Edge effect on the population structure and the reproductive success of two *Bursera* species

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Abstract

Background. Environmental conditions in edges of vegetation fragments affect life cycle characteristics of the native biota (edge effect). We evaluated the edge effect on two *Bursera* species, which are representative of the mature community of the tropical deciduous forest (TDF) in Mexico.
Hypothesis. We expected a population structure reflecting the affectation to reproduction, survival and growth in the edges of TDF fragments.
Studied species. *Bursera fagaroides*, *B. palmeri*.
Study site and years of study. Querétaro (Qro.), Apaseo el Grande (Gto.), México. Field survey: May-September 2012.
Methods. Within each of nine TDF fragments, we drew plots in two environmental contrasting conditions (edge and interior), between which we compared the density, population structure and reproductive success of the two *Bursera* species, as well as estimators of the solar radiation and soil compaction.
Results. Solar radiation and soil compaction were not different between environmental conditions. In both species density of individuals was larger in the edge, where individuals with middle and large sizes were predominant. Reproductive potential of individuals, and the viability and germination of their seeds were similar between edge and core environments.
Conclusions. Density and population structure showed a congruent variation with higher rates of recruitment, growth and survival in the edge environment, which could have been present under initial conditions of greater incidence of radiation in the edges. The similarity currently observed in the solar radiation between edge and core areas of fragments, could be a result of the fast recovery of the canopy under conditions of higher light incidence in edges.
Key words: *Bursera fagaroides*, *Bursera palmeri*, dioecious species, germination, tropical deciduous forest.

Efecto de borde sobre la estructura poblacional y el éxito reproductivo de dos especies de *Bursera*.

Resumen

Antecedentes. Las condiciones ambientales en los bordes de los fragmentos de vegetación afectan las características del ciclo de vida de la biota nativa (efecto de borde). Evaluamos el efecto de borde en dos especies de *Bursera*, las cuales son representativas de la comunidad madura del bosque tropical caducifolio (BTC) en México.
Hipótesis. Esperábamos una estructura poblacional que reflejara la afectación de la reproducción supervivencia y crecimiento en los bordes de los fragmentos de BTC.
Especies en estudio. *Bursera fagaroides*, *B. palmeri*.
Sitio de estudio y fechas. Querétaro (Qro.), Apaseo el Grande (Gto.), México. Trabajo de campo: mayo-septiembre 2012.
Métodos. Dentro de cada uno de los nueve fragmentos de BTC, trazamos parcelas en dos condiciones ambientales contrastantes (de borde e interior), entre las que se comparó la densidad, estructura de la población y el éxito reproductivo de las dos especies de Bursera, así como estimadores de la radiación solar y la compactación del suelo.
Resultados. La radiación solar y la compactación del suelo no fueron diferentes entre las condiciones ambientales. En ambas especies la densidad de individuos fue mayor en el borde, donde los individuos con tamaños medianos y grandes fueron predominantes. El potencial reproductivo de los individuos, así como la viabilidad y la germinación de sus semillas, fueron similares entre los ambientes de borde e interior.
Conclusiones. La densidad y la estructura poblacional mostraron una variación congruente con mayores tasas de reclutamiento, crecimiento y supervivencia en el ambiente de borde, las cuales podrían haberse presentado en las condiciones iniciales de mayor incidencia de la radiación en los bordes. La similitud que se observa actualmente en la radiación solar entre el borde y el interior de los fragmentos, pudo ser el resultado de la recuperación rápida del dosel bajo condiciones de una incidencia de la luz más alta en los bordes.
Palabras clave: bosque tropical caducifolio, *Bursera fagaroides*, *Bursera palmeri*, especies dioicas, germinación.

Anthropogenic alterations of natural ecosystems creates fragmented landscapes with isolated remnants of natural vegetation separated by a matrix of contrasting environmental conditions (Saunders *et al*. 1991), where the edges of fragments are transition zones with biotic and abiotic conditions differing from those of the original ecosystem (Murcia 1995, Suzán *et al*. 1999, Broadbent *et al*. 2008). Environmental conditions in edges of fragments often affect several parameters of the life cycle in the native biota, which is a phenomenon commonly known as "border or edge effects" (Saunders *et al*. 1991, Murcia 1995, Honnay *et al*. 2005).

Changes in the environmental conditions in the edges of vegetation fragments are associated to factors such as the increase in the incidence of solar radiation, higher temperatures and dryness modifying the composition of the soil microbiota and the nutrients cycles, as well as increasing environmental stress conditions for the macroorganisms (Didham *et al*. 1996, Gehlhausen *et al*. 2000). Modifications in the edge environmental conditions will depend on the resulting surrounding matrix (*i.e*. grasslands, agricultural fields, urban settlements) (Jules & Shahani 2003). Additionally, colonization of vegetation fragments by exogenous species and the restrictive factors associated to the degree of fragmentation (*i.e*. distances among vegetation patches) creates adverse conditions for the persistence of mature community species (Turner 1996, Laurance *et al*. 1998, Benitez-Malvido 1998, Honnay *et al*. 1999, Zhu *et al*. 2004).

The reduction in the regeneration ability of species from mature communities is an important effect of habitat fragmentation (Benitez-Malvido 1998). For example, in a dominant palm species in Mexican tropical rain forests (*Astrocaryum mexicanum*), reduction in fragment sizes increased the competition among pollinators and non-pollinators floral visitors, because pollinator density is positively correlated to fragment size (Aguirre *et al*. 2011). Other examples such as *Samanea saman*, a common species in the tropical dry forests of Costa Rica, decreases in the germination percentages and seedling vigor, results from isolation among conspecific individuals increasing geitonogamic crosses and incompatible pollen deposition (Cascante *et al*. 2002). In Chilean and Argentinean forest, habitat fragmentation affects the survival of seedlings and decreases the fruit size of the common creeper *Lapageria rosea* (Henríquez 2004).

Alterations caused by the vegetation fragmentation on the life cycles of mature communities species, can be evaluated comparing the age or size structure of populations, in areas with different disturbance levels such as cores and edges of the vegetation gaps fragments, since the structure of ages and/or sizes reflects predominant patterns of growth, reproduction and survival (Silvertown 1987, Silvertown & Lovett-Doust 1993). Frequently, species from mature vegetation exhibit a decrease in the recruitment rates, and an increase in the mortality in the border of fragments (Benitez-Malvido 1998). In contrast, the recruitment of species from early successional stages, often increases in the fragment borders (Laurance *et al*. 1998).

The Tropical Deciduous Forest (TDF) is one of the must threatened ecosystems in the world, as consequence of the deforestation associated to extensive grazing, agriculture expansion and wood extraction (Janzen 1988, Maass *et al*. 2002). In Mexico, around 60 % of the tropical communities correspond to TDF (Trejo 1996, Trejo & Dirzo 2000), which is an ecosystem characterized by high biological diversity and an important number of endemic species (Ceballos & García 1995, Lott & Atkinson 2002, Rzedowski 2006). Nevertheless, the areas with TDF in the country face serious conservation problems, remaining only 26 % of its original distribution in México for 2002 (Challenger *et al*. 2009, Koleff *et al*. 2012), and only a 10 % of their surface remains in conservation zones (Sánchez-Azofeifa *et al*. 2005, Koleff *et al*. 2012). Therefore, the implementation of suitable practices of handling and conservation of areas with TDC becomes fundamental. Additionally, it is important to consider that several species of trees that characterize tropical communities are particularly vulnerable to the effects of the fragmentation (Cascante *et al*. 2002), because many species have low densities, are pollinated by animals, and they have out-crossing pollination and complex self-incompatibility systems (Bawa 1974, Zapata & Arroyo 1978, Hamrick & Murawsky 1990).

