THE SOUTHWESTERN NATURALIST 51(1):11–21 MARCH 2006

SEED DISPERSAL OF *BURSERA FAGAROIDES* (BURSERACEAE): THE EFFECT OF LINKING ENVIRONMENTAL FACTORS

RAÚL ORTIZ-PULIDO* AND VICTOR RICO-GRAY

Departamento de Ecología Vegetal, Instituto de Ecología A.C., A.P. 63, Xalapa, Veracruz, 91000, México (ROP, VRG)
Present address of ROP: Laboratorio de Ecología de Poblaciones, Centro de Investigaciones Biológicas,
Universidad Autónoma del Estado de Hidalgo, A.P. 69, Pachuca, Hidalgo, 42001, México
**Correspondent: raulortizpulido@yahoo.com*

ABSTRACT—We studied the seed dispersal process of a population of *Bursera fagaroides* (Burseraceae) on the coast of the Gulf of Mexico by considering 1) all phases of the dispersal process (i.e., fruit removal, effect of seed passage through digestive tract, seed deposition, removal of seeds from the ground, germination, growth and survival of seedlings and adults, and seed set); 2) plant and animal components and their interaction; and 3) spatial variation in these components using different subpopulations. Hill aspect and surrounding microenvironment or habitat affected individuals of *B. fagaroides*, and this effect depended on life stage (seed, seedling, or adult). Seed germination was greater in moderately-shaded areas (below the perennial plant species *Coccoloba barbadensis*) than in relatively open sites (below *B. fagaroides* or on bare sand); seedlings grew less on sites in bright sunlight; adult individuals were not detected in highly-shaded places; and females inhabiting open sites (grassland) had more removed seeds than those of shaded areas (shrubland and dry forest). *Vireo griseus* and *Dumetella carolinensis,* the only species consuming fruits of *B. fagaroides* during our study, differed in their effect on seeds: seeds ingested by *V. griseus* did not germinate, whereas 17% of seeds ingested by *D. carolinensis* germinated. Additionally, even though both bird species preferred the tropical dry forest, their foraging behavior differed. *Vireo griseus* was mostly found at mid-canopy height in tree-dominated sites, and *D. carolinensis* used the understory of shrubby areas; *B. fagaroides* does not inhabit tree-dominated sites. Our results indicated that there was no ''best'' place for a seed to land. What is suitable for a seed might not be optimal for a fruiting plant. Thus, patterns of seed dispersal are almost certainly altered by processes that happen long after seed deposition.

RESUMEN—Estudiamos el proceso de dispersión de semillas de una población de *Bursera fagaroides* (Burseraceae) en la costa del Golfo de México considerando 1) todas las fases del proceso de dispersión (por ejemplo, remoción de frutos, efecto en las semillas del paso por el tracto digestivo, deposición de la semilla, remoción de la semilla del suelo, germinación, crecimiento y supervivencia de plántulas y adultos y producción de semillas); 2) componentes animales y vegetales y su interacción; y 3) la variación espacial de estos componentes usando diferentes subpoblaciones. El aspecto de las laderas y el microambiente circundante o hábitat afectaron a los individuos de *B. fagaroides,* y este efecto dependió de la fase de desarrollo (semilla, plántula o adulto). La germinación de semillas fue mayor en sitios de sombra moderada (bajo una planta perenne, *Coccoloba barbadensis*) que en sitios relativamente abiertos (bajo *B. fagaroides* o sobre arena desnuda); las plántulas crecieron menos en sitios abiertos; no se detectaron individuos adultos en lugares altamente sombreados, y en las hembras que habitaban sitios abiertos (pastizales) se removieron más semillas que en las zonas sombreadas (matorrales y bosque seco). *Vireo griseus* y *Dumetella carolinensis,* las únicas especies de aves que consumieron frutos de *B. fagaroides* durante nuestro estudio, difirieron en su efecto en las semillas; semillas ingeridas por *V. griseus* no germinaron, mientras que el 17% de las semillas ingeridas por *D. carolinensis* sí germinaron. Además, a pesar de que ambas especies de aves prefirieron el bosque seco tropical su conducta de forrajeo difirió. *Vireo griseus* se encuentró usualmente a media altura del dosel en sitios arbolados, y *D. carolinensis* usó el sotobosque de áreas arbustivas; *B. fagaroides* no habita áreas dominadas por árboles. Nuestros resultados indicaron que no hubo un ''mejor'' lugar para que caigan las semillas. Lo que es un lugar adecuado para que se deposite una semilla puede no ser óptimo para una planta en fructificación. Por lo tanto, los patrones de dispersión de semillas probablemente son susceptibles de ser modificados por procesos que suceden mucho tiempo después de la deposición de las semillas.

Levey and Benkman (1999) have recently suggested that the study of seed dispersal by vertebrates lacks a guiding paradigm. From the early 1970s to the later 1980s, the study of seed dispersal by vertebrates was under the untested paradigm that vertebrate frugivores and ornithocorous plants had coevolved (Wheelwright, 1991; Howe, 1993), a hypothesis that has been rejected by most studies (Levey and Benkman, 1999). Many factors hinder coevolution between plants and frugivorous vertebrates because the result of primary dispersal (i.e., transport of propagules from the parent plant to a different site) can be modified by variables affecting subsequent steps of the process (e.g., Herrera, 1989, 2002; Jordano, 1993; Schupp, 1993; Herrera et al., 1994). The lack of a central paradigm has caused this field of study to stagnate (Fleming and Estrada, 1993; Levey and Benkman, 1999). Novel approaches to the study of seed dispersal systems by vertebrates might lead to new discoveries and new paradigms.

