0.001$, adjusted $r^2 = 0.59$). However, only the partial correlation coefficients (B) of the above-ground dry weight of *M. robusta* ($B = 0.38, \beta = 0.76, t_{115} = 12.92, P < 0.001$) and the intensity of light in the environment ($B = -0.07, \beta = -0.16, t_{115} = -2.07, P < 0.01$) were significant; that is, the slope values (β) ≠ 0 (Fig. 1).

The multiple regression model that best explained arthropod richness within grass using the log of the plant size and the environmental light treatment as independent variables was significant ($F_{2,117} = 84.66, P < 0.001$, adjusted $r^2 = 0.58$). The model obtained was:

$$S + 1 = (0.275)X_1^{0.757}10^{-0.15X_2}$$

where S is the arthropod richness within *M. robusta*, X_1 is the above-ground dry weight of the grass (g) and X_2 is the environmental light condition at the site where the grass is established (shady = 1 or sunny = 2).

Best functional models for community attributes

All regression models developed using the five grass-size variables (height, cover, basal area, above-ground dry weight, volume) and the three community attributes (abundance, biomass, diversity index) were positive and significant. The above-ground dry weight of *M. robusta* was the plant-size variable that showed the highest coefficient of determination, followed by the basal area, volume, foliage cover and grass height, for any attribute of the arthropod community (Table 1). However, the functions of best fit models varied among the arthropod community attributes. The abundance was best explained by the power function, but the diversity index by the logarithmic function, for all the plant-size variables (Table 1, Figs 2,3). On the other hand, the arthropod biomass (dry weight) was best explained by the exponential function for the grass dry weight and volume (Table 1, Fig. 4), but by the power function for the basal area, foliage cover and height (Table 1).

Factors affecting arthropod community structure

ANCOVA (Table 2) revealed that shade, plant phenophases and plant isolation did not significantly affect community attributes (abundance, biomass, diversity index per basal area of the grass). This was also true for the interactions among these factors.

DISCUSSION

Species–area relationship

Our study confirmed the species–area relationship (SAR) between individual plants in this plant-arthropod system, as in other studies on bromeliads (Richardson

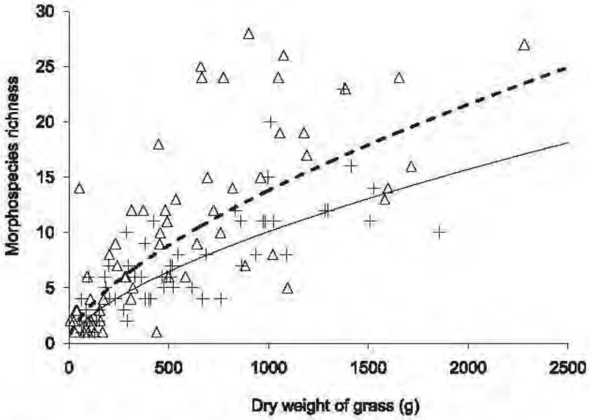

Figure 1 Species-area relationship (SAR) curves and observed data describing the relationship between the above-ground dry weight of *Muhlenbergia robusta* and the morphospecies richness of arthropods within plants under two remarkable light conditions, shady (△, dotted line) and sunny (+, continuous line).

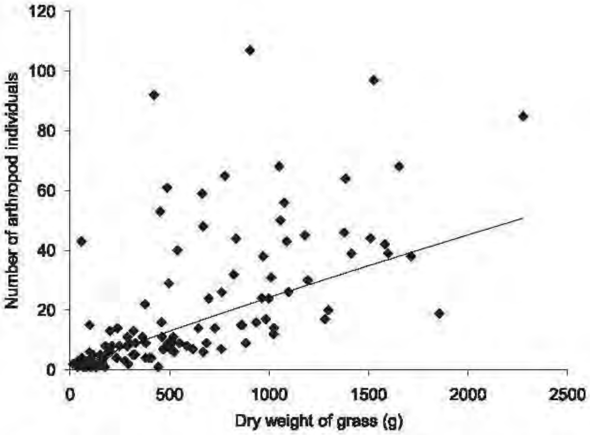

Figure 2 The best-fit power model curve and observed data describing the relationship between the above-ground dry weight of *Muhlenbergia robusta* and the arthropod abundance among plants ($r^2 = 0.58$).

Table 1 Best fit models of regressions among five size-variables of *Muhlenbergia robusta* and three community attributes of arthropods

	Arthropod community attributes		
Size-variables of grass	Abundance (+1)	Dry weight (g + 1)	Diversity index (H')
Height (cm)	$y = 1.4 \times 10^{-3} x^{1.96}$ (0.14)**	$y = 0.59x^{0.13}$ (0.09)*	$y = 1.52 \ln x – 4.50$ (0.17)**
Foliage cover (cm^2)	$y = 0.6 \times 10^{-3} x^{1.03}$ (0.28)**	$y = 0.58x^{0.06}$ (0.16)**	$y = 0.75 \ln x – 4.64$ (0.30)**
Basal area (cm^2)	$y = 0.18x^{0.69}$ (0.46)**	$y = 0.86x^{0.04}$ (0.21)**	$y = 0.51 \ln x – 0.50$ (0.52)**
Volume (cm^3)	$y = 0.6 \times 10^{-4} x^{0.88}$ (0.41)**	$y = 1.01e^{6 \times 10^{-8x}}$ (0.20)**	$y = 0.61 \ln x – 5.88$ (0.41)**
Dry weight (g)	$y = 0.05x^{0.90}$ (0.58)**	$y = 1.01e^{1 \times 10^{-4x}}$ (0.28)**	$y = 0.62 \ln x – 1.24$ (0.57)**

*$P = 0.001$, **$P < 0.0001$, $n = 120$. Determination coefficients are in parentheses.

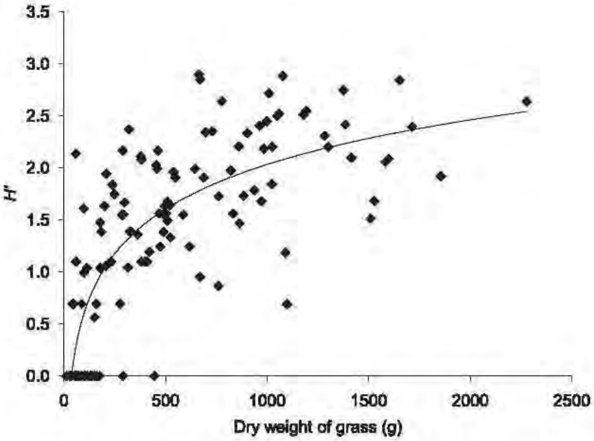

Figure 3 The best-fit logarithmic model curve and observed data describing the relationship between the above-ground dry weight of *Muhlenbergia robusta* and the Shannon–Wiener diversity index (*H'*) of arthropods within plants ($r^2 = 0.57$).

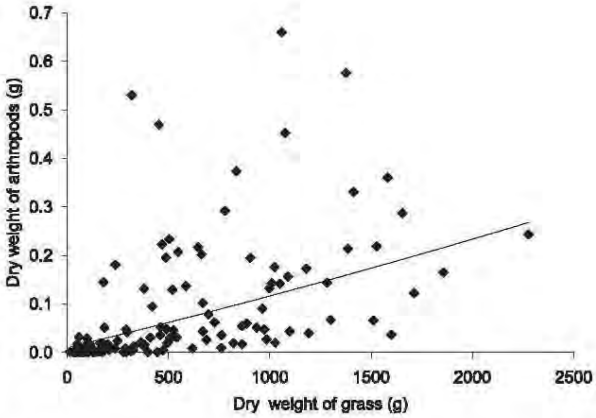

Figure 4 The best-fit exponential model curve and observed data describing the relationship between the above-ground dry weight of *Muhlenbergia robusta* and the dry weight of arthropods within plants ($r^2 = 0.28$).

Table 2 Results of ANCOVA to determine the influence of shade, plant phenophases, and plant isolation on attributes (abundance, biomass, diversity index per basal area of the grass) of arthropod community living within *Muhlenbergia robusta*

Arthropod community attribute Effect	d.f.[†]	*F*	*P*
Abundance			
Shade (S)	1	1.94	0.17
Plant phenophases (PP)	1	0.56	0.45
Plant isolation (PI)	1	1.16	0.28
S × PP	1	0.02	0.89
S × PI	1	1.48	0.22
PP × PI	1	0.73	0.39
S × PP × PI	1	0.04	0.82
Biomass			
Shade (S)	1	0.72	0.40
Plant phenophases (PP)	1	0.03	0.86
Plant isolation (PI)	1	0.29	0.59
S × PP	1	1.15	0.29
S × PI	1	0.42	0.52
PP × PI	1	<0.01	0.96
S × PP × PI	1	1.09	0.29
Diversity index			
Shade (S)	1	1.08	0.30
Plant phenophases (PP)	1	0.15	0.70
Plant isolation (PI)	1	0.01	0.92
S × PP	1	0.44	0.51
S × PI	1	0.82	0.36
PP × PI	1	0.14	0.71
S × PP × PI	1	0.40	0.53

[†] For all tests the degrees of freedom (d.f.) of the error were 112.