In this study we evaluated the population structure and the reproductive success of *Bursera fagaroides* (Kunth) Engl. and *B. palmeri* S. Watson in the borders and core areas of TDC fragments in Querétaro, México. *Bursera fagaroides* and *B. palmeri* are two important species in mature vegetation of TDF in central México. Both species are particularly vulnerable to fragmentation because are dioecious (Rzedowski & Guevara-Féfer, 1992; Rzedowski *et al*.,

2005), and in consequence, its reproductive success may be related to changes of density by the fragmentation and the consequent alteration of environmental conditions in the edges of TDF fragments.

Material and methods

Study area. Study area encompasses nine fragments of TDF distributed in a polygon with co-ordinates: (20° 26' N and 20° 47' N, 100° 26' W and 100° 37' W; Figure 1), located in the municipalities of Querétaro, Qro., and Apaseo el Grande, Guanajuato, México. Climates in the study area are semidry semiwarm and semidry temperate, and dominant soils are vertisol and phaeozem (INEGI, 2010). Dominant vegetation type is TDF surrounded by xeric shrub-lands (Zamudio *et al.* 1992). Average altitudes of fragments varied between 1,847 and 2,002 m a.s.l.

Species studied. *Bursera fagaroides* is a dioecious small tree or shrub occasionally hermaphrodite that reach 10 m in height and a trunk wit 30 cm in diameter. It has an exfoliation external crust of yellowish color and produces an off-white latex (Rzedowski & Guevara-Féfer 1992). It's distributed between southeast USA to Oaxaca, in Mexico), and is considered an important element of the TDF, secondary vegetation from TDF and xerophytic shrub-lands, with a recent severe abundant reduction in the TDF (Rzedowski *et al.* 2004). The phenophase starts in April and May, with fructification between November and December and foliage present from June to November (Rzedowski & Guevara-Féfer 1992).

Bursera palmeri is a dioecious small tree or shrub that reach 8 m in height, which produce an aromatic resin, with a trunk reaching up to 30 cm in diameter with a green to reddish-green exfoliating cortex (Rzedowski & Guevara-Féfer 1992). In Mexico it's distributed in TDF from the following states: Aguascalientes, Durango, Guanajuato, Jalisco, Michoacán, Querétaro and Zacatecas. This species inhabit at altitudes higher than 1,400 m a.s.l., and its abundance shows a significant decrease due to extraction for fuel (Rzedowski *et al.* 2005). The flowering period range between May and June, and the species preserve the foliage between May and November (Rzedowski & Guevara-Féfer 1992).

Fragments selected for the study. In order to evaluate de edge effect in fragmented vegetation we selected nine TDF fragments using orthophotos scale 1:10,000 (INEGI 2008), and field sur-

Figure 1. I) Location of tropical deciduous forest (TDF) fragments in the study zone (numbered from the 1 to the 9); II) scheme of one of the fragments showing the edge and interior zones and the disposition of the Whittaker plots; III) scheme of the structure of the modified Whittaker plots.
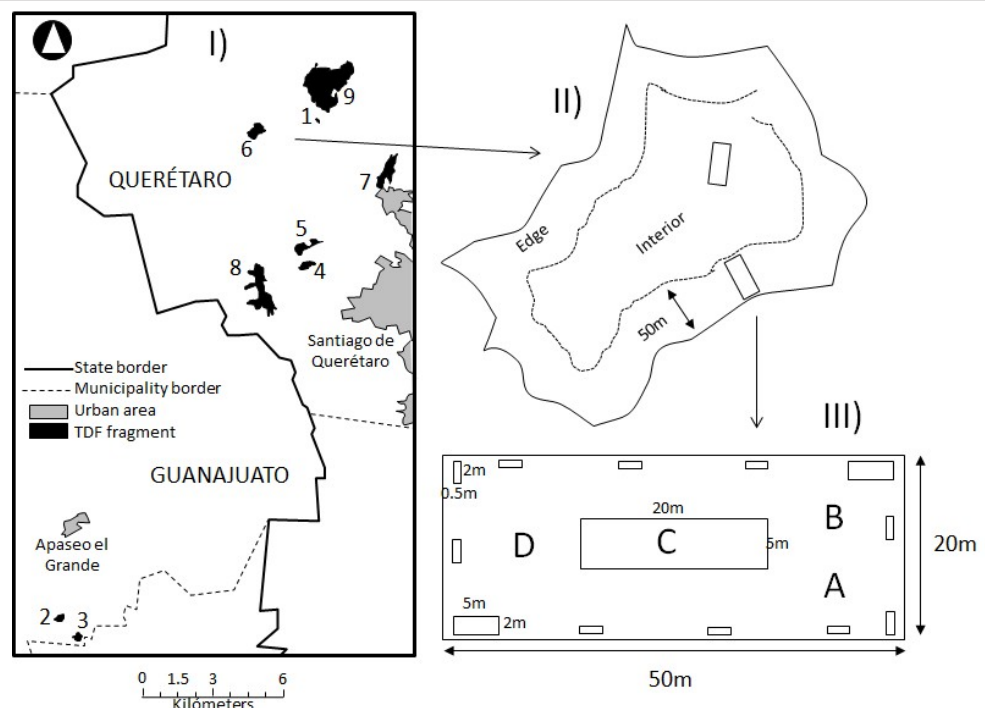
vey between May and September 2012. The fragments were selected considering the presence of the two *Bursera* species and a qualitative conservation status that considered the presence of edges clearly distinguishable of the surrounded matrix, appreciable abundance of primary tree species with DBH ≥ 15 cm (*e.g. Cedrela dugesii, Ceiba aesculifolia, Erythrina coralloides, Eysenhardtia polystachia* and *Ipomoea murucoides, Lysiloma microphylla, Senna polyantha*), and an average canopy height of 8 m. Each fragment was mapped, and the plots for environmental contrasting conditions (edge and interior of the fragment) were randomly selected by using a network of cells (50 × 20 m) with the program ArcMAp v. 10.1, and defining their central geographic coordinates to locate Whittaker modified plots of 25 × 50 m (Stohlgren *et al.* 1995) in the field. When selected coordinates of two or more plots were too close, within the same condition (interior or edge) in a fragment, we maintained a minimum distance of 200 m between centers of plots. The total area and surrounding matrix for each fragment was calculated with the software ESRI® ArcMapTM 10.0. The surrounding matrix considered a buffer outside area of 500 m wide according to Charbonneau and Fahrig (2004) and Houlahan *et al.* (2006).

For each condition (edge and interior of the fragments) we measured respectively 16 and 41 Whitakker plots. The number of plots per fragment differs according to the fragment size (Table 1). The plots in the edges were located in a buffer zone (0-50 m) from the edge to inside of fragments, while plots in the interior were located close to the center of each fragment (Figure 1), excluding the possible border effects (Williams-Linera 1990a, Chen *et al.* 1992).

Environmental conditions in the edges and interior of the fragments. Plant area index (PAI) and soil compaction were obtained for each Whitakker plot in the fragments. PAI was selected as an estimator of the canopy cover and solar radiation within the plots, and soil compaction as an indirect estimator of the effect of anthropogenic activities in the area.

Plant Area Index (PAI) of the fragments.- A couple of Licor LAI 2000 (PCA, LI-COR®, Lincoln, NE, USA) instruments were used to calculate the PAI of the plots according to Asner *et al.* (2003) and de Wasseige *et al.* (2003), including leafs and branches for each measurement. All the measurements were conducted between 5.00 and 7.00 h with clear skies, in the rain season (October-November) 2012. One instrument sensor installed at 1 m height, beneath the vegetation canopy with a 90° cap, and the second instrument in an open area measuring automatically every 30 seconds as an outside-canopy control. In the fragment, three PAI measurements were conducted with a systematic sampling across the central longitudinal axis of each Whittaker plot, and with 10 m in distance between measurements. Each PAI measurement consists on the average of three beneath canopy measurements, and one outside measurement from the control sensor. A Wilcoxon T test was used to compare plots in edges and interior of TDF fragments (Sokal & Rohlf 1995).