A literature survey on seed dispersal systems by vertebrates (e.g., Levey, 1988; Wiens, 1989; Willson and Whelan, 1990; Loiselle and Blake, 1991; Jordano, 1993, 1995; Jordano and Herrera, 1995; Schupp, 1995; Schupp and Fuentes, 1995; Traveset, 1995; Herrera, 1998) clearly shows the need to consider all steps in the process (i.e., fruit removal, seed dispersal, seed establishment, seed germination, and seedling and adult establishment). We also need to consider both plants and animals, as well as their interactions, the spatio-temporal variability intrinsic to these systems (Wiens, 1989; Kotliar and Wiens, 1990), and the ecological scale for each studied phase (e.g., subpopulation, population, community; Allen and Hoekstra, 1990). Thus, the study of seed dispersal should address 2 great difficulties: the natural variability of the system and the conflicts among different steps of the process. These difficulties, naturally inherent to these systems (Sallabanks and Courtney, 1993), might be the cause for the lack of major generalizations about the mechanisms and processes of seed dispersal by vertebrates. Spatio-temporal variability has been detected even in the simplest systems (Sallabanks and Courtney, 1993), and the conflicts among different steps of the process have been predicted theoretically (Schupp, 1995) and found experimentally (Jordano and Herrera, 1995). The most studied conflicts among phases are those between juveniles and adults (Schupp, 1995), where, for example, an adequate site for adult establishment might not be adequate for a seed. A researcher considering all phases and the spatio-temporal variability of these systems faces 2 problems: 1) joint coordination of 3 research methods (i.e., for birds, plants, and their interaction) (Bronstein, 1994), and 2) appropriate data analysis. The use of statistical tools for the analysis of multiphased processes is only recent (e.g., path analysis; Horvitz and Schemske, 1986; Petraitis et al., 1996; Shipley, 1997). The process of seed dispersal comprises several phases, and each part of this system can be subdivided for study in many ways. For example, plants can be divided into seeds, seedlings, and adults, and the seed stage can be analyzed in different ways (e.g., consumption, removal, deposition, germination). Thus, problems arising in the study of seed dispersal by vertebrates originate from different methods that must be combined, as well from the independence among phases of the process and the natural variability of the system. Complexity increases when we realize that certain phases of the process have not been studied in detail (e.g., there is no direct method to follow, in the field, a seed ingested by a vertebrate).

To assess our understanding of this system, we analyzed the seed dispersal process of the Neotropical small tree, bird dispersed, *Bursera fagaroides* (H.B.K.) Engl. (Burseraceae). We considered all phases of the process, the 3 components of the system (i.e., plant, animal, interaction), and the spatial variation of its components (using different subpopulations). We hypothesized that a detailed knowledge of the system will allow us to detect patterns. In particular, we answered the following questions: What happens after *B. fagaroides* seeds are deposited on the ground by birds? How is recruitment in *B. fagaroides* affected by environmental conditions experienced by seeds? What environmental factors affect the establishment of *B. fagaroides* propagules? After considering the answers to these questions, we further asked: Is it possible to say which bird species are effective dispersal agents of *B. fagaroides*?

METHODS—*Study Area*—Fieldwork was conducted at Centro de Investigaciones Costeras La Mancha (CICOLMA) located on the coast of the Gulf of Mexico (19°36′N, 96°22′W, elevation <100 m). The climate is warm and subhumid, with summer rains. Annual precipitation varies from 900 to 1,800 mm, and annual maximum, minimum, and mean temperature are 33°C, 12°C, and 22°C, respectively (Moreno-Casasola, 1982; Ortiz-Pulido, 1994; Martínez et al., 2002). CICOLMA is a mosaic of plant communities, including tropical dry and deciduous forest, sand dune scrub, mangrove forest, seasonally flooded forest, maize and sugarcane plantations, and human-induced grasslands (Novelo, 1978). *Bursera fagaroides* and *Coccoloba barbadensis* (Polygonaceae) are the most abundant shrub species on cliff tops, and the grasses *Trachypogon gouinii, Schizachyrium scoparium,* and *Aristida adscensionis* are the most abundant species in the herbaceous stratum. The general lack of seeds and seedlings has been explained by high predation rates by the red land crab, *Gecarcinus lateralis,* which is abundant in certain years and at certain times of the year; furthermore, there are no other seed predators (e.g., mice, birds) with a similar abundance and effect on seed banks (García-Franco et al., 1991; Delfosse, 1992).

Plant Species—The genus *Bursera* includes over 100 species of deciduous, bark-exfoliating shrubs and trees distributed from the southern United States to central Brazil. *Bursera* are usually codominant elements in tropical dry forests (Rzedowski and Calderón, 1996). *Bursera fagaroides* var. *purpusii* is present at the study site (Rzedowski and Calderón, 1996). Individuals of this variety are usually dioecious (rarely hermaphroditic) tree-like shrubs, less than 4 m in height, but occasionally reaching up to 8 m, and they live at least 70 y, with one seed per fruit (Toledo, 1982; Rzedowski and Guevara-Féfer, 1992; Rzedowski and Calderón, 1996; J. Rzedowski, pers. comm.). At CICOLMA, *B. fagaroides* is phenologically synchronous. Vegetative growth and flowering of adult individuals occurs at the onset of the rainy season (May to June), mature fruits are present from mid to late dry season (December to May), and seedlings grow during the rainy season (July to September). Most (>99%) individuals shed their leaves during the dry season. Reproductive females are easily detected throughout the year by fruit peduncles that remain attached to branches after fruit detachment. Many species in this genus have toxins, generally terpenes, that act to deter herbivory by arthropods (e.g., Becerra and Venable, 1990; Becerra, 1994, 1997; Peraza-Sánchez et al., 1995). Such protection might not exist for *B. fagaroides* seedlings, which has yet to be studied. Preliminary data suggest that after one year, seedlings with physical protection (covered by 11-mm wire mesh) had 37% higher survival than seedlings without this protection.

Fieldwork—Fieldwork was conducted in 1996 and 1997 on 2 hills separated by 150 m, which represent the general study area. East and west aspects of each hill were characterized microclimatically by measuring 5 variables (light [μmol/s/m^2], air temperature, soil temperature, air moisture, and soil moisture) with a Licor DataLogger (Licor Biosciences, Lincoln, Nebraska) every 5 min during 2 d on February 12 to 13 and August 27 to 28 (near of the middle of the dry and wet seasons, respectively) in each of 3 microhabitats: under an evergreen shrub, under a deciduous shrub, and in an open site, separated by 30 to 40 m from each other. The data collected in each season were averaged to obtain only one measure by microhabitat (mean ± 1 *SE*). Data of dry and wet seasons were compared and analyzed with a randomized block design, with hills as blocks and aspects as treatments; microhabitat was a subplot effect in a split plot arrangement, and changes over seasons were analyzed in a repeated measures analysis. Vegetative cover was estimated with a belt transect (100 m long, 2 m wide) in each plot in the wet season, and differences between plots related to microhabitat cover were analyzed using an ANOVA.