1999) and shrubs (Sanchez & Parmenter 2002). The increase in the richness of arthropods on larger grasses indicates a growing variety and number of habitats available to the arthropod community, which enables the coexistence of a greater variety of species with different requirements (Soulé & Simberloff 1986) as a result of niche differentiation and habitat segregation (Kuris *et al.* 1980).

Our results indicate that diverse host-plant attributes have an unequal ability to predict the SAR, which is similar to the results of other studies. For example, Southwood *et al.* (1982) and Anglade and Bigot (2001) did not record a SAR relationship when using the height of host-plants. Their results correspond with the findings of this study, in which the height of the plant was found to be the plant attribute with the lowest determination coefficient ($r^2 = 0.16$). Conversely, in studies that used other host-plant attributes such as the volume of shrubs (Sanchez & Parmenter 2002) or the cover of bromeliads (Richardson 1999), a clear SAR relationship between arthropods and their individual host-plants was found.

The above-ground dry weight of the grass was the best plant attribute indicator for the SAR ($r^2 = 0.57$) of the arthropod community within *M. robusta*. It suggests that this attribute can more accurately determine the variety and quantity of microhabitats and resources available for arthropods in host-grasses. However, for other plants, the best plant attributes for the SAR may differ. For example, Marques *et al.* (2000) did not find a correlation between insect herbivore richness and the mean dry weight of five species of woody fabaceous plants. Nevertheless, when host-plant resources were broken down into different types of resources (flowers, fruits, leaves, stems) and correlated with the number of insect species that used those resources, most correlations were significant. The results of our study and those of Marques *et al.* (2000) indicate that the best plant attribute for the SAR in individual plants depends on the plant growth form and the type of arthropod resource.

To estimate the biota richness in grasses at the individual host-plant level, it is suggested that the above-ground dry weight of the plant be used. However, if this requires expensive and laborious work, the level of prediction for the SAR at different attributes of the host-plant can be determined first, after which a cost–benefit analysis can be conducted to determine the most practical plant attribute to use to predict the biota richness. In this study, the most practical plant attribute was the basal area ($r^2 = 0.47$) because it provided a good level of prediction and was easy to measure in the field. This knowledge could be useful when identifying concentrations of arthropod diversity for conservation reasons (Drakare *et al.* 2006).

Best functional models for community attributes

The regression analyses that produced the highest determination coefficients (the best functional mathematical models) for abundance, dry weight and the diversity index of arthropods in response to increases in grass size (above-ground dry weight) were the power, exponential and logarithmic models, respectively. These models could be useful to enable estimation of arthropod community attributes based on plant size when we study the arthropod community within a given ecosystem, or evaluate the potential of an area to host the local fauna of arthropods with a focus on conservation or restoration. However, before these models can be relied on, further studies using different types of vegetation and plant growth forms must be conducted.

The above-ground dry weight of *M. robusta* was the best plant attribute for prediction of the abundance, dry weight and diversity index of the arthropod community (Table 1), indicating that this attribute of *M. robusta* is best able to determine the number of resources of an arthropod community within *M. robusta* when compared to other plant attributes (height, cover, basal area, volume). In this case, the above-ground dry weight of *M. robusta* represents the food for arthropod herbivores and, in an indirect way, the level of prey available to predators. Greater availability of food permits an increase in the populations that shape the community, as has been described in other studies conducted to evaluate arthropod communities within different species of plants (Marques *et al.* 2000; Araújo *et al.* 2003; Veldtman *et al.* 2007).

Effects of light

Multiple regression analysis revealed that the light conditions in the area in which the grass was established contributed to the SAR to explain the variance of arthropod richness within *M. robusta*. Additionally, this analysis revealed that grasses found in shady environments had higher arthropod richness than those found in sunny areas (Fig. 1). The greater biodiversity found on grasses in shady areas could indicate that the arboreal stratum over *M. robusta* provides a more favorable microhabitat, such as lower wind speed, less radiation from the sun, smaller variation in diurnal temperature and better physical protection against rain, than sunny areas (Cano-Santana 1994). For this reason, shade allows a more complex assembly of arthropod species. Conversely, harsh habitats appeared to be associated with low species richness, which was likely because such environments reduce the possibility of a species establishing itself (Townsend *et al.* 1983; Hartley & Jones 2003).

Plant phenophase effect

The lack of influence of plant phenophase of *M. robusta* on the arthropod community attributes suggests that the availability of vegetation is not an important source of food and energy for the arthropod community within this ecosystem. Further study (López-Gómez *et al.* 2009), however, showed that the arthropod community within *M. robusta* had higher morphospecies richness, abundance, biomass and diversity index during the rainy season (August–October) than the dry season (February–March). The highest levels of precipitation in the study site are associated with a higher level of primary productivity for many plant species (Cano-Santana 1994), which results in a greater quantity and variety of vegetation as food available for herbivores, and consequently a higher abundance of prey for the next trophic levels. It is possible that our results reflect two transition times of the arthropod community within *M. robusta* between the rainy and dry seasons when the community attributes are contrasting.

Isolation effect

The results of this study indicated that the distance between conspecific grasses (1.95 ± 1.33 m) had no effect on any attributes of the arthropod community within *M. robusta*. These findings were likely because our distance records were smaller than the distance records of other studies in which the distance between individual neighboring plants was found to impact community characteristics (e.g. 103 ± 65 m, Sanchez & Parmenter 2002). Seemingly, in this ecological reserve, the level of isolation among grasses did not affect the ability of arthropods to colonize other conspecific habitats, even when isolation affected their ability to disperse, escape from adverse circumstances or find optimum conditions (Schowalter 2006). The results of a study conducted by Sanchez and Parmenter (2002) suggest that an isolation distance of >100 m between host plants could be important to the diversity of a resident arthropod community.

ACKNOWLEDGMENTS

The authors thank Santiago Zaragoza Caballero, Harry Brailowsky, Rafael Gaviño Rojas, Iván Castellanos Vargas and Cristina Mayorga Martínez for their valuable contributions to the identification of specimens. Thanks also to Marco Romero-Romero for technical laboratory support, and Susana Alejandre Grimaldo, Erick Daniel Villamil, David Humberto Basilio Hernández and Isael Victoria Salazar for field assistance. This research was made possible through a scholarship from CONACYT-Mexico within the Postgraduate Department of Biological Sciences of the UNAM. Additionally, we thank the English Communications Consultant/Editor, Susan M. French.

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III. Host-plant specialization and diurnal dynamic of arthropod community within *Muhlenbergia robusta* (Poaceae)

Víctor López-Gómez and Zenón Cano-Santana. Enviado a *Entomological News.*

Abstract

Most literature about the arthropod community within plants makes the assumption that all arthropod species carry out their activities in their host-plant. Nevertheless, studying arthropod communities with a high level of specialization in the use of their host-plant could also provide important information about the dynamics of the arthropod community. In this study, the ratio of taxa arthropods was determined considering high specialization in the use of the host-plant. The *Muhlenbergia robusta*: Poaceae was compared with two adjacent habitats with similar conditions (herbaceous patches and litter) at different diurnal schedules (0100, 0700, 1300 & 1900 h) in the xerophilous scrubland. Results point to the conclusion that the arthropod community in *M. robusta* exhibited few species with a high level of specialization in the use of this habitat (4.3%). Arthropod community structure (richness, abundance, and index diversity) in the grass was constant throughout the day.

Key words. Arthropods, diurnal dynamic, grass, habitat specialization, herbaceous patches, litter.

INTRODUCTION

It is well known that herbivorous insects are very specialized in terms of their food. It has been reported that they feed on only one or on a few genera of plants, even in a single family (Bernays and Graham, 1988; Schoonhoven *et al.*, 2005). Certain factors have been found to be decisive in determining the range of hosts of herbivorous insects. Among the most important are (1) the secondary compounds in the plants, (2) the presence of predators, and (3) mating behavior. These factors are discussed below.

Secondary compounds are one of the most effective strategies that plants use to avoid predation by herbivores, for example, toxins or feeding deterrents that kill insects or slow their development rates (Lill and Marquis, 2001; Schowalter, 2006). The noxious effects of secondary compounds on insects are crucial to the preferences of feeding insects, and therefore, the host plant's range of phytophagous insects (Cates, 1980; Bernays and Graham, 1988).

Natural enemies can influence the host range of phytofagous specialization. Moreover, it has been proposed that species are looking for enemy-free spaces to reduce their mortality (Gilbert and Singer, 1975; Lawton, 1978). In fact, Price et al. (1980) recorded some insect herbivores that changed their host plant to a new toxic plant that provided protection against enemies.

Literature has described that some phytophagous insects restrict their host range due to patterns of mate-finding behavior. This is true even in plants that do not have a relationship with the food preferences of insects(Labeyrie, 1978).