Soil compaction.- Soil compaction was estimated by means of its apparent density and texture (Siebe *et al.* 1996), and classified according to texture ranges suggested by the Mexican system of integrated differential diagnosis of soils (Soto *et al.* 2003, Córdoba-Athanasiadis 2010). A total of 342 samples, 246 from the edges and 96 from the fragment interiors plots, were obtained with metal cylinder cores (124.35 cm^3). In each Whittaker plot six equidistant samples were collected. In order to measure apparent density, the soil samples were weighted in fresh and after being dried in an oven (105 °C, 24 h), and the cylinder and aluminum foil weights were subtracting from the total weight of each sample. Soils densities for each condition (edge and interior of fragments) were compared with a Wilcoxon T test (Sokal & Rohlf 1995).

Population structure. The population structure of *Bursera fagaroides* and *B. palmeri* in the edge and interior of fragments was estimated within Whittaker modified plots (Stohlgren *et al.* 1995), which include a nested design with four sub-plot levels (A, B, C and D). In the subplots A (0.5 × 2 m), we register frequencies of individuals with height ≤ 50 cm (juvenile type 1); for the subplots B (2 × 5 m) we register individuals with height > 50 cm, and diameter at breast height (DBH) between 1 and 5 cm (juvenile type 2); in the subplots C (5 × 20 m) individuals between 5 and 10 cm in DBH (juvenile 2), and in subplots D (20 × 50 m) individuals > 10 cm in DBH (adults) Seedling recruitment was not estimated because the majority of seedling die in few weeks.

Comparisons of densities of individuals between the edge and interior of the fragments were

analyzed by a bi-factorial analysis of variance (ANOVA) with a randomized block design, with condition (edge and interior) and size categories (juveniles type 1 and 2 and adults) as factors and fragments as blocks. Density data were square root transformed (Sokal & Rohlf 1995). Within each fragment, population structures in edge and interior were compared by a G hetero-geneity test (Sokal & Rohlf 1995).

Additionally, in order to explore the contribution of surrounding matrix in the population structure of *Bursera* species, we conducted a Spearman correlation analysis with values for fragments of the proportion of surrounding matrix corresponding to the area covered by princi-pal components of matrix (*i.e.* roads, paddocks, rainfed agriculture, rural settlements and areas with secondary vegetation), and values of density and proportion of individuals of two *Bursera* species in the three categories (juvenile 1, juvenile 2 and adults).

Reproductive individual size and reproductive potential in the fragments. Sex, height and two perpendicular canopy diameters of reproductive trees in the "D" subplots within each plot were recorded. The volume of reproductive individuals was calculated as a unique estimator of indi-vidual size with the inverted truncated cone formula:

$$V = 3^{-1}\pi h(R^2 + r^2 + R \times r) \tag{1}$$

Where h is the cone height, R is the mean radius of the circumference corresponding to the canopy and r is the radius of the circumference corresponding to the DBH.

The volume of reproductive individuals was compared between the edge and interior of the fragments with a Student "t" test, with volume data previously log-transformed (Sokal & Rohlf 1995).

Reproductive potential (*PR*) in the edge and interior of each fragment was estimated as:

$$PR = (d\,♀ + d\,♂)d_{Ad}\,n_s\,2^{-1} \tag{2}$$

Where $d♀$ and $d♂$ represent densities for female and male reproductive individuals in 1,000 m²; d_{Ad} adult densities/1,000m²; and ns the number of sexes in the Plot (equal to two if both sexes are present in the plot). *PR* values ranges between cero (no reproductive individuals) and one (all adult individuals reproductive, and both sexes in the plot). *PR* values were compared with a Wilcoxon T test (Sokal & Rohlf 1995).

For each species we compared adult densities between edge and interior of fragments, and between sexes with a bifactorial ANOVA in a randomized block design (fragments as blocks). Density data were transformed by the square root function (Sokal & Rohlf 1995).

Seeds viability and germinative ability. Seeds were collected between April and May 2013 for *Bursera fagaroides*, and between January and February 2013 for *Bursera palmeri*. In each fragment, for each species and each condition, seeds from at least five adult trees with similar DBH (15 cm < DBH < 20 cm) were collected. Percentages of viable seeds for each species and condition were calculated by a flotation test from a random sample of 100 seeds. Additionally, in *B. fagaroides* viability was also estimated with a tetrazolium chloride (TC) test, from seeds selected after the flotation test. In each condition for each fragment 30 seeds were selected and then scarified and exposed to a 0.2 % solution of TC for 24 h (Henríquez 2004). TC evaluation was not conducted in *B. palmeri* because the insufficient amount of seeds. The proportion of viable seeds in each condition was compared with a paired t test with proportions transformed with the arc-sine function (Sokal & Rohlf 1995).

Mature seeds of *B. fagaroides* selected after a flotation test were used to compare germination percentages between the edge and interior of fragments (100 seeds each) in laboratory condi-tions. Seeds were disinfected with sodium hypochlorite (30 %, 5 min) and then washed in dis-tilled water for 5 min (Godínez-Álvarez *et al*. 2008). Seeds were revised daily and germination was considered after root emergence. Seed germination percentages between conditions were compared with a pair *t* test after the transformation of data with the arc-sine function (Sokal & Rohlf 1995).

All the statistical analysis was conducted with JMP 8.0 software.

Results

Fragment description. The arboreal stratum in most of the fragments was dominated by species such as *Bursera fagaroides*, *Ipomoea murucoides*, *Lysiloma microphyllum*, *Myrtillocactus geometrizans* y *Senna polyantha*, other common species were, *Bursera palmeri*, *Ceiba aesculifolia*, *Celtis caudata*, *Erythrina coralloides*, *Prosopis laevigata*. Evidence of wood extraction for the arboreal species was very scarce or null in some fragments. The shrub stratum was highly disturbed by cattle and goat grazing, and the dominant species were *Acacia farnesiana*, *Celtis pallida*, *Forestiera phillyreoides* and *Karwinskia humboldtiana*. The more abundant surrounding matrices were rainfed agriculture (28.8 %) and paddocks (27.2 %), while roads and rural areas were the least commons.

The Plant Area index (PAI) values for the fragment edges range between 0.86 and 2.36 m²/m² with a mean and standard error (SE) = 1.78 ± 0.17 m²/m², while in the interior range between 1.32 and 2.83 m²/m², with mean and SE = 2.02 ± 0.19 m²/m² (Table 1), but no significant differences were detected for PAI values between the edge and interior of the fragments ($W = 12.0$, d.f. = 7, $P = 0.10$).

Apparent densities of soil according to the texture ranks suggested by the integrated differential diagnosis had small values, indicating non-compaction in the fragments studied (Table 1). Average and SE soil densities for all edge fragments were 0.64 ± 0.05 g/cm3, and for the interiors 0.71 ± 0.04 g/cm3. No significant differences between the edge and interior of fragments were detected ($W = 8.5$, d.f. = 7, $P = 0.27$).