To assess seed removal, seeds collected from 11 *B. fagaroides* individuals were placed in 2 Petri dishes with 5 seeds each in each experimental combination (hill, exposure, and microhabitat); seed removal after 2 d was recorded. To assess germination, we planted 80 seeds in 2 subplots (20 × 20 cm) at a 1-cm depth in each experimental combination. Plots were monitored every week, and after 3 mo, the number of germinated seeds was determined. Seedling survival was studied in 2 subplots in each experimental combination; seedlings were 1.5 cm in height and less than 1 mo old at the time of transplanting. Seedling height was monitored to assess seedling growth. Subplots used in these experiments were protected from herbivores with an 11-mm mesh. Percentage data (e.g., seed removal, seed germination, and seedling survival) were analyzed as a binomial distribution with a generalized linear model that allowed for a mixed model using the GLIMMIX procedure (SAS, 2003). Seedling growth data were normally distributed and were analyzed with a randomized block design, with hills as blocks and aspect as treatment; microhabitat was a subplot factor in a split plot arrangement. With this design, the error degrees of freedom are a function of the number of blocks and treatments (instead of the number of observations).

The effect of environmental conditions on size of adult individuals was studied by marking each adult individual in each of 4 habitats: bare sand (without vegetation), with herbs (grassland), with shrubs (shrubs), or with trees and shrubs (dry forest) on each hill. For each individual, we measured height and trunk diameter (at 0.15 m above ground level) and classified the crown into one of 2 categories (covered by other plants, either more or less than 50%). We considered an individual as an adult if it was >0.8 m in height (first reproductive event of *B. fagaroides* occurs approximately at that size; R. Ortiz-Pulido, unpubl. data). Fruit production was assessed by marking a 0.4-m^2 area under each of 82 randomly selected female trees, counting the number of fruits directly above this area, and multiplying the number of times this area fitted under the tree crown. Height, diameter, and fruit production were compared in an ANOVA that included block and aspect in a randomized block design, with habitat as a subplot effect and crown cover (2 levels) as a subplot effect. We did not test the bare sand habitat because in some aspects inside hills, there were no individuals in this kind of habitat.

We determined habitat preference (tropical deciduous forest, tropical dry forest, sand dune scrub, grassland) for each bird species observed eating fruits of *B. fagaroides.* The relative abundance (individuals/ha) of every bird species in each habitat was considered as habitat preference, and it was obtained by walking monthly (April 1992 to March 1993) along a 1-km transect in every habitat (following Emlen, 1971) and registering the vegetative stratum where every individual was observed. Data were standardized among vegetation associations with different bird detectability (only individuals observed nearer than 20 m were counted; sensu Emlen, 1971; see Ortiz-Pulido et al., 2000). Bird species were determined using 7 × 35 mm binoculars and field guides (Peterson and Chalif, 1989; National Geographic Society, 1991).

To assess the number of fruits removed by birds, we used the 82 female individuals at fruit production. The number of seeds removed (NSR) by birds was estimated as: NSR = fruits produced − (fruits left on branches + fruits in traps). The data used were obtained only from the fraction of the tree crown directly above a seed trap. Fruits produced were those counted at the onset of the fruiting season, fruits left on branches were those still attached to a branch at the end of the season, and fruits in traps were those within a trap that remained during all the fruiting season below the plant. Seed traps were checked every month during the fruiting season. To estimate the number of visits to plants and the number of seeds removed by each bird species, we conducted 4-h focal observations for each of the 82 female plants considered, recording bird visiting species and number of individuals.

Laboratory experiments were conducted to determine seed viability after passage through the digestive tract of each bird species we observed ingesting fruits of *B. fagaroides.* Birds were captured within the area of distribution of *B. fagaroides,* placed in independent metal cages containing water, chopped banana and soy flour, and allowed to rest through the night with the cage covered with a semitransparent fabric. The next morning, we placed in each cage a Petri dish containing 10 mature fruits of *B. fagaroides.* Birds were released after they had eaten the fruits and regurgitated or defecated the seeds. The recovered seeds were planted 1 cm deep in plastic containers filled with soil obtained from *B. fagaroides* sites. The containers were placed in a shade house at the field station at room temperature and watered until sand was saturated once per day. We recorded the number of germinated seeds, and observations stopped after a month without new seeds germinating. For controls, we used seeds obtained directly from fruits, which were treated the same as regurgitated seeds or seeds from feces. Seed germination differences between treatments were separated with the least significance test using least square means.

Normal distribution of data was tested with a Shapiro-Wilk test (alpha = 0.05). We used a stepwise regression (with generalized linear models; GLIM; Royal Statistical Society, 1992; Crawley, 1993) to determine the effect of the 5 climatic variables, measured in 2 seasons (see Table 1) on growth of seedlings. When we used GLIM, in all cases we evaluated data overdispersion using a deviance analysis and the residual degrees of freedom of the minimum models, and, in the case of overdispersion, we adjusted the scale parameter (Crawley, 1993).

RESULTS—With the exception of air temperature, which was only different between seasons ($\chi^2 = 4.05$; $df = 1$; $P < 0.05$; $n = 288$), we found microclimatic differences between aspect ($F > 250$; $n > 143$; $P < 0.0001$), microhabitats ($F > 4$; $n > 143$; $P < 0.05$), and season ($F > 48$; $n > 143$; $P < 0.0001$) for all variables considered (Table 1). In addition, west aspects had more area covered by trees and shrubs than east aspects ($\chi^2 = 243$; $df = 9$; $P < 0.001$; Table 2).

Ninety-five percent of exposed seeds were removed. Variation in removal was not related to aspect ($F = 0.68$; $df = 1, 1$; $P > 0.05$), microenvironment ($F = 0.614$; $df = 2, 4$; $P > 0.05$), or to the aspect by microenvironment interaction ($F = 0.614$; $df = 2, 4$; $P > 0.05$).

Seed germination was low (10.5%) and was related to microenvironment ($F = 14.62$; $df = 2, 6$; $P > 0.005$) but not to aspect ($F = 3.85$; $df = 1, 2$; $P = 0.10$) or to the interaction between aspect and microenvironment ($F = 0.14$; $df = 2, 6$; $P > 0.05$). We recorded significantly fewer germinated seeds below *B. fagaroides* and bare sand than below *C. barbadensis* (in both cases $t > 3.89$; $df = 6$; $P < 0.01$; Fig. 1).