Conversely, arthropod predators are generalized in their food selection (Sabelis, 1992). For this reason, habitat selection depends on the services that the habitat provides to increase their chances of survival. It has been reported that the abundance of arthropod predators within plants is related to habitats offering (1) abundant prey, (2) refuge from predation, e.g., cannibalism and intraguild predation, (3) easier and more effective spotting and capture of prey, (4) a more favorable microclimate, and (5) access to alternative resources (Langellotto and Denno, 2004).

In spite of the knowledge gathered about host-plant specialization within several arthropod species (Feeny, 1976; Cates, 1980; Bernays and Graham, 1988), there is little data about the level of arthropod specialization in the use of its habitat at the community level (i.e., species that carry out all their activities in the host-plant). Descriptions of arthropod communities within host plants assume that all species have the same level of specialization in the use of their habitat. In order to address this theoretical problem, only the most abundant taxa of the community have been studied. Previous studies about the ratio of arthropods with high specialization in the use of their habitats are difficult to find. This kind of research could provide important data about the dynamics of the arthropod community in their host plant, and about the possible main flows of matter and energy within the arthropod-plant ecosystem.

The main goals of this study are (1) to determine the ratio of species in the arthropod community in a grass (*Muhlenbergia robusta*: Poaceae) with high levels of specialization in the use of the host plant (i.e., species that carry out all their activities in the host plant), by studying arthropod communities with similar habitats (i.e., herbaceous patches and litter) at four different times throughout the day, and (2) to determine the diurnal variation of the arthropod community structure in three different herbaceous habitats (*M. robusta*, herbaceous patches, and litter).

METHODS

Area of Study

This study was done in the Reserva Ecológica del Pedregal de San Ángel (REPSA) (19°19’N, 99°11’W), which is located in the main campus of the Universidad Nacional Autónoma de México, southwest of Mexico City. This ecological reserve has an extension of 237 ha and an elevation of 2300 m. Vegetation at the reserve can be characterized as a xerophilous scrubland; the area has a sub-humid climate. This site has an annual mean temperature of 16.1 °C, and its annual mean rainfall is 835 mm (César-García, 2002). The reserve has a wet season between May and October. The area is located over a basaltic substratum that was deposited 1650 to 2000 years ago, during the eruption of the volcano Xitle (Carrillo, 1995). Most plant species are herbaceous or shrub-like; however, there are a few small trees 3 to 7 m high.

Study system

Muhlenbergia robusta (Fourn.) Hitchc. (Poaceae) is a perennial grass 1 to 2 m high. This plant contributes about 15% of the aboveground net primary productivity in the REPSA (Cano-Santana, 1994). This plant flowers between June and August and bears fruit between September and June (César-García, 2002). This grass has a distribution between 2250 and 3200 m elevation (Rzedowski and Rzedowski, 2001).

Collection

In each collection we had the intention to trap the most quantity of arthropods possible for the different habitats; unfortunately the heterogeneous geomorphology in the REPSA did not allow using the same trapping technique. For this reason were used the most suitable technique for each kind of habitat (*M. robusta*, herbaceous patches and litter).

24 *M. robusta* plants—that show about 48 and 73 cm of basal perimeter at ground level— were collected at random, at four different times of day (0100 to 0300 h, 0700 to 0900 h, 1300 to 1500 h and 1900 to 2100 h). Six grasses were collected during each time period. The collection took place in July of 2006, in a large site in the nuclear zone of the REPSA with the presence of some arboreal stratum. Each selected grass was completely wrapped and protected using a plastic bag, and was later extracted using a pick and shovel.

To obtain an authentic epiphyte arthropod community from the herbaceous patches of each grass, an entomological net was struck ten times in the four nearest patches where the herbaceous patches were dominant and *M. robusta* was not present.

To acquire the arthropods associated with a litter habitat, for each plant, the litter of the four nearest patches without vegetation was collected using a 24 cm diameter circle as a sampling unit.

The same day of the collection, the three habitat samples (*M. robusta*, herbaceous patches, and litter) were taken to the laboratory, where arthropods were manually extracted from them. Only organisms ≥ 3 mm in corporal length were considered. Extracted fauna were initially sorted into morphospecies, a common practice in biodiversity studies that does not compromise scientific accuracy (Oliver and Beattie, 1996) and has some clear advantages when expertise in all taxonomic groups is not available (Gaston ,1996). The morphospecies were identified and then sent to several taxonomists for species identification. The community attributes for each sample were recorded considering richness per plant, abundance per plant, and diversity. Diversity was recorded using the Shannon-Wiener's index with natural logarithm (*H'*).

The aboveground dry weight of each plant was obtained by drying the plant in an electric oven at 50°C to a constant weight, and was then weighed using an analytical balance (Ohaus AV812, ± 0.005 g).

In August of 2007, the relative coverage of the principal landscape elements in the site were determined (*i.e., M. robusta*, herbaceous patches, litter, exposed rock, and shrubbery and arboreal plants) using Canfield´s method with two lines of 8 m that traversed the site.

Statistical Analysis

To determine the effects of the sampling schedule (0100, 0700, 1300, and 1900 h) and the type of habitat (grass, herbaceous patches and litter) on community attributes (richness, abundance, and *H'*), the Wilks MANOVA tests were calculated (Zar, 2010). Afterward, factorial ANOVA tests were calculated for each fauna attribute, using only independent variables showing significant effects on previous MANOVA tests. Tukey's multiple comparison tests were then done on significant ANOVA tests. Richness and abundance were transformed using the formula $X' = \sqrt{0.5 + X}$, because they are discrete variables (Zar, 2010).

To determine the similarity of species composition among diverse communities, Jaccard's index of similarity was applied, considering the twelve treatments (four schedules × three habitats). Next, a single linkage cluster analysis using Jaccard's index was done.

RESULTS

Arthropod-fauna on three kinds of habitats

On 24 grasses, a total of 139 arthropod taxa and 1529 individuals were found; the herbaceous patches sampling registered 150 arthropods taxa and 1594 individuals; the litter sampling found 60 arthropod taxa and 248 individuals.

Wilks' MANOVA tests showed significant effects, depending on the kind of habitat, the schedule sampling, and the interaction between these two variables (kind of habitat × schedule sampling) on community arthropod attributes (richness, abundance, and diversity). Likewise, two ways factorial ANOVA tests showed a significant effect in the kind of habitat, the hour of sample collection, and in the type of habitat interaction × the hour of collection, on richness ($F_{3,\ 60}$=8.1, P=0.001; $F_{2,\ 60}$=84.1, P<0.001; $F_{6,\ 60}$=7.6, P<0.001, respectively), abundance ($F_{3,\ 60}$=3.1, P=0.03; $F_{2,\ 60}$=41.9, P<0.001; $F_{6,\ 60}$=4.1, P=0.001, respectively), and index diversity ($F_{3, 60}$=7.5, P<0.001; $F_{2, 60}$=40.4, P<0.001; $F_{6, 60}$=4.0, P<0.001, respectively).

Different schedules did not result in significant changes in arthropod mean richness and abundance, nor in *H'* in *M. robusta* (Figs. 1A, B, C). In contrast, the lowest richness and abundance averages on the herbaceous patches habitat were at 0100 h. At 0700 h they showed a sudden increase, and at 1300 and 1900 they showed a slight decrease (Figs. 1A, B). The mean of the arthropod index diversity was unchanged at different schedules on the herbaceous patches habitat (Fig. 1C). On litter habitat, the lowest arthropod richness and diversity averages were at 1300 h, and the highest averages were at 0700 h (Figs. 1A, C). Abundance averages were constant at different schedules (Fig. 1B).

On *M. robusta* habitat, the highest average abundance of Formicidae was at 1300 h. Diplopoda, Coleoptera, Hemiptera, Blattodea, and Araneae did not show a clear peak average abundance (Fig. 2A). Othoptera, Homoptera, Coleoptera, and Diptera showed their lowest average abundance at 0100 on the herbaceous patches habitat. Afterwards, these taxonomic groups increased their average abundance between 0700 and 1300 h, and then they showed a slight decrease at 1900 h (Fig. 2B). There was a clear peak of abundance at 0700 h for Coleoptera, Araneae, Formicidae, and Diplopoda on litter habitat, while Chilopoda did not appear (Fig. 2C).