Population structure. Population structure of *Bursera fagaroides* and *B. palmeri* showed higher densities of individuals for all size classes in the edge of fragments ($F = 43.92$, d.f. = 1, $P < 0.0001$ and $F = 31.39$, d.f. = 1, $P < 0.0001$, respectively). In *B. fagaroides* differences in densities among size classes were not significant ($P = 0.92$), and the interaction between condition (edge, interior) and size classes was also no significant ($P > 0.53$). In contrast, for *B. palmeri* densities of juvenile 1 size class was smaller compared to other size classes ($F = 10.11$, d.f. = 2,

Table 1. Characteristics of the Tropical Deciduous Forest fragments. Numbers within the parentheses in the column 2 indicate the number of Wittaker plots in each condition. Values in columns 4 and 6 represent the average and the standard error of the plant area index (PAI) and the apparent density. Abbreviations in column five mean textures: clay-loam (CL), coarse-silty-clay (CoSC), fine-clay-loam (FCL), sandy-clay (SC), sandy-clay-loam (SaCL) and silty-clay-loam (SCL).

| Fragment	Area (has)	Condition	PAI (m² / m²)	Texture	Apparent density (g/cm³)	Soil Compaction
1	7.68	Edge (1)	2.2 ± 0.19	SaCL	0.52 ± 0.16	Very low
		Interior (2)	2.83 ± 0.12	CL	0.5 ± 0.16	Very low
2	7.72	Edge (2)	1.75 ± 0.14	SCL	0.61 ± 0.12	Very low
		Interior (1)	2 ± 0.14	SCL	0.6 ± 0.14	Very low
3	9.39	Edge (1)	1.75 ± 0.22	SCL	0.61 ± 0.14	Very low
		Interior (1)	1.73 ± 0.3	SCL	0.93 ± 0.2	Very low
4	11.43	Edge (1)	0.86 ± 0.44	SCL, FCL	0.55 ± 0.09	Very low
		Interior (4)	1.32 ± 0.15	CL	0.62 ± 0.16	Very low
5	26.57	Edge (1)	ND	FCL	0.69 ± 0.09	Very low
		Interior (2)	ND	FCL	0.72 ± 0.19	Very low
6	26.93	Edge (1)	2.36 ± 0.17	FCL	0.89 ± 0.1	Very low
		Interior (3)	2.82 ± 0.31	FCL	0.82 ± 0.04	Very low
7	44.19	Edge (1)	2.1 ± 0.13	CL, SC	0.16 ± 0.61	Very low
		Interior (5)	1.73 ± 0.26	SCL	0.43 ± 0.05	Very low
8	104.08	Edge (2)	1.5 ± 0.11	SCL, SC, CoSC, FCL, CL	0.79 ± 0.04	Very low
		Interior (12)	1.82 ± 0.14	SaCL, SCL	0.69 ± 0.09	Very low
9	249.59	Edge (6)	1.75 ± 0.15	SC, SaCL, CL, SCL	0.36 ± 0.33	Very low
		Interior (11)	1.89 ± 0.14	SaCL, SCL, CL	0.66 ± 0.06	Very low
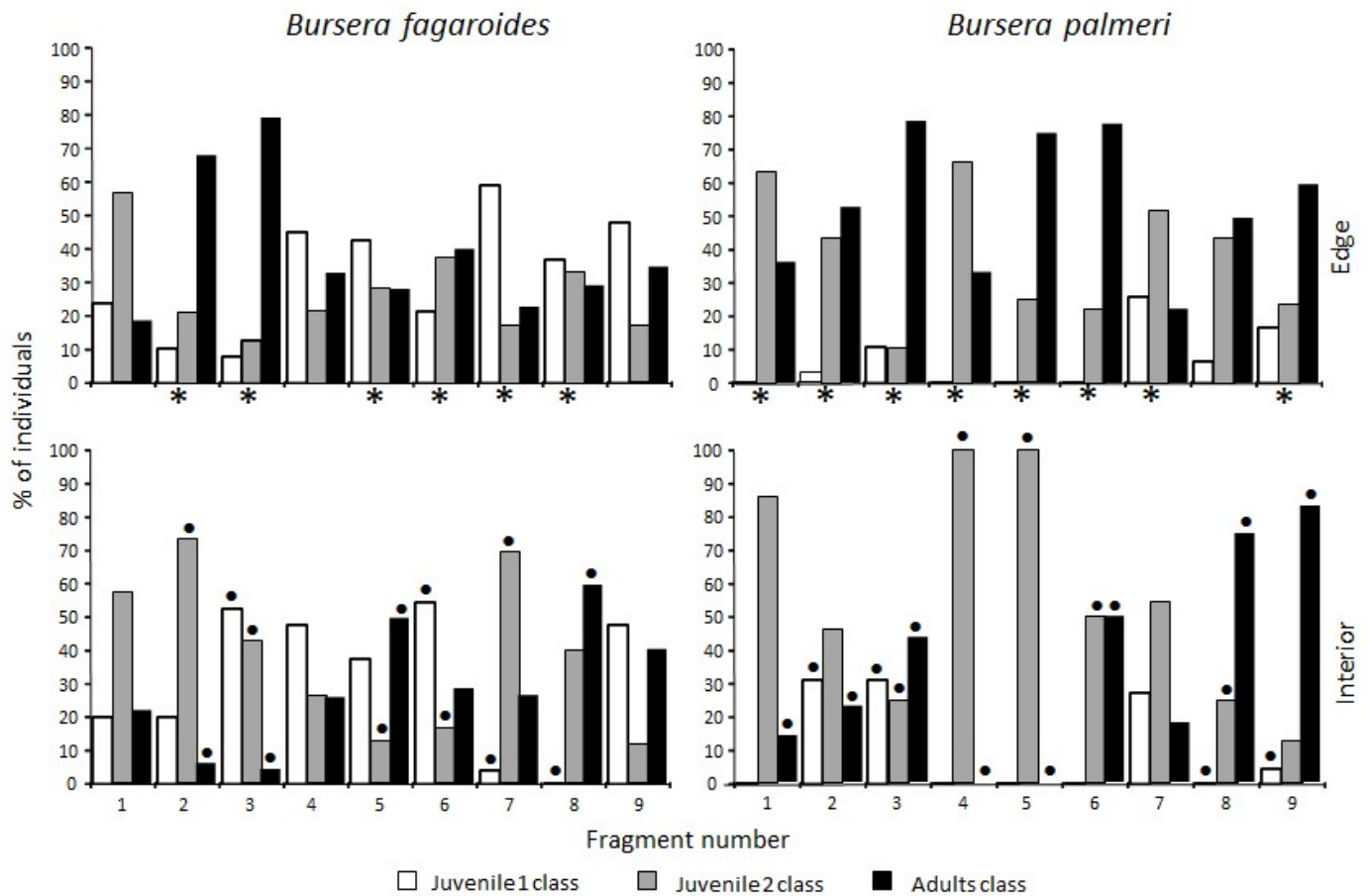
Figure 2. Population structure of *Bursera fagaroides* and *B. palmeri* in the edge and the interior of tropical deciduous forest fragments (1 to 9). The fragments in which the population structure was significantly different between the edge and the interior are indicated with an asterisk (*). The categories (juvenile 1, juvenile 2 and adults) that differ significantly between edge and interior in each one of fragments is indicated with a full circle (●).

$P = 0.0003$), and the interaction between condition and size classes was significant ($F = 5.12$, d.f.= 2, $P = 0.0105$), due to the similarities on juvenile 1 for both conditions (Table 2). On the other hand, *B. fagariodes* had higher densities than *B. palmeri* ($F = 18.83$, d.f. = 1, $P = 0.0002$). However, even that total densities of *B. fagaroides* individuals were higher in the edges ($F = 38.8$, d.f. = 1, $P < 0.0001$), densities of this species in the interior were intermediate between densities of *B. palmeri* in the edges and interior of the fragments, leading to a significant interaction between the factors species and condition ($F = 7.63$, d.f. = 1, $P = 0.0108$).

Table 2. Densities (individuals/1,000 m²) of *Bursera fagaroides* and *B. palmeri* in the edge and interior of tropical deciduous forest fragments in Queretaro, Mexico. Data are the average ± standard errors for fragments.