TABLE 1—Summary of environmental parameters measured (mean ± 1 *SE*): 2 seasons, 2 aspects, and 3 microhabitats (under *Bursera fagaroides* [BF] and *Coccoloba barbadensis* [CB], and on bare sand [BS]) at Centro de Investigaciones Costeras La Mancha on the coast of the Gulf of Mexico.

Environmental parameters	Micro-habitat	Dry season		Wet season	
		East	West	East	West
Light (μmol/s/m^2)[ac]	BF	582.7 ± 4.9	697.2 ± 4.6	663 ± 5	—
	CB	39.3 ± 1.2	44.3 ± 1.3	38.9 ± 1.2	21.2 ± 1.4
	BS	584.5 ± 5	699.7 ± 4.8	662.4 ± 5.1	495.2 ± 5
Air temperature (°C)[ad]	BF	23 ± 0.3	26.2 ± 0.4	28.6 ± 0.3	26.6 ± 0.2
	CB	22.3 ± 0.2	23.5 ± 0.2	26.2 ± 0.2	26.1 ± 0.2
	BS	23.8 ± 0.3	26.2 ± 0.4	28.8 ± 0.4	27.8 ± 0.3
Soil temperature (°C)[bd]	BF	25.7 ± 0.3	26.7 ± 0.3	28.8 ± 0.2	27 ± 0.2
	CB	—	22.7 ± 0.2	25.6 ± 0.1	25.9 ± 0.1
	BS	25.8 ± 0.3	28.3 ± 0.4	28.7 ± 0.3	28.3 ± 0.3
Air moisture (%)[ae]	BF	<5	<5	61 ± 0.5	82.2 ± 0.6
	CB	<5	<5	85.7 ± 0.3	98.6 ± 0.4
	BS	<5	<5	61.3 ± 0.6	64.4 ± 0.7
Soil moisture (%)[be]	BF	<5	<5	11.9 ± 0.3	22.2 ± 0.3
	CB	<5	<5	17.4 ± 0.4	18.3 ± 0.4
	BS	<5	<5	7.9 ± 0.4	28.3 ± 0.4

[a] Taken 1.5 cm over ground.

[b] Taken 5 cm below soil surface.

[c] $n = 144$ to each mean.

[d] $n = 288$ to each mean.

[e] $n = 24$ to each mean.

Mean height of seedlings (growth) was 86.0 ± 5.7 mm (mean ± 1 *SE*). Height was not affected by aspect ($F < 0.10$; $df = 1, 6$; $P > 0.05$), microenvironment ($F = 2.43$; $df = 2, 6$; $P > 0.05$), or by the aspect by microenvironment interaction ($F = 1.16$; $df = 2, 6$; $P > 0.05$). Photosynthetic active radiation during the dry season and soil moisture during the wet season were associated with seedling growth ($\chi^2 = 31.58$ and $\chi^2 = 18.97$, respectively, with $df = 1$; $P < 0.05$; χ^2 reported due to overdispersed data).

Most seedlings (84.6%) survived for at least one year. Survival was not associated with aspect ($F < 0.10$; $df = 1, 6$, $P > 0.05$), microenvironment ($F = 0.66$; $df = 2, 6$; $P > 0.05$), or by the aspect by microenvironment interaction ($F = 0.60$; $df = 2, 6$; $P > 0.05$).

TABLE 2—Percent of area covered by vegetation associations in the 4 hills studied at Centro de Investigaciones Costeras La Mancha on the coast of the Gulf of Mexico.

Hill	Vegetation association			
	Bare sand	Grassland	Shrub	Dry forest
E1	12.50	48.25	39.25	0
E2	16.00	40.75	43.25	0
W1	3.75	13.50	82.75	0
W2	4.75	11.25	66.25	17.75
Total (m^2)	74	227.50	463	17.75

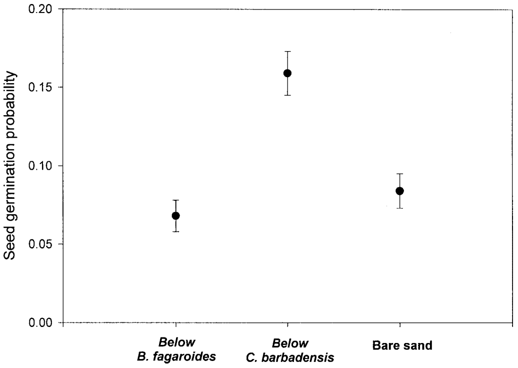

FIG. 1—Seed germination recorded to individuals of *Bursera fagaroides* in 3 microenvironments in central Veracruz, Mexico. Bars represent 1 *SE*.

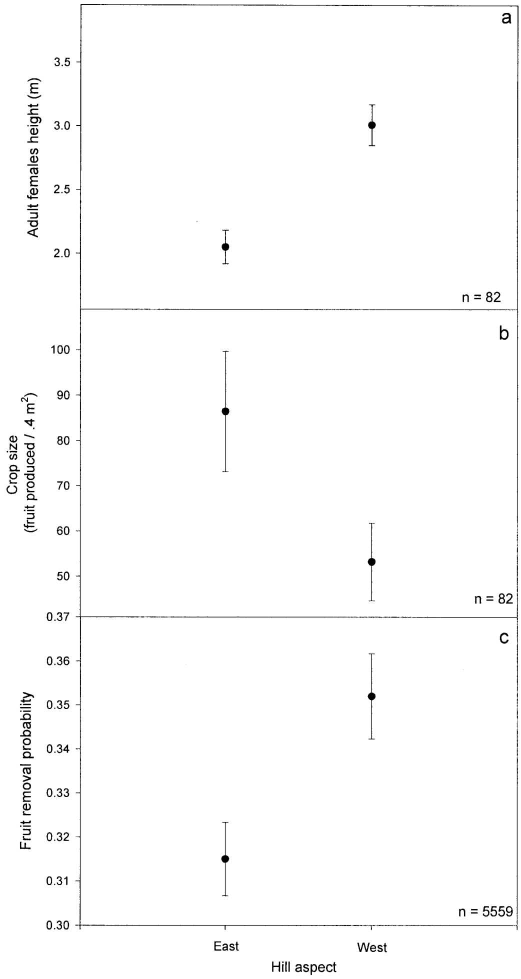

FIG. 2—Height (a), crop size (b), and fruit removal (c) of female *Bursera fagaroides* trees related to aspect of hills in central Veracruz, Mexico. Bars represent 1 *SE.*