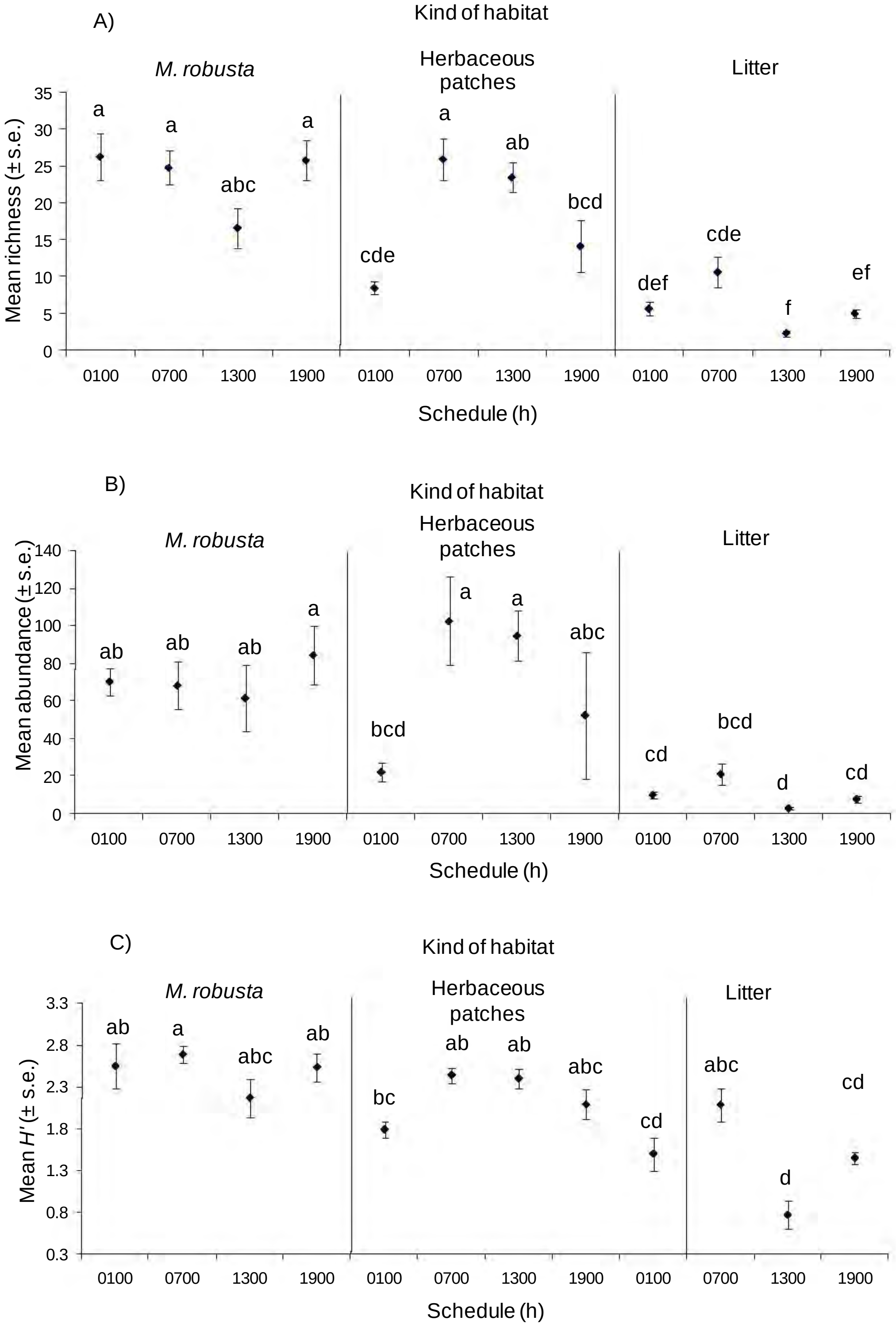

Figure 1. Arthropod-fauna average richness (a), abundance (b), and index diversity (c) (*H'*) in three different kinds of habitats (*M. robusta*, Herbaceous patches and Litter) during four different sampling schedules (0100, 0700, 1300, 1900 h). Collection, July 2006, Reserva Ecológica del Pedregal de San Ángel, Mexico City. Letters denote significant differences (α=0.05). Values are means ± s.e.

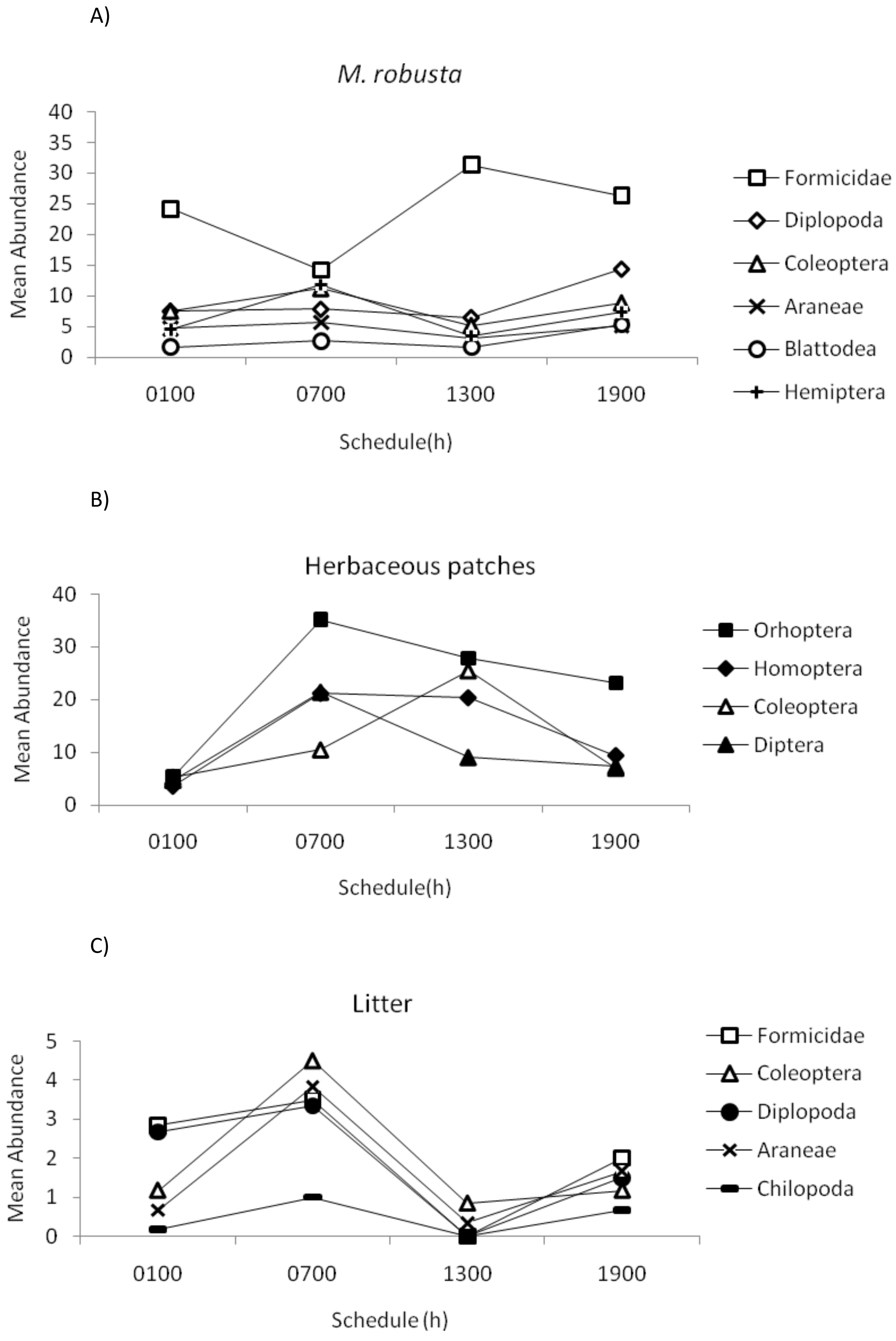

Figure 2. Taxonomic group mean abundance during four different schedules (0100, 0700, 1300, 1900 h) in three different habitats: *Muhlenbergia robusta* (a), Herbaceous patches (b), and Litter (c). For *M. robusta* and herbaceous patches habitats, only shown-taxonomic groups with an average abundance greater than 5. Collection, July 2006, Reserva Ecológica del Pedregal de San Ángel, Mexico City.

Habitat specialization of arthropods

There were six taxa that appeared only in *M. robusta*, four of which were registered at all schedules (Thomisidae 10: Araneae, *Phlegyas* sp.: Hemiptera, Armadillidiidae 2: Isopoda, *Blatta* sp.: Blattodea), and two of which were registered at three schedules (*Novalene* sp.: Araneae and *Dinocheirus tenoch* Chamberlin 1929: Pseudoscorpiones). There were three exclusive taxa for herbaceous stratus habitat, of which, only Cidadellidae 10 (Homoptera) was present at all schedules. In litter habitat, Chrysomelidae 12 (Coleoptera) was present in almost all schedules, except at 1300 h.

Sphenarium purpurascens Charpentier 1842 (Orthoptera), *Crematogaster* sp. (Formicidae), and Melyridae 14 (Coleoptera) were registered on *M. robusta* and on herbaceous patches habitats. Polydesmida 3 (Diplopoda), *Paratrechina* sp. (Formicidae) and Coleoptera 41 were registered on *M. robusta* and litter habitats. There were no taxa found on herbaceous patches or on litter habitats; there were no fauna that used all the three kinds of habitats.