	Bursera fagaroides		*Bursera palmeri*	
Class	**Edge**	**Interior**	**Edge**	**Interior**
Juvenile 1	33.1 (± 12.8)	4.0 (± 1.3)	1.9 (± 0.8)	1.1 (± 0.7)
Juvenile 2	28.2 (± 9.2)	4.5 (± 1.5)	8.7 (± 2.8)	1.9 (± 0.7)
Adults	40.2 (± 12.7)	2.3 (± 0.6)	11.6 (± 3.2)	1.9 (± 0.9)
TOTAL	101.5 (± 24.7)	10.9 (± 2.6)	22.1 (± 5.9)	4.9 (± 1.9)
	REPRODUCTIVE			
Adults ♀	2.8 (± 0.6)	0.9 (± 0.3)	0.8 (± 0.3)	0.3 (± 0.3)
Adults ♂	4.7 (± 1.1)	1.3 (± 0.3)	0.9 (± 0.3)	1.0 (± 0.5)

For both species, population structure was different between the edges and interior for most of the fragments ($12.74 \le G \le 152.13$, d.f. = 2, $P < 0.05$) (Figure 2). In the interior of the fragments, the higher proportion of individuals was concentrated in juvenile 1 and juvenile 2 classes, while in the edges the biggest proportion on individuals were concentrated on juvenile 2 and/or adult classes (Figure 2, Table 1). The comparisons of population structure between the edge and interior of different fragments in both species, suggest that juvenile trees grow slowly in the interior of fragments, leading to a concentration of individuals on juvenile 1 and juvenile 2 classes, while in the edge of fragments, juvenile trees seem grow faster, changing toward upper size classes in smaller times, and leading to a concentration in juvenile 2 and adult categories.

Regarding the relationship between characteristics of surrounding matrix of fragments and the population structure, no significant associations were detected between the area covered by predominant components of the surrounding matrix, and the density and proportion of individuals of both *Bursera species* ($P > 0.05$).

Reproductive individual size and reproductive potential in the fragments. The size of the reproductive trees (average volume ± SE) for both species tend to be higher in the interior than the edges of fragments, for *Bursera fagaroides* 35.0 ± 2.8 m^3 vs 29.8 ± 1.9 m^3 respectively, and for *B. palmeri* 36.0 ± 3.1 m^3 *vs* 27.7 ± 2.6 m^3 respectively. However, differences among conditions were non-significant: *B. fagaroides*: $t = 1.67$, d.f. = 203, $P = 0.10$; and *B. palmeri*: $t = 1.45$, d.f. = 104, $P = 0.14$. The reproductive potential of *B. fagaroides* was higher in the interior of the fragments than in the edges ($W = 20.5$, d.f. = 1, $P = 0.012$; Table 3), and for *B. palmeri* a similar but no significant trend was detected ($W = 14.0$, d.f. = 1, $P = 0.10$; Table 3).

Density of reproductive individuals were higher in the edge than in the interior of fragments for *Bursera fagaroides* ($F = 20.15$, d.f. = 1, $P = 0.0002$), but not for *B. palmeri* ($F = 1.29$, d.f. = 1, $P = 0.27$). In two species density of male individuals tends to be higher than females, both in edge and interior of fragments (Table 2), but differences between sexes were not significant (*B. fagaroides*: $F = 3.16$, d.f. = 1, $P = 0.09$; and *B. palmeri*: $F = 3.07$, d.f. = 1, $P = 0.09$), like the

Table 3. Reproductive potential (*RP*), viability (*Vb*) and germination (*Gm*) in the edges and interior of Tropical Deciduous Forests in Queretaro, Mex. Viability estimated by flotation technique (*Vb*) and with tetrazolium chloride (*Vb*$_{CT}$).

Fragment	Condition	*Busera fagaroides*			*Bursera palmeri*	
		PR	*Vb / Vb*$_{CT}$ (%)	*Gm* (%)	*PR*	*Vb* (%)
1	Edge	0.41	52 / 37	82	0.00	43
	Interior	0.89	28 / 78	76	1.00	25
2	Edge	0.09	26 / 66	89	0.04	39
	Interior	1.00	18 / 53	87	0.33	18
3	Edge	0.09	32 / 56	88	0.05	38
	Interior	0.50	56 / 72	85	0.57	41
4	Edge	0.14	73 / ND	77	0.50	74
	Interior	0.50	57 / ND	70	0.00	43
5	Edge	0.25	69 / ND	98	0.25	65
	Interior	0.50	27 / ND	93	0.00	33
6	Edge	1.00	54 / 44	89	0.21	62
	Interior	0.88	59 / 78	80	0.00	63
7	Edge	0.12	35 / 36	79	0.00	42
	Interior	0.57	20 / 51	75	0.50	44
8	Edge	0.14	67 / 49	87	0.19	60
	Interior	0.17	55 / 64	84	0.89	57
9	Edge	0.52	43 / 38	93	0.56	60
	Interior	1.00	60 / 49	93	0.90	57
Mean (EE)	Edge	0.31 (0.10)	50.11 / 46.54 (5.74) / (4.23)	86.89 (2.22)	0.20 (0.07)	53.67 (4.41)
	Interior	0.67 (0.10)	42.22 / 63.69 (6.11) / (4.82)	82.56 (2.66)	0.47 (0.14)	42.33 (5.06)

interaction between conditions and sex factors (*B. fagaroides*: $F = 0.43$, d.f. = 1, $P = 0.52$; and *B. palmeri*: $F = 1.20$, d.f. = 1, $P = 0.29$).

Seeds viability and germinative ability. Seed viability estimated by flotation in *Bursera faga-roides* not showed differences among the edge and interior of fragments ($t = 1.22$, d.f. = 8, $P = 0.26$; Table 3), while in *B. palmeri* viability was higher in the edge ($t = 2.40$, d.f. = 8, $P = 0.04$; Table 3). In contrast, viability estimated with tetrazolium chloride for *B. fagaroides* was significantly higher for seeds collected in the interior of fragments ($t = 2.58$, d.f. = 6, $P = 0.04$; Table 3). Finally, germination percentages in *B. palmeri* were consistently higher in the edge than interior of fragments (Table 3), leading to significant differences between conditions ($t = 4.49$, d.f. = 8, $P = 0.002$).

Discussion

In this study we expected that the population structure and the reproductive success of *Bursera fagaroides* and *B. palmeri*, could reflect changes associated to the modification of the environmental conditions in the edges of fragments of the Tropical Deciduous forest (TDF), since both species are dioecious, have low densities and they are used frequently for fuel (Rzedowski *et al.* 2005), leading to variations in density and size structure between the edge and the interior of fragments, as a result of smaller rates of survival, growth and reproduction in the edges.

In contrast to our expectations, *Bursera. fagaroides* and *B. palmeri* seems to be favored by the environmental conditions that predominate in the edges of fragments, where the density of both species was greater. In this sense, probably the variation between edge and interior of fragments in the solar radiation that penetrates through canopy has influenced in the density. Similar results reported by Ortiz-Pulido and Rico-Gray (2006) from "El Morro de la Mancha" (Veracruz) in *B. fagaroides* shows that the presence of the species, their germination and growth, were favored by the TDF moderate shaded environment, contrasting with open exposed sites, or in heavy shaded environments within the Tropical semideciduous forests. However, our estimations of the PAI in the edge and inside fragments had similar values, suggesting two possibilities: 1) that the solar incidence of radiation is not an important factor in the variation of the density of individuals, or 2) that the differences in the incidence of the solar radiation between both conditions are currently minimum because the rapid recovery of the canopy. With respect to our estimation of the PAI, it is important to mention that the real value of LAI can be overestimated due to the contribution of trunks and branches of the canopy. Nevertheless, this bias for our instruments could be considered as non-significant (Cutini *et al.* 1998). On the other hand, is also important to consider that use of PAI to estimate the differences in the solar radiation that penetrates the canopy between edge and the interior of fragments, could be a coarse method to detect a subtle variation in the quantity and quality of light affecting growth of plants under the canopy, compared with other methods such as measuring of the photosynthetically active radiation (PAR). However, measures of LAI and PAR generally show a high correlation (*e.g.*, Buckley *et al.* 1999, Bellow & Nair 2003, Hyer & Goetz 2004), so we considered that PAI estimations derived from LAI measures have the sufficient resolution to detect differences in radiation passing through the canopy.