Mean height for all the adult population ($n = 310$) was 2.1 ± 0.2 m and diameter was 29.8 ± 2.0 cm. Female height was related to aspect ($\chi^2 = 32.60$; $df = 1$; $P < 0.05$; $n = 82$) and habitat ($\chi^2 = 28.43$; $df = 2$; $P < 0.05$; $n = 80$). Females on east-facing aspects were shorter than females on west-facing aspects (Fig. 2a), and females in grassland were shorter (mean = 1.73 ± 0.10 m) than females from shrub (mean = 2.63 ± 0.73 m) and dry forest habitats (mean = 3.86 ± 1.40 m). Female diameter was related to cover ($\chi^2 = 7.24$; $df = 1$; $P < 0.05$; $n = 82$) and a habitat by aspect interaction ($\chi^2 = 11.72$; $df = 1$; $P < 0.05$; $n = 82$). Females under <50% of canopy cover were smaller in diameter (mean = 24.89 ± 1.29 cm) than females under >50% of cover (mean = 30.00 ± 2.82 cm), and females inhabiting grassland, in both aspects, were smaller in diameter than females in shrub and dry forest (Fig. 3).

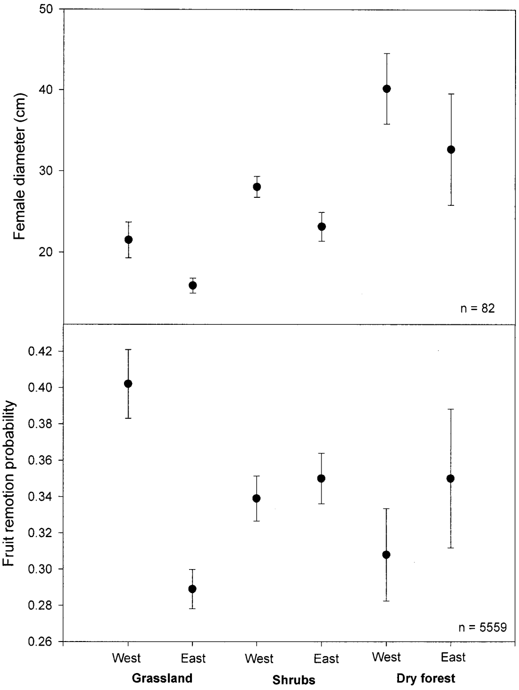

FIG. 3—Trunk diameter and fruit remotion related to hill aspect and habitat of *Bursera fagaroides* adult female trees in central Veracruz, Mexico. Bars represent 1 *SE.*

At fruit production, we detected differences only among aspect ($\chi^2 = 5.37$; $df = 1$; $P < 0.05$; $n = 82$). Those individuals on east-facing aspects had lower fruit production than those on west-facing aspects (Fig. 2b).

We did not find significant differences among aspect, habitats, or aspect by habitat interactions in terms of the number of bird visits to plants. *Vireo griseus* and *Dumetella carolinensis* comprised more than 77.5% of total bird visits ($n = 164$). The other visiting bird species were *Tyrannus forficatus, Empidonax minimus,* and *E. trailli.* Only *V. griseus* and *D. carolinensis* ingested fruit during visits to *B. fagaroides,* and no significant differences were found between species in terms of the number of fruits ingested (one-way ANOVA to data with Poisson distribution, $\chi^2 = 0.52$; $n = 108$; $P = 0.4$).

The number of fruits removed was significantly different among aspects ($\chi^2 = 4.27$; $df = 1$; $P < 0.05$; $n = 5{,}559$) and affected by aspect by habitat interaction ($x^2 = 13.65$; $df = 1$; $P < 0.05$; $n = 5{,}559$). Fewer fruits were removed on east-facing aspects than on west-facing aspects (Fig. 2c). Fewer fruits were removed on east-facing grasslands and west-facing dry forest and shrub lands than on east-facing shrub lands, east-facing dry forests, and west-facing grasslands (Fig. 3).

Landscape use differed among the bird species feeding on *B. fagaroides* fruits. *Vireo griseus* preferred the canopy (>6 m height) of the tropical dry (80% of sightings) and tropical deciduous (20% of sightings) forests. In contrast, *D. carolinensis* used the forest understory (<2.18 m height) of the tropical dry forest (74% of sightings) and the sand dune scrub (26% of sightings).

We found significant differences ($\chi^2 = 5.21$; $df = 107$; $P < 0.05$) in the percent of seeds germinating after passage through the digestive tract of *V. griseus* (0% germination, $n = 15$) and *D. carolinensis* (17% germination, $n = 93$). We also found significant differences in germination ($\chi^2 = 506.1$; $df = 512$; $P < 0.001$) between seeds passed through the digestive tract of birds and those taken directly from plants (20% germination, $n = 420$).

DISCUSSION—Our results illustrate the need to consider in detail all components of the system (plant, disperser, interaction), as well as all phases of dispersal to determine the effect of vertebrates on the process of recruitment by a plant. Failure to consider a component or a phase could lead to an erroneous conclusion about the outcome of the frugivore-ornithocorous plant system. For example, if we had only considered fruit ingestion, we would have concluded that both *V. griseus* and *D. carolinensis* were effective dispersal agents, when, in fact, they have different dispersal qualities after ingesting seeds. Similarly, considering only seed removal from the soil, we would have concluded that there are no best sites to deposit seeds, when seeds germinated best below *C. barbadensis* shrubs. The analysis of the plant and animal components individually and their interaction allowed us to detect details that would have otherwise gone unnoticed (e.g., germination patterns and landscape use by birds). The details of each component have the potential to determine the final outcome of the interaction (e.g., effect of environment and bird behavior on propagule establishment).

