

# Influence of slope orientation on sex ratio and size distribution in a dioecious plant *Bursera fagaroides* var. *purpusii* (Brandeg.) McVaugh and Rzed. (Burseraceae)

Raúl Ortiz-Pulido · Numa P. Pavón

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**Abstract** It has been hypothesized that environmental variability can influence the sex ratio of a plant population, and it has been observed that in stressful environments, male plants are more abundant than females. However, it is unknown whether this is due to differential mortality rates between males and females. In this study, we analyzed sex ratio, mortality, and size distribution in a population of the neotropical tree/bush *Bursera fagaroides* in two different environments (east- and west-oriented slopes) over a 10-year period. We determined that the sex ratio favored males in the more stressful environment (east-facing slope) and that females were significantly larger in the less stressful environment (west-facing slope). Despite a significant difference in size between sexes by slope aspect, the difference in sex ratio cannot be explained by slope or by mortality during the 10 years of observation.

**Keywords** Sex ratio · *Bursera fagaroides* · Slope aspect · Plant sex · Mortality

## Introduction

Slope aspect can have marked effects on the growth and development of plants (Pavón 2002; Flores-Palacios and Ortiz-Pulido 2005; Ortiz-Pulido and Rico-Gray 2006). It is known that solar radiation differs by aspect, causing variations in temperature and air humidity, conditions that influence the stomatic conductivity of plants (Dubayah 1994), which could affect their growth. This assumes that the prevailing conditions in some slope orientations could be less appropriate for the establishment and regeneration of plant populations (Ferrer et al. 1995; González-Hidalgo et al. 1996; Erefur et al. 2008). Environmental variation influenced by slope aspect offers an appropriate system for studying the effect of environmental variation on sex ratio and size distribution in plants.

It has been hypothesized that under nonstressful conditions, dioecious plant populations maintain a sex ratio of 1:1 (Charnov 1982; Carroll and Mulcahy 1993; Allen and Antos 1993). In harsh environments (e.g., low precipitation and/or poor soil), populations show a tendency toward greater numbers of males (Ortiz et al. 1998, 2002). For example, in several species of *Juniperus* (Cupressaceae), higher proportions of males have been reported in populations

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R. Ortiz-Pulido (✉) · N. P. Pavón  
Centro de Investigaciones Biológicas, Universidad  
Autónoma del Estado de Hidalgo, A.P. 69, Pachuca,  
Hidalgo 42001, México  
e-mail: raulortizpulido@yahoo.com

R. Ortiz-Pulido  
Laboratorio de Ecología de la Conducta, Centro Tlaxcala  
de Biología de la Conducta UAT-UNAM, Carretera  
Tlaxcala-Puebla km 1.5 Colonia Xicohtencatl S/N,  
90070 Tlaxcala, Tlaxcala, México

growing in environments with scarce water resources at elevations above 2,600 m above sea level (Ortiz et al. 1998; Ortiz et al. 2002). This deviation in the sex proportion was not always found to be connected with environmental conditions (e.g., Obeso et al. 1998; Decker and Pilson 2000), but with differential energy requirements by sex (Obeso et al. 1998).

In dioecious species, females, in comparison to males, designate more resources to reproduction than to maintenance and growth; they are smaller and shorter-lived (Willson 1983; Allen and Antos 1993; Obeso et al. 1998; Pavón and de Luna 2008). Energy consumption would, therefore, cause greater mortality among females, changing the sex ratio in the population accordingly (Lovett-Doust and Lovett-Doust 1988; Allen and Antos 1993). This may be why females are the predominant individuals in some populations located in high-quality habitats (e.g., deep, well-drained soils), as they can maintain an equilibrium between energy resources obtained and used (Dawson and Ehleringer 1993; Freeman et al. 1993; Ramadan et al. 1994; Pavón and de Luna 2008).

For *Bursera fagaroides* (Burseraceae), a dioecious neotropical bush-tree, it was found that size and reproduction are related to slope aspect. Individuals growing on slopes with a west-facing aspect had greater height and trunk diameter, but lower fruit production than those on slopes with an eastern aspect (Ortiz-Pulido and Rico-Gray 2006). However, there is no information about how environmental conditions, as determined by slope aspect, affect *B. fagaroides* individuals by sex.

In this study, we analyzed the relationship between sex ratio, size distribution, mortality, and slope aspect of a population of *Bursera fagaroides* (Burseraceae) growing in a region of stable dunes along a coastal area of the Gulf of Mexico. We measured plant size and mortality of individuals of *B. fagaroides* during a period of 10 years (1995–2005) to determine whether these two variables could influence the sex ratio found on different slope orientations.