In addition to the potential effect of differences in the solar radiation between edge and interior of fragments on species densities, other factors must be considered. For example, a lower density of individuals in the interior of fragments may be the result of higher rates of seed predation than in edges, whether seed predators concentrate their activity away of edges to avoid their own predation (*e.g.*, Guzmán-Guzman & Williams-Linera 2006, Penido *et al.* 2015). On the other hand, higher density of plants in the edge, in contrast with the interior of fragments, may be the result of higher rates of removal and deposition of fruits that are more conspicuous for frugivore birds in the edges (Galetti *et al.* 2003). However, this seems unlikely for *Bursera fagaroides*, because germination rate of its seeds are reduced when pass through the digestive tract of birds (Ortiz-Pulido & Rico-Gray 2006).

Soil compaction is a non- relevant factor for understanding differences in densities and population structure in the edges and interior of the fragments. Soil compaction values were simi-

lar for both conditions and exhibited very low values according to the integrated differential diagnosis system for mexican soils (Soto *et al.* 2003, Córdoba-Athanasiadis 2010). Even that paddocks were a common surrounding matrix in the regions, and cattle was frequently observed for small periods of time, this activity seems not to affect significantly the soil compaction. It is important to consider that we used an indirect estimator of soil compaction, which probably did not detected differences between edge and interior of fragments. Nevertheless, the measures of apparent density of soil are frequently used as reliable estimators of compaction (Carter 1990, Håkansson & Lipiec 2000, Blanco-Sepúlveda 2009). Even more, compaction generally has detrimental effects on the growth of plants (Kozlowski 1999), which apparently did not happening in the studied fragments as is suggested by high densities of both *Bursera* species in the edges.

Previously, we mentioned that the similarity in values of the PAI between the interior and the edge of fragments could be the result of a relatively fast recovery of the canopy under the initial conditions of greater incidence of radiation in the edges. A recovery of the relatively accelerated canopy can be possible if the incidence of greater solar radiation leads to an increase of the recruitment rates, survival and growth of some common arboreal species in the mature and/or secondary communities of the TDF, such as *Bursera fagaroides* and *B. palmeri* (Rzedowski & Guevara-Féfer 1992). Generally, the arboreal species that comprise the mature vegetal communities are affected by modifications from environmental conditions after ecosystem fragmentation, showing higher mortality rates and smaller recruitment in the edges (*e.g.*, Williams-Linera 1990b, Benitez-Malvido 1998, Nascimento & Laurance 2004). Nevertheless, has been documented that recruitment and growth of some species from mature communities increased in conditions of moderate disturbance such as in the edges fragments, becoming, dominant elements of the secondary communities (Chen *et al.* 1992, Oliveira-Filho *et al.* 1997, McDonald & Urban 2004, Laurance *et al.* 2006).

Differences in the population structure of *Bursera fagaroides* and *B. palmeri* between the edge and the interior of TDF fragments, is congruent with the idea that environmental conditions in the edges of fragments are or were favorable for increasing growth rates. Nevertheless, since the size or age structure of a population depends on the patterns of recruitment and survival (Silvertown 1987, Caswell 2001), a higher growth rate in the edges is not sufficient to explain the differences observed in the population structure of both species between edges and interior of the fragments. In this sense, one more reasonable explanation is than a higher individual growth rate in the edges has been accompanied with high recruitment and survival rates, as is suggested by the considerably high density of individuals of all size categories in the edges of fragments. Nevertheless, it is necessary to demonstrate by long term demographic studies that the recruitment, survival and growth rates of *B. fagaroides* and *B. palmeri* increased under conditions of greater light intensity. Additionally, it is necessary to evaluate the importance of other factors that contribute in the differences of density and variations of the population structure like the seeds and seedlings predation (Benitez-Malvido 1998, Cascante *et al.* 2002, Guzmán-Guzman & Williams-Linera 2006, Penido *et al.* 2015), changes in the density of common species in the mature community, which are less tolerant to the light, high temperatures and drying (Benitez-Malvido 1998, Laurance *et al.* 2006), and the modification of the abundance of generalist and specialist dispersers (Restrepo *et al.* 1999, Albrecht *et al.* 2013).

The increase in the recruitment rate of *Bursera fagaroides* and *B. palmeri* in the edge of fragments, indicates differences in juvenile densities between the edge and the interior of the fragments, and does not seem to be a consequence of the increasing densities of reproductive adult individuals, since in the edge of fragments the density of reproductive individuals was slightly higher than in the interior, which is reflected in the reproductive potential, showing smaller values for the edges compared to the interior of the fragments. Also, the similarity in the proportion of masculine and feminine reproductive individuals in the edge and inside fragments, as well as the similarity in the percentage of viability and germination, does not provide indications that these factors have important effects in the difference of density for juvenile individuals between both conditions. Even when germination percentages were significantly greater in the edges than in the interiors, the values obtained were high in both conditions (87 % and 83 %, respectively). A possible explanation for this small but significant difference could be a greater temperature fluctuation in the edge condition that increases the seeds germination, which has been

demonstrated for several species of *Bursera* under experimental conditions (Bonfil-Sánders *et al*. 2008).

Finally, it is important to consider that our evaluations for densities of reproductive individuals, sex rates and the viability and germination for both species, represent only one snapshot in the process that have determined the variation in the density and the population structure between the edge and interior of fragments. In this way, it is necessary to consider the temporary variation to improve our estimation of the edge effects on the reproduction of studied species. For example, although we could not currently detect a bias between sexes, which, by the way, may depend on several factors as differences between male and female plants in the age or size to the sexual maturity, or differences in the flowering frequency between plants of different sexes (Meagher 1980), to long term, bias in sexual rates between edge and interior of fragments may be expected, because in contrast with male plants, survival rates of female plants can be decreased in stressed environments as consequence of a less resources allocation to the survival and a high allocation to the reproduction (*e.g*., Agren 1988, Gehring & Linhart 1993, Yu & Lu 2011). Additionally, it is important to consider other factors that can influence juvenile densities in the edge and the interior of the fragments. For example, the high production of seeds in the edge of fragments as consequence of a greater environmental stress on the female individuals, which has been observed in *Bursera fagaroides* (Ortiz-Pulido & Pavón 2010); and the ability of seeds to remain viable in seeds banks, and to germinate massively under conditions of greater luminosity. With respect to this second point, the time that seeds can remain viable is an aspect still little explored in species of the genus *Bursera*. Nevertheless, the available information suggests that the period in which the seeds remain viable in natural conditions, can be relatively short (Bonfil-Sánders *et al*. 2008, Sánchez-Martínez *et al*. 2011, Morgan & Jose 2013).

Acknowledgments

Literatura Cited

Agren J. 1988. Sexual differences in biomass and nutrient allocation in the dioecious *Rubus chamaemorus*. *Ecology* **69**:962–973. DOI: 10.2307/1941251

Aguirre A, Guevara R, Dirzo R. 2011. Effects of forest fragmentation on assemblages of pollinators and floral visitors to male- and female-phase inflorescences of *Astrocaryum mexicanum* (Arecaceae) in a Mexican rain forest. *Journal of Tropical Ecology* **27**:25-33. DOI: 10.1017/S0266467410000556

Albrecht J, Berens DG, Blüthgen N, Jaroszewicz B, Selva N, Farwing N. 2013. Logging and forest edges reduce redundancy in plant-frugivore networks in an old-growth European forest. *Journal of Ecology* **101**:990-999. DOI: 10.1111/1365-2745.12105

Asner GP, Scurlock JMO, Hicke JA. 2003. Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. *Global Ecology and Biogeography* **12**:191–205. DOI: 10.1046/j.1466-822X.2003.00026.x

Bawa KS. 1974. Breeding systems of tree species of a lowland tropical community. *Evolution* **28**:85-92. DOI: 10.2307/2407241

Bellow JG, Nair PKR. 2003. Comparing common methods for assessing understory light availability in shaded-perennial agroforestry systems. *Agricultural and Forest Meteorology* **114**:197-211. DOI: 10.1016/S0168-1923(02)00173-9

Benitez-Malvido J. 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Conservation Biology* **12**:380-389. DOI: 10.1111/j.1523-1739.1998.96295.x

Blanco-Sepúlveda R. 2009. La relación entre la densidad aparente y la resistencia mecánica como indicadores de la compactación del suelo. *Agrociencia* **43**:231-239.