Environmental conditions (hill aspect and surrounding microenvironment or habitat) affected the life histories of individuals of *B. fagaroides* depending on the phase of development of the individual (seed, seedling, or adult). For instance, the seedling phase was not affected by these variables in our study, but seed and adult phases were affected. Seed germination and adult growth were higher in moderately shaded areas (below *C. barbadensis* and dry forest, respectively) than in relatively open areas (below *B. fagaroides* and shrubland, respectively) and non-shaded areas (bare sand and grassland, respectively), but seedlings and adult individuals were not detected in highly-shaded places (deciduous forest). Additionally, females inhabiting open sites (grassland) had more removed seeds of their crop than those of shaded areas (shrubland and dry forest).

Seed removal was relatively high in all conditions, although less on east-facing aspects and bare sand. This pattern can be explained if we consider the abundance of the red land crab, *G. lateralis,* the main seed consumer in our study site. *Gecarcinus lateralis* is a predator exerting a strong effect on the population dynamics of some plant species (it can ingest >70% of their seed bank; Blain, 1988; García-Franco et al., 1991; Delfose, 1992). The marks of activity by *G. lateralis* found at the sites where our seed removal experiments were conducted suggest that individuals of this species removed seeds of *B. fagaroides* (although the white-tipped dove, *Leptotila verreauxi,* could also remove some seeds). In a study conducted simultaneously with our research, A. Capistrán (unpubl. data) found that *G. lateralis* exhibited higher abundance on west-facing hills and under the crowns of shrubs and trees (ca. 7,000 individual/ha) than on east-facing hills and bare sand sites (2,300 individuals/ha). The abundance data for *G. lateralis* and our seed removal data suggest that there was less removal of *B. fagaroides* seeds at sites with fewer crabs (east-facing hills and bare sand). However, we did not detect significant differences.

We do not know if seed removers can directly determine that some populations of *B. fagaroides* will exhibit the survival and growth characteristics observed in this study, but we consider it improbable. Instead, we suggest that the phenotypic characteristics of *B. fagaroides* and the removal activities of *G. lateralis* are determined by environmental conditions, with no direct association between them. Other studies have shown that environmental conditions, such as light intensity, have an effect on abundance of seedeaters and herbivores (Maiorana, 1981; Sommaggio et al., 1995; Hanley et al., 1996).

Seed germination was related to environmental conditions. Seeds had a better chance of germination if deposited in a moderately shaded microenvironment, for example, under non-deciduous shrubs, such as *C. barbadensis,* but not in dry forest or deciduous forest (i.e., sites with more shadow) nor on bare sand (i.e., sites hardly shaded). This kind of ''nursing'' has been previously observed in *Bursera graveolens,* another species inhabiting dry environments (Clark and Clark, 1981). Plants growing under a nurse plant in dry sites lose less water than those living in open sites, where lack of water and high temperatures can kill seeds and seedlings. Light availability under non-deciduous shrubs was lower than under deciduous shrubs, but higher than in the dry forest (where no *B. fagaroides* seedlings were found). Lower germination under *B. fagaroides* than under *C. barbadensis* could be the result both of differences in light intensity or the effect of toxic allelopathic substances produced by adult *B. fagaroides* individuals (Becerra, 1997).

We did not find an effect of environmental conditions on seedling survival. However, there could be other environmental effects that we did not test (e.g., effect of predators and herbivores). For example, in preliminary studies, we found that seedlings protected from predators had 37% higher survival probabilities than seedlings without protection. High seedling mortality is known for 2 other *Bursera* species: *B. graveolens,* where it is believed that it is the result of herbivory by goats (Clark and Clark, 1981), and *B. aloexylon,* where lack of seedlings has been attributed to cattle (Colina, 1987). For *B. fagaroides,* it is possible that *G. lateralis* has a strong effect on seedling survival, although this effect could be limited by toxic substances produced by these plants (Becerra and Venable, 1990; Becerra, 1994, 1997).

We detected an effect of environmental conditions on fruit production, where individuals inhabiting east-facing aspects had higher crop size than those on west-facing hills. Fruit production is the least affected variable by environmental conditions, and it has been interpreted as an effect of plasticity of individuals to allocate resources first to reproduction (Caldwell and Pearcy, 1994). In view of our results, the effect of habitat on the fruit production of *B. fagaroides* remains to be determined.

The size of adult individuals was related to environmental conditions, with light in the dry season and moisture in the wet season having the most influence. The tallest and largest individuals were recorded in the dry forest, and the shortest and smallest individuals in grassland, suggesting that although temperature should be adequate for growth of *B. fagaroides,* light is a limiting factor (<45 μmol/s/m^2 in dry forest vs. >450 μmol/s/m^2 in bare sand), as is moisture (near 10% in dry forest vs. $<5\%$ in bare sand, both measures during the dry season), both affecting plant growth. In the forest, individuals might have to be taller to reach the canopy and receive light directly; however, this is not a factor in grassland, where water is a factor in the dry season. Several studies using different species (e.g., Morgan and Smith, 1979; Grime and Campbell, 1991; Ballaré, 1994) offer evidence supporting the latter consideration and indicate that height and cover of individual plants are related to the height of the surrounding vegetation.

In summary, the environment exerts a significant effect on the development of the plant component. The propagules of *B. fagaroides* have specific requirements related to their phase of development. Thus, the development of a propagule will increase in a slightly shaded site, perhaps with few herbivores (e.g., under a non-deciduous shrub of another species), and fruit production will be affected by aspect of the hill where the individual is established.