Similarity among arthropod communities with diverse habitats and schedules

The highest Jaccard similarity index among arthropod communities within *M. robusta* at different local times was between 0700 and 1700 (0.717); the lowest was between 0100 and 1300 (0.448, Table 1). The average of all similarity indices was 0.59 (± 0.04 s.e.). A dendrogram cluster analysis based on Jaccard's index of similarity showed that arthropod communities are grouped principally by habitat, rather than by sampling schedules (Fig. 3).

Table 1. Jaccard similarity indices among arthropod communities within *M. robusta* at different local solar hours (0100, 0700, 1300, 1900). Collection, July 2006, Reserva Ecológica del Pedregal de San Ángel, Mexico City.

	Local solar time (h)		
	0100	**0700**	**1300**
0700	0.603		
1300	0.448	0.566	
1900	0.673	0.717	0.518

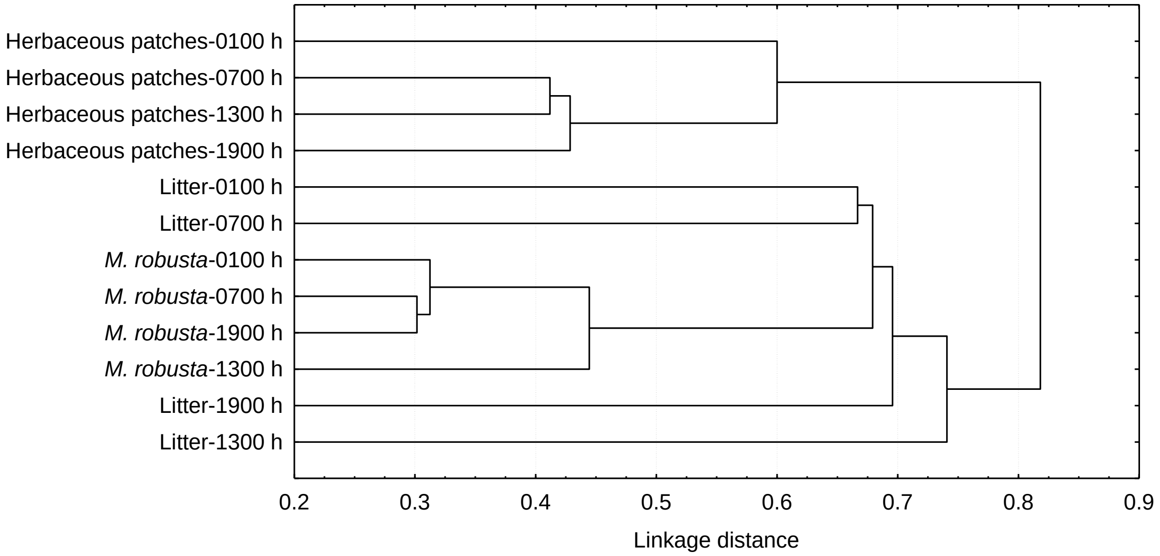

Figure 3. Dendrogram based on Jaccard's index of similarity; considering 12 different arthropod communities using a design of three kinds of habitats (*M. robusta*, Herbaceous patches and Litter) × four sampling schedules (0100, 0700, 1300 and 1900). Collection, July 2006, Reserva Ecológica del Pedregal de San Ángel, Mexico City.

M. robusta sizes and landscape elements

The one-way ANOVA test did not find a significant effect of the sampling schedule on the ground dry weight of *M. robusta* ($F_{3,\,20}$=1.09, P=0.37). Results suggest that habitat size does not have influence over arthropod community attributes, which was described for animal-plant interaction (Lawton, 1978; Southwood *et al.*, 1982; Ozanne *et al.*, 2000; Marshall and Storer, 2006).

Canfield's method showed that *M. robusta*'s presence was the most dominant at the site of the study. Following that, in order of importance, were the herbaceous patches, litter, exposed rock, and finally, shrubbery and tree plants (Fig. 4).

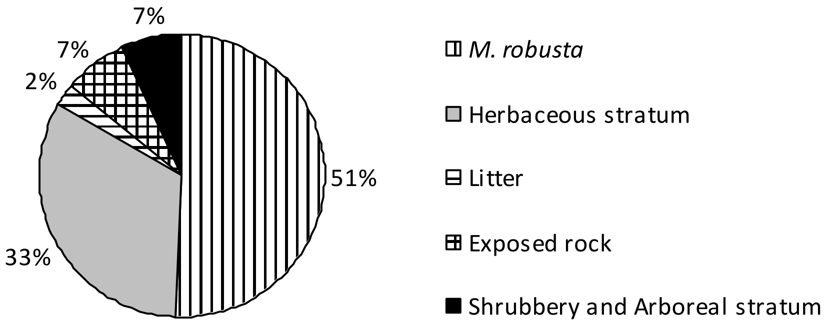

Figure 4. Relative coverage of *M. robusta* and landscape elements (herbaceous patches, litter, exposed rock, and shrubbery and tree plants) on a sunny site in the Reserva Ecológica del Pedregal de San Ángel. Collection, August 2007.

DISCUSSION

Only 4.3% of the arthropod taxa (six morphospecies) was specialized in *M. robusta* in the use of habitat, which suggests that they carry out most of their activities (foraging, hiding and meeting) within this grass. These specialist arthropods showed a complex community formed by the main functional groups in an ecosystem: herbivorous (*Phlegyas* sp.: Hemiptera), saprophagous (Armadillidiidae 2: Isopoda and *Blatta* sp.: Blattodea) and predators (Thomisidae 10: Araneae, *Novalene* sp.: Araneae and *Dinocheirus tenoch*: Pseudoscorpiones). This indicates, on one hand, that grass conditions offer most of the requirements of these taxa in a microhabitat, i.e., alternative prey or food resources and refuge from predation. On the other hand, these taxa seem to share a very close trophic relationship among themselves, and probably form the main flows of energy and matter in the *M. robusta* system. Nevertheless, more studies are needed to support this assertion.

Study results indicate that *Phlegyas* sp. (Hemiptera) could be a probable phytophaguous specialist feeding on this grass. As literature has reported, herbivorous insects are very specialized in the selection of their food (Bernays and Graham, 1988). The three predators with significant habitat specialization to grass (Thomisidae 10: Araneae, *Novalene* sp.: Araneae and *Dinocheirus tenoch*: Pseudoscorpiones) show signs that the *M. robusta* structure facilitates their hunting strategies and provides suitable refuge to avoid predation (Langellotto and Denno, 2004). It was observed that the habitat structure of the host plant can influence a community of spiders in plants. This was shown through a robust pattern of growth in the natural enemies of arthropods (hemipterans, mites, parasitoids and spiders) in complex structural habitats. These complex habitats provide a broad range of favorable conditions that attract natural enemies and decrease the need to move in search of more suitable conditions (Sunderland and Samu, 2000). In the same way, the two saprophagous taxa specialists on *M. robusta* (Armadillidiidae 2 and *Blatta* sp.) indicate that the layer of dead organic matter typical on *M. robusta* (located in its base at ground level), could be an appropriate source of food and protection against predators (Jabin *et al.*, 2004; Schmidt *et al.*, 2005).

Study results showed that most of the arthropod community taxa, within *M. robusta* (i.e., 133 morphospecies), were generalized in their use of the different available herbaceous habitats. This could be attributed to the great variety of life forms and requirements that are characteristic of the Phylum Arthropoda. These organisms can be categorized as (1) taxa with a regular association with *M. robusta*, and (2) taxa that use *M. robusta* and other herbaceous habitats.

One example of taxa with a regular association with this grass could be *Sphenarium purpurascens* (Orthoptera), a grasshopper that eats the pollen and fruit of *M. robusta* (Mendoza and Tovar-Sánchez, 1996). Results show that this Orthoptera was found in herbaceous patches at all schedules, but was recorded in *M. robusta* only at 1300 h. This grasshopper is likely foraging the reproductive structures of the grass only at this specific hour of the day because of favorable environmental conditions—as has been recorded for floral visitors in this Ecological Reserve (Figueroa-Castro and Cano-Santana, 2004).

For taxa that use *M. robusta* and other herbaceous habitats, Polydesmida 3 (Diplopoda) was registered in the grass at all times, and in the litter habitat at three schedules. This can be interpreted to mean that the saprophagous use these two habitats simultaneously because they offer food and refuge against adverse conditions. Other studies have also registered a direct relationship between saprophagous abundance and the amount of litter available (Jabin *et al.*, 2004; Schmidt *et al.*, 2005).

Apparently there is no taxon that uses all three kinds of habitats. However, there are arthropods that likely use all described habitats. Of these, most are probably fliers. Unfortunately, their numbers cannot be registered due to their high mobility and the limitations of our sampling techniques.

The *M. robusta* habitat had the greatest coverage of all landscape types (51%), which explains the richness and abundance of the arthropods (139 taxa and 1529 individuals) found within this habitat. This landscape provides a greater quantity and variety of habitats, as well as resources for the fauna. Likewise, species-area relationship (SAR) has described a direct link between the richness of arthropods and the extension of their host plant distribution (Lawton, 1978; Southwood *et al.*, 1982; Ozanne *et al.*, 2000; Marshall and Storer, 2006).