Bonfil-Sanders C, Cajero-Lázaro I, Evans RY. 2008. Germinación de semillas de seis especies de *Bursera* del centro de México. *Agrociencia* **42**:827-834.

Broadbent EN, Asner GP, Keller M, Knapp DE, Oliveira PJC, Silva JN. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biological Conservation* **141**:1745-1757. DOI: 10.1016/j.biocon.2008.04.024

Buckley DS, Isebrands JG, Sharik TL. 1999. Practical field methods of estimating canopy cover, PAR, and LAI in Michigan oak and pine stands. *Northern Journal of Applied Forestry* **16**:25-32

Carter MR. 1990. Relative measures of soil bulk density to characterize compaction in tillage studies on fine sandy loams. *Canadian Journal of Soil Sciences*: **70**: 425-433. DOI: 10.4141/cjss90-042

Cascante A, Quesada M, Lobo JJ, Fuchs EA. 2002. Effects of dry tropical forest fragmentation on the reproductive success and genetic structure of the tree *Samanea saman*. *Conservation Biology* **16**:137-147. DOI: 10.1046/j.1523-1739.2002.00317.x

Caswell H. 2001. *Matrix population models: construction, analysis and interpretation*. Massachussetts: Sinauer Associates Inc.

Ceballos G, García A. 1995. Conserving neotropical biodiversity: the role of dry forests in western Mexico. *Conservation Biology* **9**:1349-1356. DOI: 10.1046/j.1523-1739.1995.09061349.x

Challenger A, Dirzo R. 2009. Factores de cambio y estado de la biodiversidad. *In*: Dirzo R, González R, March IJ, comps. *Capital Natural de México, Volumen II: Estado de conservación y tendencias de cambio*. México DF: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.

Charbonneau NC, Fahrig L. 2004. Influence of canopy cover and amount of open habitat in the surrounding landscape on proportion of alien plant species in forest sites. *Ecoscience* **11**:278-281. DOI: http://dx.doi.org/10.1080/11956860.2004.11682833

Chen J, Franklin JF, Thomas AS. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecological Applications* **2**:387-396. DOI: 10.2307/1941873

Córdoba-Athanasiadis M. 2010. *Priorización de áreas para recuperar la función hidrológica de la subcuenca Támbula-Picachos, Guanajuato*. MSc. Thesis. Universidad Autónoma de Querétaro.

Cutini A, Matteucci G, Mugnozza GS. 1998. Estimation of leaf area index with the Li-Cor LAI 2000 in deciduous forests. *Forest Ecology and Management* **105**:55–65. DOI: 10.1016/S0378-1127(97)00269-7

de Wasseige C, Bastin D, Defourny P. 2003. Seasonal variation of tropical forest LAI based on field measurements in Central African Republic. *Agricultural and Forest Meteorology* **119**:181–194. DOI: 10.1016/S0168-1923(03)00138-2

Didham RK, Ghazoul J, Stork NE, Davis AJ. 1996. Insects in fragmented forests: a functional approach. *Trends in Ecology and Evolution* **11**:255-260. DOI: 10.1016/0169-5347(96)20047-3

Galetti M, Alves-Costa CP, Cazetta E. 2003. Effects of forest fragmentation, anthropogenic edges and fruit colour on the consumption of ornithocoric fruits. *Biological Conservation* **111**:269-273. DOI: 10.1016/S0006-3207(02)00299-9

Gehlhausen SM, Schwartz MW, Augspurger CK. 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. *Plant Ecology* **147**:21-35. DOI: 10.1023/A:1009846507652

Gehring JL, Linhart YB. 1993. Sexual dimorphisms and response to low resources in the dioecious plant *Silene latifolia* (Caryophyllaceae). *International Journal of Plant Sciences* **154**:152–162.

Godínez-Álvarez H, Jiménez M, Mendoza M, Pérez F, Roldán P, Ríos-Casanova L, Lira R. 2008. Densidad, estructura poblacional, reproducción y supervivencia de cuatro especies de plantas útiles en el Valle de Tehuacán, México. *Revista Mexicana de Biodiversidad* **79**:393-403.

Guzmán-Guzmán J, Williams-Linera G. 2006. Edge effect on acorn removal and oak seedling survival in Mexican lower montane forest fragments. *New Forests* **31**:487-495. DOI: 10.1007/s11056-005-2015-0

Håkansson I, Lipiec J. 2000. A review of the usefulness of relative bulk density values in studies of soil structure and compaction. *Soil and Tillage Research* **53**:71-85. DOI: 10.1016/S0167-1987(99)00095-1

Hamrick JL, Murawski DA. 1990. The breeding structure of tropical tree populations. *Plant Species Biology* **5**:157-165. DOI: 10.1111/j.1442-1984.1990.tb00200.x

Henríquez CA. 2004. Efecto de la fragmentación del hábitat sobre la calidad de las semillas en *Lapageria rosea*. *Revista Chilena de Historia Natural* **77**:177-184. DOI: 10.4067/S0716-078X2004000100013

Houlahan JE, Keddy PA, Makkay K, Findlay CS. 2006. The effects of adjacent land use on wetland species richness and community composition. *Wetlands* **26**:79-96. DOI: 10.1672/0277-5212(2006)26[79:TEOALU]2.0.CO;2

Honnay O, Hermy M, Coppin P. 1999. Impact of habitat quality on forest plant species colonization. *Forest Ecology and Management* **115**:157-170. DOI: 10.1016/S0378-1127(98)00396-X

Honnay O, Jacquemyn H, Bossuyt B, Hermy M. 2005. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New Phytologist* **166**:723-736. DOI: 10.1111/j.1469-8137.2005.01352.x

Hyer EJ, Goetz SJ. 2004. Comparison and sensitivity analysis of instruments and radiometric methods for LAI estimation: assessments from a boreal forest site. *Agricultural and Forest Meteorology* **122**:157-174. DOI: 10.1016/j.agrformet.2003.09.013

INEGI. 2008. Inventario de productos geográficos digitales. <http://www.inegi.org.mx/geo/contenidos/topografia/productos_geograficos.aspx> (consulted 1 January 2012)

INEGI. 2010. Compendio de información geográfica municipal. <http://mapserver.inegi.org.mx/dsist/prontuario/index2.cfm> (consulted 1 January 2012)

Janzen DH. 1988. Tropical dry forests. *In*: Wilson EO, ed. *Biodiversity*. Washington DC: National Academies Press, 130–137.

Jules ES, Shahani P. 2003. A broader ecological context to habitat fragmentation: Why matrix habitat is more important than we thought. *Journal of Vegetation Science* **14**:459-464. DOI: 10.1111/j.1654-1103.2003.tb02172.x

Koleff P, Urquiza-Haas T, Contreras B. 2012. Prioridades de conservación de los bosques tropicales en México: reflexiones sobre su estado de conservación y manejo. *Ecosistemas* **21**:6-20.