Through their physiology and behavior, vertebrate frugivores can affect the establishment pattern of a plant (Schupp, 1993), because they will deposit propagules with different viability in a variety of microsites. This is due to the specific treatment that the digestive tract of each vertebrate species exerts on seeds (Traveset and Verdú, 2002), and seeds will be deposited within the habitat of each vertebrate species. Dispersal effectiveness (i.e., the capacity of an animal to successfully disperse seeds) has been a central topic in the analysis of the ecological and evolutionary consequences of seed dispersal by vertebrates (Schupp, 1993). *Vireo griseus* and *D. carolinensis,* the species consuming fruits of *B. fagaroides,* differed in their treatment of seeds. Seeds ingested by the former did not germinate, whereas 17% of the seeds ingested by the latter did germinate. Thus, *V. griseus* apparently is not an effective dispersal agent of *B. fagaroides.* Although the number of seeds recovered from *V. griseus* was low (n = 15), limiting our ability to make inferences, there is another difference establishing *D. carolinensis* as a better seed dispersal agent of *B. fagaroides.* Even though both bird species prefer the tropical dry forest, their foraging behavior differed. *Vireo griseus* was mostly found at mid-canopy height in tree-dominated sites, whereas *D. carolinensis* used the understory of shrubby areas. Our results show that *B. fagaroides* does not inhabit tree-dominated sites, and, thus, only the dispersal by *D. carolinensis* might be considered successful in the long term. However, we found that seed taken directly from the plant had higher germination than seeds consumed by both bird species. Assessing the effect of the digestive tract of a vertebrate on seed germination has been difficult, and results of published studies have been contradictory (Traveset and Verdú, 2002). A recent meta-analysis found that, globally, birds as a group increased germination rates of seeds that go through their digestive track; however, there is high variability in these results, with germination ranging from 0 to 100% (Traveset and Verdú, 2002). Our results show one of many possible results for the system studied. We suggest that a spatio-temporal approach, where many sites and years are studied, is a better way to understand the effect of birds on seed germination of *B. fagaroides.*

In summary, our data on fruit consumption in the field, on germination of seeds passed through the digestive tract of birds, and on landscape use by birds indicate that *D. carolinensis* should be considered the best seed dispersal agent of *B. fagaroides* at our study site. To more successfully assess the final outcome in studies of seed dispersal by vertebrates (and not reach biased or erroneous conclusions), we should consider the 3 components of the interaction (plant, animal, and their interaction) and all the phases of dispersal (fruit removal, effect of seed passage through digestive tract, seed deposition, removal of seeds from the ground, germination, growth and survival of seedlings and adults, and seed set). The fact that germination of seeds, and later fruit removal from adults (=fitness), vary so much from one habitat to another means that there is no ''best'' place for an individual to land. What is suitable for a seed might not be optimal for a fruiting plant. Thus, for our study species, study site, and study time, the patterns of seed dispersal affected by birds are almost certainly likely to be altered by processes that happen long after seed deposition.

We appreciate the help during fieldwork of R. Valenzuela, R. Ortiz, J. Marín, M. Carvallo, C. Díaz-Castelazo, R. Díaz, and E. Flores. We thank O. Briones, D. O'Dowd, D. R. Folkerts, D. J. Levey, R. Dirzo, and 3 anonymous reviewers for their comments and suggestions at different times during the preparation of the manuscript. Research was supported by Instituto de Ecología, A. C. (No. 902-16), CONACyT (No. 9352171 to ROP and 95-137 to VRG), and Sigma XI (ROP). Universidad Autónoma del Estado de Hidalgo and Instituto de Ecología A.C. support a stay of ROP, where a part of this paper was finished.

Literature Cited

Allen, T. F. H., and T. W. Hoekstra. 1990. The confusion between scale defined levels and conventional levels of organizations in ecology. Journal of Vegetation Science 1:5–12.

Ballaré, C. L. 1994. Light gaps: sensing the light opportunities in highly dynamic canopy environments. In: M. M. Caldwell and R. M. Pearcy, editors. Exploitation of environmental heterogeneity by plants. Academic Press, New York. Pages 73–110.

Becerra, J. X. 1994. Squirt-gun defense in *Bursera* and the chrysomelid counterploy. Ecology 75: 1991–1996.

Becerra, J. X. 1997. Insects on plants: macroevolutionary chemical trends in host use. Science 276: 253–256.

Becerra, J. X., and D. L. Venable. 1990. Rapid-terpene-bath and ''squirt-gun'' defense in *Bursera schlechtendalii* and the counterploy of chrysomelid beetles. Biotropica 22:320–323.

Blain, D. 1988. Factors affecting the early stages of regeneration of three tropical tree species in a seasonal forest, Veracruz, Mexico. Unpublished M.S. thesis, York University, Toronto, Canada.

BRONSTEIN, J. L. 1994. Our current understanding of mutualism. Quarterly Review of Biology 69:31–51.

CALDWELL, M. M., AND R. M. PEARCY. 1994. Exploitation of environmental heterogeneity by plants. Academic Press, New York.

CLARK, D. A., AND D. B. CLARK. 1981. Effects of seed dispersal by animals on the regeneration of *Bursera graveolens* (Burseraceae) on Santa Fe Island, Galápagos. Oecologia 49:73–75.

COLINA S., M. G. DEL P. 1987. Estudio de una población natural de linaloe, *Bursera aloexylon,* en Chaucingo, Guerrero. Unpublished B.S. thesis, Facultad de Ciencias, U.N.A.M., México.

CRAWLEY, M. J. 1992. Seed predators and plant population dynamics. In: M. Fenner, editor. Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford, United Kingdom. Pages 157–191.

CRAWLEY, M. J. 1993. GLIM for ecologists. Blackwell Scientific Publications, Oxford, United Kingdom.

DELFOSSE, B. 1992. The effect of the red land crab *Gecarcinus lateralis* on the litter and nutrient cycling of a coastal semi-deciduous tropical forest. Unpublished M.S. thesis, York University, Toronto, Canada.

EMLEN, J. T. 1971. Population densities of birds derived from transect counts. Auk 88:323–342.

FENNER, M. 1985. Seed ecology. Chapman and Hall, London, United Kingdom.

FLEMING, T. H., AND A. ESTRADA. 1993. Frugivory and seed dispersal: ecological and evolutionary aspects. Klumer Academic Publishers, Dordrecht, The Netherlands.

GARCÍA-FRANCO, J. G., V. RICO-GRAY, AND O. ZAYAS. 1991. Seed and seedling predation of *Bromelia pinguin* L. by the red land crab *Gecarcinus lateralis* Frem. in Veracruz, Mexico. Biotropica 23:96–97.

GRIME, J. P., AND B. P. CAMPBELL. 1991. Growth rate, habitat productivity, and plant strategy as predictors of stress response. In: H. A. Mooney, W. E. Winner, and E. J. Pell, editors. Response of plants to multiple stresses. Academic Press, New York. Pages 143–159.

HANLEY, M. E., M., FENNER, AND P. J. EDWARDS. 1996. The effect of mollusc grazing on seedling recruitment in artificially created grassland gaps. Oecologia 106:240–246.