Despite the low coverage (33%) of the herbaceous patches, this habitat shows the highest arthropod richness (150 taxa) in comparison with the other two kinds of habitats. This could be because herbaceous patches habitat comprises many species of plants that offer a greater variety of habitats and food for the arthropod community; this permits the establishment of more species with contrasting requirements (Symstad *et al.*, 2000).

Results show that the structure of the arthropod community within *M. robusta* is constant throughout the day, based on the richness and abundance per plant, and the diversity (*H'*). Additionally, records on the abundance of the principal taxonomic groups within the grass were regular throughout the day. However, Jaccard's index of similarity indicates that arthropod communities change their composition throughout the day, on average, 42% (59 species). This evidence indicates that all available habitats for arthropods in *M. robusta* are fully occupied all day long; and that arthropod communities in grass are very dynamic, retaining only 58% of its species composition throughout the day.

Cluster analysis points out that arthropod communities within *M. robusta* present a remarkably different species composition compared to herbaceous patches and litter habitats. This could be explained because *M. robusta* offers diverse (1) microclimatic conditions, (2) types of resources and (3) interactions with other species. These factors are decisive in determining the establishment of species (Begon *et al.*, 2006). Nevertheless, the arthropod community composition within *M. robusta* has more in common with litter habitat than herbaceous patches, most likely because *M. robusta* shows a layer of dead organic matter around its base. For this reason, similar conditions should be observed with the litter habitat.

In the herbaceous patches habitat, arthropod richness and abundance—and the abundance of the principal taxonomic groups—showed a sudden increase at 0700 h; following that, the recorded numbers decreased gradually. This indicates that arthropods experience a peak of activity at 0700 h in this habitat. Results agree with a study of arthropod floral visitor activity of four Asteraceous (*Eupatorium petiolare*, *Dahlia coccinea*, *Tagetes lunulata* and *Verbesina virgata*) in the REPSA (Figueroa-Castro and Cano-Santana, 2004). The authors found that the highest frequency of visits of anthophiluos were between 0845 and 1645 h. The number of Arthropod visitors on flowers was related to higher temperatures and lower relative humidity levels, which is directly related to its physiological response to the environment.

In comparison to other habitats, litter habitat showed the lowest richness, abundance, and diversity. This may be true because, for the majority of the arthropod community, this habitat is used only as a passing location for dispersion; results showed that the peak of arthropod mobility is at 0700 h. Moreover, this habitat represents an exposed location to predators due to the absence of vegetation; nevertheless, records indicate that it could be an appropriate habitat for saprophagous.

We are conscientious that our results have limitations in their interpretation, because the difficult to compare these arthropod communities from different habitats when different trapping techniques were used; however this study is an approach of the level of specialization of the community arthropods to their host-plant, and besides shows the diurnal dynamic of the whole arthropods within a plant, which both have been few recorded. For studies that will try to corroborate our records, could be appropriate use the same trapping technique on the treatments, if it is possible.

We conclude that the ratio of arthropod species with a high level of specialization in the use of the *M. robusta* host plant was very little (4.3%). Further, the structure of the arthropod community (richness, abundance, and index diversity) in the grass was constant throughout the day, although the diurnal variation of species composition shows a remarkable change (42%).

ACKNOWLEDGEMENTS

We thank Santiago Zaragoza Caballero, Harry Brailowsky, Rafael Gaviño Rojas, Iván Castellanos, and Cristina Mayorga Martínez for the identification of specimens. Thanks to Marco Romero-Romero for technical laboratory support. We thank Susana Alejandre Grimaldo, Erick Daniel Villamil, for field assistance. VLG had a scholarship from CONACYT-Mexico within the Posgrado en Ciencias Biológicas. Thanks to Susan French for editing the English-language text.

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IV. The Relationships Between Maximum Food-Chain Length, Ecosystem Size, and Species Richness in an Arthropod Community Within a Grass

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Abstract

1. Food-chain length (FCL) is a crucial attribute of ecosystems. Today, the importance of species richness in the relationship between ecosystem size and the FCL is unclear. Likewise, there is little evidence that supports the ecosystem size theory in small terrestrial environments.

2. In this study was determined the dependence of maximum FCL on the ecosystem size (dry weight) and on arthropod species richness within the grass *Muhlenbergia robusta*.

3. The maximum FCL was determined with the enrichment of $\delta^{15}N$ between basal species (herbivorous and saprophagous) and top predators within grasses with different sizes.

4. In this study neither was obtained relationships between maximum FCL and ecosystem size, nor with arthropod richness, probably due at the high variability on the $\delta^{15}N$ signatures of arthropods, in consequence at high dynamic of the community.

Key words: Ecosystem size theory, Maximum Food-Chain length, Path analysis, Species-area relationship, Insect-Plant relationship.

Introduction

Food-chain length (FCL) is the number of transfers of energy or nutrients from the base to the top of a food web. This is a central ecosystem trait because it modifies trophic structure (Schoener, 1989; Post *et al.*, 2000) and ecosystem processes (Post, 2002), and determines contaminant concentrations in top predators (Kidd et al., 1998). Stable isotope ratios of nitrogen and carbon are powerful tools for estimating trophic structure in ecological communities (Peterson and Fry, 1987; Post, 2002). Although the importance of FCL in ecosystems is recognized, our current understanding of FCL variability is limited (Post, 2002).

It has been proposed that ecosystem size can modify FCL in natural ecosystems (Post, 2002). Most of the evidence, however, is found in aquatic ecosystems such lakes, streams and marine ecosystems (Vander Zanden and Fetzer, 2007); there is little actual evidence in terrestrial ecosystems (Schoener, 1989), we did not find studies that test this patterns on plant-arthropod interaction, either.

The ecosystem size hypothesis affirms that larger ecosystems support food webs with longer FCLs than smaller ones (Schoener, 1989; Cohen and Newman, 1991). This is because an increase in species richness promotes the addition of intermediate predators, which causes changes in the identity of the apical predator. Moreover, larger ecosystem size often provides greater habitat heterogeneity and refuge from prey, thus reducing the efficiency of predator foraging and decreasing their degree of trophic omnivory. This increases the possibility that top predators will consume other predators, and consequently increase the FCL (Post *et al.*, 2000; Post and Takimoto, 2007).

The goals of this study are (1) to determine the dependence of the maximum FCL of a arthropod community within the grass *Muhlenbergia robusta* with the host plant size (dry weight), likewise (2) the dependence of the maximum FCL with the arthropod richness.

Materials and methods

Area of Study

This study was conducted in the Reserva Ecológica del Pedregal de San Ángel (REPSA) (19°19'N, 99°11' W, 2300 m a.s.l., 237 ha), located on the main campus of the Universidad Nacional Autónoma de México, southwest of Mexico City. The area supports a xerophilous scrubland and a temperate sub-humid climate. This site has an annual mean temperature of 16.1°C, and rainfall averages of 835 mm (César-García, 2002), with a wet season from May until October. The area is located over a basaltic substratum that was deposited 1,650 years ago, during the eruption of the volcano Xitle (Siebe, 2000). Most plant species are herbaceous or shrub-like; however, there are a few small trees 3 to 7 m high.

Study System

Muhlenbergia robusta (Fourn.) Hitchc. (Poaceae) is a perennial grass 1 to 2 m high. The plant contributes about 15% of the aboveground net primary productivity in the REPSA (Cano-Santana, 1994). This plant flowers between June and August and bears fruit between September and June (César-García, 2002). This grass has a distribution between 2250 and 3200 m elevation (Rzedowski and Rzedowski, 2001). Previous studies (López-

Gómez et al., 2009) show that fauna within grasses are composed mostly of arthropods (158 species), as well as two kinds of mollusks and salamanders.

Methods

Muhlenbergia robusta was sampled in November 2003 and in May 2004 in the REPSA. For each sampling, ten random sites were chosen. At each site, circular plots of 20 m diameter were drawn in both sunny and shady locations. In each plot, three individual grass plants of different sizes were selected. For each collecting, 60 plants were sampled. The selected grass plants were cut at ground level using a garden shears and then wrapped carefully in plastic bags. The field sampling was carried out between 0700 and 1000 h. The aboveground dry weight of each plant was obtained by drying the plant in an electric oven at 50°C to constant weight. The samples were then weighed using an analytical balance (Ohaus AV812, ± 0.005 g).

Extraction of the fauna was done through direct exploration and examination of the leaves of the grass in the laboratory immediately following the gathering of samples. Only those organisms with $\geq$ 3 mm body length were collected. Species were initially sorted into morphospecies, a common practice in biodiversity studies that does not compromise scientific accuracy (Oliver and Beattie, 1996) and has clear advantages when expertise in all taxonomic groups is not available (Gaston, 1996). The morphospecies were identified by the author of this study and then sent on to several taxonomists for species identification. For each morphospecies, their alimentary preferences were determined based on a study of the food web of arthropods within *M. robusta* (Blanco-Becerril, 2009), and using related literature. Organisms were stored in ethanol at 70%, as this preservation technique does not modify the stable isotope signature of δN^{15} and δC^{13} (Sarakinos *et al.*, 2002; Halley *et al.*, 2008).