Kozlowski TT. 1999. Soil compaction and growth of woody plants. *Scandinavian Journal of Forest Research* **14**:596-619. DOI: 10.1080/02827589950154087

Laurance WF, Ferreira LV, Rankin-De Merona JM, Laurance SG, Hutchings RW, Lovejoy TE. 1998. Effects of forest fragmentation of recruitment patterns in Amazonian tree communities. *Conservation Biology* **12**:460-464. DOI: 10.1111/j.1523-1739.1998.97175.x

Laurance WF, Nascimento HEM, Laurance SG, Andrade AC, Fearnside PM, Ribeiro JEL, Capretz RL. 2006. Rain forest fragmentation and the proliferation of successional trees. *Ecology* **87**:469-482. DOI:10.1890/05-0064

Lott EJ, Atkinson TH. 2002. Biodiversidad y fitogeografía de Chamela-Cuixmala, Jalisco. *In*: Noguera FA, Vega-Rivera JH, García-Aldrete AN, Quesada-Avendaño M, eds. *Historia natural de Chamela*. México DF: Universidad Nacional Autónoma de México, 83-98.

Maass JM, Jaramillo V, Martínez-Yrízar A, García-Oliva F, Pérez-Jiménez A, Sarukhán J. 2002. Aspectos funcionales del ecosistema de selva baja caducifolia en Chamela, Jalisco. *In*: Noguera FA, Vega-Rivera JH, García-Aldrete AN, Quezada-Avendaño M, eds. *Historia natural de Chamela*. México DF: Universidad Nacional Autónoma de México, 525-542.

McDonald RI, Urban DL. 2004. Forest edges and tree growth rates in the North Carolina piedmont. *Ecology* **85**:2258-2266. DOI: 10.1890/03-0313

Meagher TR. 1980. Population biology of *Chamaelirium luteum* a dioecious lily. I. Spatial distributions of males and females. *Evolution* **34**:1127-1137. DOI: 10.2307/2408293

Morgan M, Jose S. 2013. Increasing seed germination of *Bursera graveolens*, a promising tree for the restoration of tropical dry forests. *Tree Planters' Notes* **56**: 74-83.

Murcia C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* **10**:58-62. DOI: 10.1016/S0169-5347(00)88977-6

Nascimento EM, Laurance WF. 2004. Biomass dynamics in Amazonian forest fragments. *Ecological Applications* **14**: 127-138. DOI: 10.1890/01-6003

Oliveira-Filho AT, de Mello JM, Scolforo JRS. 1997. Effects of past disturbance and edges on tree community structure and dynamics within a fragment of tropical semideciduous forest in southeastern Brazil over a five-year period (1987-1992). *Plant Ecology* **131**:45-66. DOI: 10.1023/A:1009744207641

Ortiz-Pulido R, Rico-Gray V. 2006. Seed Dispersal of *Bursera fagaroides* (Burseraceae): The Effect of Linking Environmental Factors. *The Southwestern Naturalist* **51**:11-21. DOI: 10.1894/0038-4909(2006)51[11:SDOBFB]2.0.CO;2

Ortiz-Pulido R, Pavón NP. 2010. Influence of slope orientation on sex ratio and size distribution in a dioecious plant *Bursera fagaroides* var. *purpusii* (Brandeg.) McVaugh and Rzed. (Burseraceae). *Plant Ecology* **208**:271-277. DOI: 10.1007/s11258-009-9704-2

Penido G, Ribeiro V, Fortunato DS. 2015. Edge effect on post-dispersal artificial seed predation in the southeastern Amazonia, Brazil. *Brazilian Journal of Biology* **75**:347-351. DOI: 10.1590/1519-6984.12813

Restrepo C, Gomez N, Heredia S. 1999. Anthropogenic edges, treefall gaps, and fruit-frugivore interactions in a neotropical montane forest. *Ecology* **80**:668-685. DOI: 10.1890/0012-9658(1999)080[0668:AETGAF]2.0.CO;2

Rzedowski J, Guevara-Féfer F. 1992. Flora del Bajío y de Regiones Adyacentes, Fascículo 3. Familia Burseracea. Pátzcuaro: Instituto de Ecología AC.

Rzedowski J, Medina RL, Calderón de Rzedowski G. 2004. Las especies de *Bursera* (Burseraceae) en la cuenca superior del Río Papaloapan (México). *Acta Botánica Mexicana* **66**:23-151.

Rzedowski J, Medina RL, Calderón de Rzedowski G. 2005. Inventario del conocimiento taxonómico, así como de la diversidad y del endemismo regionales de las especies mexicanas de *Bursera* (Burseraceae). *Acta Botánica Mexicana* **70**:85-111.

Rzedowski J. 2006. *Vegetación de México*. México DF: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.

Sánchez-Azofeifa GA, Kalacska M, Quesada M, Calvo-Alvarado JC, Nassar JM, Rodríguez JP. 2005. Need for integrated research for a sustainable future in tropical dry forests. *Conservation Biology* **19**:285-286. DOI: 10.1111/j.1523-1739.2005.s01_1.x

Sánchez-Martínez E, Hernández-Oria JG Hernández-Martínez MM, Maruri-Aguilar B, Torres-Galeana LE, Chávez-Martínez R. 2011. *Técnicas para la propagación de especies nativas clave para la forestación, la reforestación y la restauración en el municipio de Querétaro y su área de influencia*. Santiago de Querétaro: CONCYTEQ.

Saunders DA, Hobbs RJ, Margules CR. 1991. Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* **5**:18-32. DOI: 10.1111/j.1523-1739.1991.tb00384.x

Siebe C, Jahn R, Stahr K. 1996. *Manual para la descripción y evaluación ecológica de suelos en el campo*. Chapingo: Sociedad Mexicana de la Ciencia del Suelo A.C, Publicación Especial 4.

Silvertown JW. 1987. *Introduction to plant population ecology*. Ed. 2. Essex: Longman Scientific & Technical.

Silvertown JW, Lovett-Doust J. 1993. *Introduction to plant population biology*. Oxford: Blackwell Scientific Publications.

Sokal RR, Rohlf FJ. 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*. New York: W. H. Freeman and Company.

Soto JM, Uvalle JX, Sánchez E, Yánez RM, Montes F. 2003. Diagnóstico Diferencial Integrado: una herramienta para el uso racional de fertilizantes. *Fruticultura profesional* **139**:152-156. ISSN: 1131-5660

Stohlgren TJ, Falkner MB, Schell LD. 1995. A modified-Whittaker nested vegetation sampling method. *Vegetatio* **117**:113-121. DOI: 10.1007/BF00045503

Suzán H, Malda G, Patten TD, Nabhan GP. 1999. Effects of exploitation and park boundaries on legume trees in the Sonoran Desert. *Conservation Biology* **13**:1497-1501. DOI: 10.1046/j.1523-1739.1999.98177.x

Trejo I. 1996. Características del medio físico de la selva baja caducifolia en México. *Investigaciones Geográficas Boletín* **4**:95-110.

Trejo I, Dirzo R. 2000. Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico. *Biological Conservation* **94**:133-142. DOI: 10.1016/S0006-3207(99)00188-3

Turner IM. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology* **33**:200-209. DOI: 10.2307/2404743

Williams-Linera G. 1990a. Origin and early development of forest edge vegetation in Panama. *Biotropica* **22**:235-241. DOI: 10.2307/2388533

Williams-Linera G. 1990b. Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology* **78**:356-373. DOI: 10.2307/2261117

Yu L, Lu J. 2011. Does landscape fragmentation influence sex ratio of dioecious plants? A case study of *Pistacia chinensis* in the Thousand-Island Lake region of China. *Plos ONE* 6, e22903. DOI: 10.1371/journal.pone.0022903

Zamudio S, Rzedowski J, Carranza E, Calderón de Rzedowski G. 1992. *La vegetación en el estado de Querétaro*. Pátzcuaro: Instituto de Ecología AC.

Zapata TR, Arroyo MTK. 1978. Plant reproductive ecology of a secondary deciduous tropical forest in Venezuela. *Biotropica* **10**:221-230. DOI:10.2307/2387907

Zhu H, Xu ZF, Wang H, Li BG. 2004. Tropical rain forest fragmentation and its ecological and species diversity changes in southern Yunnan. *Biodiversity and Conservation* **13**:1355-1372. DOI: 10.1023/B:BIOC.0000019397.98407.c3