HERRERA, C. M. 1989. Seed dispersal by animals: a role in angiosperm diversification? American Naturalist 133:309–322.

HERRERA, C. M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. Ecological Monographs 68:511–538.

HERRERA, C. M. 2002. Seed dispersal by vertebrates. In: C. M. Herrera and O. Pellmyr, editors. Plant-animal interactions, an evolutionary approach. Blackwell Publishing, Oxford, United Kingdom. Pages 185–208.

HERRERA, C. M., P. JORDANO, L. LÓPEZ-SORIA, AND J. A. AMAT. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecological Monographs 64:315–344.

HORVITZ, C. C., AND D. W. SCHEMSKE. 1986. Seed dispersal of a Neotropical myrmecochore: variation in removal rates and dispersal distance. Biotropica 18:319–323.

HOWE, N. F. 1993. Specialized and generalized dispersal systems: where does ‘‘the paradigm’’ stand? Vegetatio 107/108:3–13.

JANZEN, D. H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2:465–492.

JORDANO, P. 1993. Pollination biology of *Prunus mahaleb* L.: deferred consequences of gender variation for fecundity and seed size. Biological Journal of the Linnean Society 50:65–84.

JORDANO, P. 1995. Spatial and temporal variation in the avian-frugivore assemblage of *Prunus mahaleb*: patterns and consequences. Oikos 71:479–491.

JORDANO, P., AND C. M. HERRERA. 1995. Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. Ecoscience 2:230–237

KOTLIAR, N. B., AND J. A. WIENS. 1990. Multiple scales of patchiness and structure: a hierarchical framework for the study of heterogeneity. Oikos 59: 253–260.

LEVEY, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. Ecological Monographs 58:251–269.

LEVEY, D. J., AND C. W. BENKMAN. 1999. Fruit-seed disperser interactions: timely insights from a long-term perspective. Trends in Ecology and Evolution 14:41–43.

LOISELLE, B. A., AND J. G. BLAKE. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology 72:180–193.

MAIORANA, V. C. 1981. Herbivory in sun and shade. Biological Journal of Linnean Society 15:151–156.

MARTÍNEZ, M. L., G. VÁZQUEZ, D. A.WHITE, G. THIVET, AND M. BRENGUES. 2002. Effect of burial by sand and inundation by fresh- and seawater on seed germination of five tropical beach species. Canadian Journal of Botany 80:416–424.

MORENO-CASASOLA, P. 1982. Ecología de la vegetación de dunas costeras: factores físicos. Biotica (México) 7:577–602.

MORGAN, D. C., AND H. SMITH. 1979. A systematic relationship between phytochrome-controlled development and species habitat, for plant grown in simulated natural radiation. Planta 145:253–258.

National Geographic Society. 1991. Field guide to the birds of North America. National Geographic Society, Washington, D.C.

Novelo, A. 1978. La vegetación de la Estación Biológica El Morro de La Mancha, Veracruz. Biotica (México) 3:9–23.

Ortiz-Pulido, R. 1994. Frugivoría y dispersión de semillas por aves en el Morro de La Mancha, Ver. Unpublished B.S. thesis, Universidad Veracruzana, Xalapa, Veracruz, México.

Ortiz-Pulido, R., J. Laborde, and S. Guevara. 2000. Frugivoría por aves en un paisaje fragmentado: consecuencias en la dispersión de semillas. Biotropica 32:473–488.

Peraza-Sánchez, S., N. E. Salazar-Aguilar, and L. M. Peña-Rodríguez. 1995. A new triterpene from the resin of *Bursera simaruba*. Journal of Natural Products 58:271–274.

Peterson, R. T., and E. L. Chalif. 1989. Aves de México. Editorial Diana, México, D.F.

Petraitis, P. S., A. E. Dunham, and P. H. Niewiarowski. 1996. Inferring multiple causality: the limitations of path analysis. Functional Ecology 10:421–431.

Royal Statistical Society. 1992. GLIM (computational program) release 4. London, United Kingdom.

Rzedowski, J., and G. Calderón. 1996. Burseraceae. In: V. Sosa, editor. Flora de Veracruz. Instituto de Ecología, A.C., Xalapa, Veracruz, México.

Rzedowski, J., and F. Guevara-Féfer. 1992. Burseraceae. In: J. Rzedowski and G. Calderón, editors. Flora del bajío y de regiones adyacentes. Instituto de Ecología, A.C., Xalapa, Veracruz, México.

Sallabanks, R., and S. P. Courtney. 1993. On fruit-frugivore relationships: variety is the spice of life. Oikos 68:567–570.

SAS. 2003. Statistical Analysis System, version 9.1. SAS Institute, Inc., Cary, North Carolina.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107/108:12–29.

Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany 82:399–409.

Schupp, E. W., and M. Fuentes. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. Ecoscience 2:267–275.

Shipley, B. 1997. Exploratory path analysis with applications in ecology and evolution. American Naturalist 149:1113–1138.

Sommaggio, D., M. Paoletti, and S. Ragusa. 1995. The effects of microhabitat condition, nutrients and predators on the abundance of herbivores on stinging nettles (*Urtica dioica* L.). Acta Oecologica 16:671–689.

Toledo, C. 1982. El género *Bursera* (Burseraceae) en el estado de Guerrero (México). Unpublished B.S. thesis, Facultad de Ciencias, U.N.A.M., México.

Traveset, A. 1995. Spatio-temporal variation in predispersal reproductive losses of a Mediterranean shrub, *Euphorbia dendroides* L. Oecologia 103:118–126.

Traveset, A., and M. Verdú. 2002. A meta-analysis of the effect of gut treatment on seed germination. In: D. J. Levey, W. R. Silva, and M. Galleti, editors. Seed dispersal and frugivory: ecology, evolution, and conservation. CAB International, Cambridge, Massachusetts. Pages 339–350.

Wheelwright, N. T. 1991. Frugivory and seed dispersal: ''La coevolución a muerto—¡Viva la Coevolución!'' Trends in Ecology and Evolution 6: 312–313.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Willson, M. F., and C. J. Whelan. 1990. Variation in postdispersal survival of vertebrate-dispersed seeds: effects of density, habitat, location, season, and species. Oikos 57:191–198.

Zar, J. H. 1996. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Submitted 7 July 2004. Accepted 1 August 2005. Associate Editor was David Wester.