From the arthropods found within each plant, four types of organisms were selected: two base arthropods (herbivorous and saprophagous), and two predators (the morpho with the longest body length and the one most abundant in the collection). The four selected morphospecies also represented the most abundant and frequently found arthropods within the collection. The predator with the highest δN^{15} was considered the top predator; the other was considered a middle predator.

The preparation of samples took place in February 2008. Selected arthropods were packed in aluminum sheets and dried in an electric oven at 50°C for 8 h. They were then finely ground in an agate mortar cleaned with Dextran before each sample. The samples were made using the largest organism from the selected morphospecies, when single organisms did not have the needed weight for the sample; several organisms of the same morphospecies (presented in the same individual grass) were added to complete it.

In April 2008, the organisms were weighed and packed in pressed tin capsules (5 × 9 mm, Costech) to send to the UC Davis Isotope Facility Labs to determine the isotopic composition of δN^{15} and δC^{13} of the samples. To carry out the isotopic analysis, the PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer was used (Sercon Ltd., Cheshire, UK). The δN^{15} and δC^{13} values were calculated by adjusting the provisional values to ensure that correct values for laboratory standards are obtained. For every 12 samples, two laboratory standards were analyzed. Laboratory standards suitable for the types of samples and their C and N content (including NIST 1547 peach leaves, NIST 1577b bovine liver, acetanilide, cellulose, glycine, sucrose, and ammonium sulfate) were applied. Laboratory standards were calibrated against NIST Standard Reference Materials (IAEA-N1, IAEA-N2, IAEA-N3, IAEA-CH7, and NBS-22). Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed relative to an international standard (Vienna Pee Dee Belemnite [VPDB] and atmospheric N, respectively) in per mil (i.e.,

$\delta^{13}C_{Sm}=[(^{13}C_{Sm}/^{12}C_{Sm})/(^{13}C_{St}/^{12}C_{St}) - 1]\times1000$; and $\delta^{15}N_{Sm}=[(^{15}N_{Sm}/^{14}N_{Sm})/(^{15}N_{St}/^{14}N_{St}) - 1]\times1000$, where *Sm* means sample and *St* means standard).

To determine the maximum FCL of an arthropod community, only $\delta^{15}N$ of organisms were used, as this is the most reliable parameter to determine an organism's trophic level. Maximum FCL was calculated based on $\delta^{15}N$ isotopic enrichment between the first consumer arthropods (average between $\delta^{15}N$ of phytophagous and $\delta^{15}N$ of saprophagous) and the top predator. The $\delta^{15}N$ isotopic enrichment was divided by the Minagawa and Wada (1984) constant which describes the enrichment of $\delta^{15}N$ along with an increase in the trophic level of the organisms (3.4 $^{0}/_{00}$). To this resultant length was added a numerical unit that indicates the flux of matter between the first and second trophic levels, the primary producers to herbivorous, and detritus to saprophagous. The maximum FCL (FCL_{Max}) of the arthropods for each plant was calculated as:

$$FCL_{Max} = \left(\frac{\left| \left(\frac{\delta^{15}N_P + \delta^{15}N_S}{2} \right) - \delta^{15}N_{TP} \right|}{3.4} \right) + 1$$

where, $\delta^{15}N_P$ is the isotopic relationship of phytophagous morphospecies, $\delta^{15}N_S$ is the isotopic relationship of the saprophagous morphospecies, and $\delta^{15}N_{TP}$ is the isotopic relationship of the top predator morphospecies. In the case that only one of the two kinds of base morphospecies were absent, FCL_{Max} was calculated as:

$$FCL_{Max} = \left(\frac{|\delta^{15}N_B - \delta^{15}N_{TP}|}{3.4} \right) + 1$$

where $\delta^{15}N_B$ is the isotopic relationship of one of the base morphospecies (saprophagous or phytophagous). The maximum FCL for grasses without base morphospecies was not determined. The maximum FCL of grasses without organisms, or with only phytophagous or saprophagous within the grass were not considered.

Statistical Analysis

The isotopic composition of functional organisms (phytophagous, saprophagous, middle predator, and top predator) was shown with a bi-plot of $\delta^{13}C$ and $\delta^{15}N$.

To determine the dependence of the maximum FCL on the grass size (dry weight) and on arthropod richness, a regression analysis was carried out for each case, and their significance was evaluated whit the ANOVA test (Zar, 2010). These analyses were performed using Statistica software (StatSoft, 2004).

Results

There were collected 120 grasses and only 60 were used to determine the maximum FCL of the system, because in the rest of the grasses only predators, phytophagous or saprophagous were presented and there were grasses without organisms as well. The saprophagous arthropods were composed of a Blattodea (Blattidae) and Isopoda (Porcellionidae and Armadillidiidae) morphospecies. The phytophagous arthropods were Hemiptera (Lygaeidae, Coreidae, and Pentatomidae), Homoptera (Cicadellidae and Fulgoridae), a Coleoptera (Chrysomelidae), and an Orthoptera (Pyrgomorphidae) morphospecies. Some Araneae morphospecies (Linyphiidae, Salticidae, Lycosidae, Clubionidae, Dipluridae, Araneidae, and Sparassidae) were middle and top predators. A Salticidae (Araneae) and a Coccinelidae (Coleoptera) morphospecies were middle predators only. The morphospecies that were only labeled as top predators were some Araneae (Sparassidae, Thomisidae, Philodromidae, Araneidae, and Theridiidae) and a Scorpiones (Vejovidae).

The δ^{13}C and δ^{15}N signatures of middle and top predators were remarkably higher than those of the base trophic groups (phytophagous and saprophagous) (Figure 1). The mean maximum FCL of the *M. robusta* system was 1.83 ± 0.10 s.e. (range: 0 - 2.90).

Maximum FCL was not related to grass size ($F_{1,\,58}$ = 0.31, P = 0.58; Figure 2), as well as arthropod richness ($F_{1,58}$ = 0.35, P = 0.56; Figure 3).

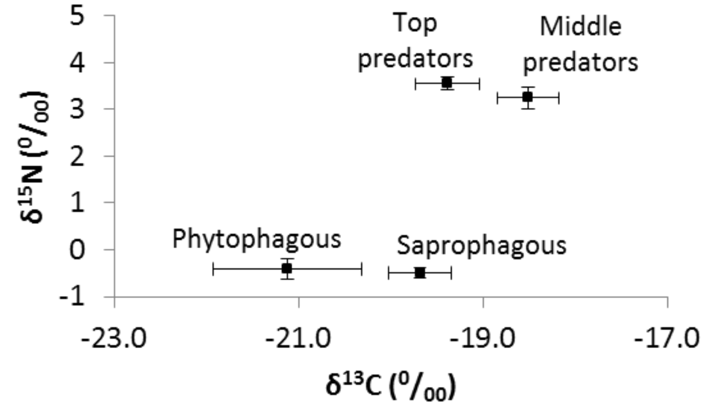

Figure 1. Bi-plot of δ^{13}C and δ^{15}N isotopes (± s.e.) for four types of trophic groups (phytophagous [*n* = 55], saprophagous [*n* = 56], middle predators [*n* = 35] and top predators [*n* = 57) of arthropods within *M. robusta*.

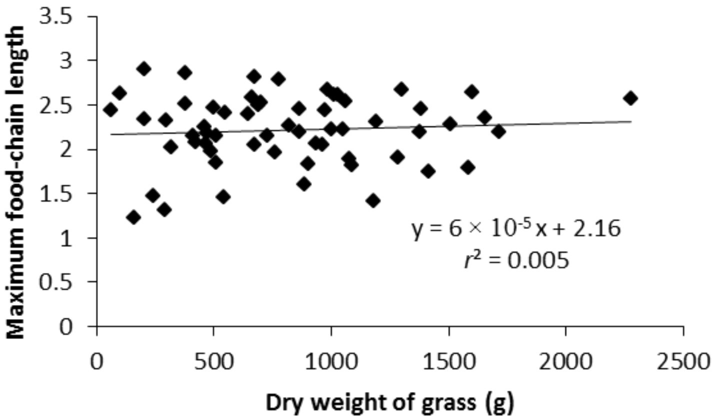

Figure 2. Regression analysis between the host-plant size (dry weight of *M. robusta*) and the maximum food-chain length of the system (n = 60).

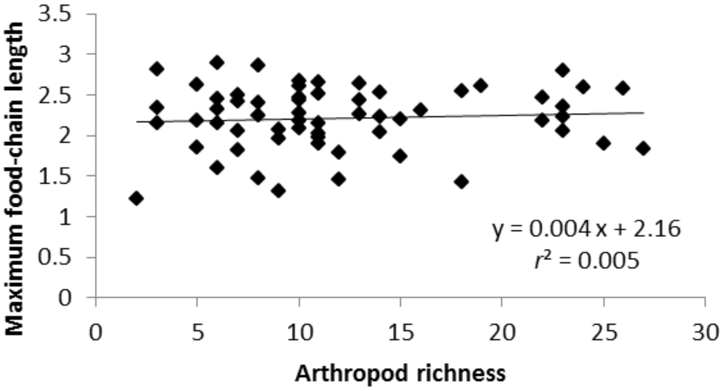

Figure 3. Regression analysis between the arthropod richness and the maximum food-chain length of the *M. robusta* system (n = 60).

Discussion

Study results did not contribute to provide evidence of the positive relationship between ecosystem size and FCL in small terrestrial ecosystems (arthropods within plants), in the same pattern that has been recorded in large aquatic ecosystems (Vander Zanden, Casselman*, et al.*, 1999; Vander Zanden, Shuter*, et al.*, 1999; Post *et al.*, 2000; Lake *et al.*, 2001). Nevertheless, results from this study are in agreement with those reported in a review of 219 aquatic ecosystems, which found a weak relationship between ecosystem size and FCL (Vander Zanden and Fetzer, 2007).

The absence of the relationship between ecosystem size and maximum FCL in *M. robusta* could be due to a high variance in the arthropods δ15N signatures, because these were determined on several morphospecies. Stable isotope ratios of nitrogen and carbon are powerful tools for trophic structure research in ecological communities (Peterson y Fry, 1987; Post, 2002). However, one the most important weakness is the variance of the δ13C and δ15N signatures due to several factors, mainly to the enrichment between prey and predator. Among the best documented factors that modify the δ13C and δ15N signatures are the nutritional stress (Oelbermann and Scheu, 2002), the biochemical form of nitrogen excretion (Vanderklift and Ponsard, 2003), dietary preferences of the organisms (Vander Zanden and Rasmussen, 2001), the tissue typeof the sample (Hobson *et al.*, 1996) and the kind of metabolism of the organisms (Bosley *et al.*, 2002). For this reason, to reduce the influence of the variation of nitrogen and carbon isotopes on arthropods in future studies, we recommended using the same morphospecies with similar size for each guild.

Results suggest that more diversity in arthropod communities will not show longer maximum FCL (Figure 3). On one hand, this result suggests that there is not addition of intermediate predators in bigger host plants, which changes the identity of top predator or reduce the predators trophic omnivory degree, in consequence of an increase in prey refuge in habitats with intraguild predation (Post and Takimoto, 2007). On the other hand, results suggest that the arthropod community within *M. robusta* has a high rate of changed species, which makes it a very dynamic community that increases the variance of the maximum FCL records. However, to test theses hypotheses, more evidence in terrestrial arthropod-plant systems is necessary.

The authors conclude from the study that the maximum FCL in *M. robusta* does not depends on habitat size, or on arthropod richness, probably due the high variation of nitrogen and carbon isotopes recorded, which has to avoid for future studies.

ACKNOWLEDGMENTS

The authors would like to thank Santiago Zaragoza Caballero, Harry Brailovsky, Rafael Gaviño Rojas, Iván Castellanos Vargas and Cristina Mayorga Martínez for their valuable contribution to the identification of specimens. The authors also thank Elsa Valiente Riveros, Manuel Hernández Quiroz and Marco Romero-Romero for technical laboratory support. Additionally, we thank Susana Alejandre Grimaldo, Erick Daniel Villamil, David Humberto Basilio Hernández and Iván Castellanos for their helpful field assistance. This research was made possible through a scholarship from CONACYT-Mexico within the Postgraduate Department of Biological Sciences of the UNAM.

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V. DISCUSIÓN GENERAL

Nuestras evidencias señalan que las plantas de mayor tamaño presentan las comunidades de artrópodos más diversas y abundantes. Esto indica que las plantas más grandes pueden soportar a comunidades más complejas porque proporcionan una mayor variedad de microambientes para el establecimiento de especies con requerimientos contrastantes (Soulé and Simberloff, 1986), así como una mayor cantidad de recursos basales que fomentan el incremento en el tamaño poblacional de las diferentes especies de artrópodos (Sanchez and Parmenter, 2002).

La alta diversidad de artrópodos presentes en los zacatones grandes no fomentó cambios en la estructura trófica del ecosistema, principalmente en su longitud máxima de la cadena trófica; probablemente por la gran variación que presentaron las firmas isotópicas del δN^{15} de los depredadores tope, a consecuencia de la gran dinámica de los artrópodos asociados a *M. robusta*, ya que sólo el 4.3% de las morfoespecies tienen una alta permanencia en esta planta a lo largo del día.

Estudios recientes señalan que los recursos biófagos y saprófagos de *M. robusta* determinan la estructura de la comunidad de artrópodos asociados. Yesenia Jiménez-Cedillo (En proceso) encontró relaciones positivas entre las hojas jóvenes de *M. robusta* y la riqueza, la abundancia y el peso seco de los artrópodos asociados. Por otro lado, al incorporar diferentes cantidades de detrito conespecífico (0%, 50%, 100%, 150% y 200%), se observó que, después de un año y medio, la cantidad de detrito incorporada no se relacionó con los atributos de la comunidad de artrópodos (riqueza, abundancia, diversidad y peso seco) y solamente la abundancia de colémbolos se relacionó positivamente con el detrito incorporado. En contraste, los atributos de la comunidad se relacionaron positivamente con el detrito que se registró en el momento de la colecta, lo cual se explicó con la estrecha relación de la comunidad de artrópodos con el detrito ya que este sustrato les proporciona refugio, alimento y sitios para encuentros (Ayala-Palma, 2010).

La comunidad de artrópodos asociada a *M. robusta* mostró una alta dinámica diurna por su elevado recambio de especies, ya que sólo el 4.3% de todas las morfoespecies encontradas en el zacatón (*S* = 139) se especializan en utilizar a esta planta como hábitat, lo cual señala, por un lado, que la comunidad de artrópodos tiene una alta dinámica a lo largo del día a consecuencia de una alta tasa de recambio de especies. Y por otro lado, que las actividades de estos organismos están muy relacionadas con esta planta así como con el flujo de materia y energía en el zacatón. Por ejemplo, en un estudio de la estructura trófica de la comunidad de artrópodos asociados a *M. robusta* se describió que la cucaracha *Blatta* sp. (una de las morfoespecies especializadas en el zacatón) incorpora materia al sistema por la vía saprófaga porque se alimenta del detrito que se presenta en la base del zacatón; además, es alimento de cuatro depredadores de la comunidad (un escorpión, una mantis y dos arañas) (Blanco-Becerril, 2009). Asimismo, Blanco-Becerril (2009) corroboró que existen artrópodos herbívoros que incorporan materia al sistema por la ruta biófaga porque encontró una larva de lepidóptero y un homóptero que se alimentan de los tejidos jóvenes de esta planta.

A partir de nuestras evidencias y de los nuevos estudios surgen las siguientes perspectivas de estudio.

(1) Determinar si la curva de especies-área (SAR) de los artrópodos asociados a *M. robusta* puede ser indicador de sistemas perturbados.

(2) Determinar los factores y los mecanismos (i.e., adición de depredadores tope o intermedios, así como cambios en el grado de omnivoría de los depredadores; Post and Takimoto, 2007) que modifican la longitud máxima de la cadena trófica de los artrópodos asociados a *M. robusta*.

(3) Conocer la importancia de las especies de artrópodos especializadas en *M. robusta* en cuanto a su papel en la estructura trófica o el flujo de materia y energía en el sistema.

(4) Describir la dinámica trófica de la depredación intragremio de los arácnidos asociados a esta planta y determinar los factores que modifican su nivel de omnivoría.

Se concluye que la sombra contribuyó a explicar la variación de la riqueza de especies de artrópodos asociados a *M. robusta*, mientras que la fenofase de la planta hospedera y su lejanía con plantas conespecíficas no afectó sobre la estructura de la comunidad de artrópodos (riqueza específica, abundancia, índice de diversidad y biomasa).

Se encontraron seis morfoespecies de artrópodos [una de araña (Thomisidae y *Novalene* sp.), una de chinche (*Phlegyas* sp.), una de cochinilla (Armadillidiidae), una de cucaracha (*Blatta* sp.) y una de pseudoescorpión (*Dinocheirus tenoch*)] con una alta especialización en el uso de *M. robusta* como su planta hospedera, las cuales representan sólo el 4.3% de los taxa de artrópodos asociados a este pasto. Lo cual señala un alto recambio de especies de artrópodos en *M. robusta* a lo largo del día.

No se registró una relación entre el tamaño de *M. robusta* (peso seco) y la longitud máxima de la cadena trófica, lo cual puede deberse a la gran dinámica que presentan las diferentes poblaciones de artrópodos asociados a esta planta.

Con base en todos los resultados se puede concluir el tamaño de la planta es determinante en la estructura de la comunidad de artrópodos asociados a *M. robusta* y que se requieren más estudios para determinar su efecto sobre la estructura trófica.

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