## Methods

### Study area

Field work was conducted at the Centro de Investigaciones Costeras La Mancha (CICOLMA) located

along the Gulf of Mexico coast (96°22' W, 19°36' N, <100 masl). The climate is warm and subhumid with summer rains. Average annual precipitation is 1,300 mm; and annual maximum, minimum, and mean temperatures are 33, 12, and 22°C, respectively (Ortiz-Pulido 1994). The soil contains between 70 and 93% sand (Duberceucq et al. 1992). *Bursera fagaroides* and *Coccoloba barbadensis* (Polygonaceae) are the most abundant shrub species on cliff tops, where the dominant vegetation type is dry low forest with xerophytic grassland patches. At this site, the effect of human perturbation is negligible because it is a protected area. The cliffs run north–south, showing only eastern and western aspects.

The study area (called “fossil dune”), where 95% of the *B. fagaroides* population is located at CICOLMA, encompassed two hills (nearly 3 ha) separated by 150 m, both with eastern and western facing slopes. The *Bursera fagaroides* population is continuous between the two aspects. Every slope aspect has particular climatic conditions due to exposure to sun radiation and sea wind (the east-facing slope receives more of both). Light [ $\mu\text{mol s}^{-1} \text{m}^{-2}$ ], air temperature, soil temperature, air moisture, and soil moisture vary with respect to slope orientation and season (Table 1). Compared to the western aspect, the eastern aspect offers more stressful conditions for plants. Soil humidity is lower throughout the year, and during rainy season (*B. fagaroides* vegetative growing period), temperatures are higher (on the ground and in the air, with a maximum air temperature of 46.6°C; Table 1) (Ortiz-Pulido and Rico-Gray 2006). This may be why some organisms, such as orchids and termites, prefer *B. fagaroides* trees situated on the west-facing slope over those on the east-facing slope (Flores-Palacios and Ortiz-Pulido 2005; López-Villalobos et al. 2008). There are more termite nests (*Nasutitermes nigriceps*) and orchid plants (*Brassavola nodosa* and *Myrmecophila grandiflora*) on adult individuals of *B. fagaroides* on the west-facing slope.

### Study species

*Bursera fagaroides* var. *purpusii* (Brandeg.) McVaugh and Rzed. is a dioecious bush-tree, commonly less than 4 m in height, but occasionally reaching heights up to 8 m, living at least 70 years (Rzedowski and Guevara-Féfer 1992; J. Rzedowski pers. comm.). At

**Table 1** Means of environmental parameters measured on hills with different aspect orientation (east-facing and west-facing) during two seasons (dry and wet seasons) in 1997 at Centro de Investigaciones Costeras La Mancha on the coast of the Gulf of Mexico

Environmental parameters	Aspect			
	E		W	
	Season		Season	
	Dry	Wet	Dry	Wet
Light (mmol/s/m <sup>2</sup> ) <sup>ac</sup>	583.60	662.70	698.45	495.20
Air temperature (°C) <sup>ad</sup>	23.40	28.70	26.20	27.80
Soil temperature (°C) <sup>bd</sup>	25.75	28.75	27.50	28.30
Air moisture (%) <sup>ae</sup>	<5	61.15	<5	64.40
Soil moisture (%) <sup>be</sup>	<5	9.90	<5	28.30

Data from Ortiz-Pulido and Rico-Gray (2006)

<sup>a</sup> Taken 1.5 cm above ground level

<sup>b</sup> Taken 5 cm below soil surface

<sup>c</sup>  $n = 288$

<sup>d</sup>  $n = 576$

<sup>e</sup>  $n = 48$

CICOLMA, *B. fagaroides* is phenologically synchronous at the population level; nearly 95% of the individuals show the same phenological stage at any time. Vegetative growth and flowering of adult individuals occur at the onset of the rainy season (May–June). Mature fruits, with one seed, are present from mid to late dry season (December–May). Seed germination occurs during the dry season (December and February), and seedlings grow during the rainy season (July–September). At the study site, seed removal, commonly by predators, is nearly 95%, while seed germination is approximately 10.5%. In a previous study, seedlings not protected from herbivores had 47.6% survival after 1 year, while 84.6% of protected seedlings survived (Ortiz-Pulido and Rico-Gray 2006). The plants shed their leaves during the dry season. At CICOLMA, fruit production is higher on the slope with eastern aspect, while the probability of fruit removal is higher on the western aspect slope (Ortiz-Pulido and Rico-Gray 2006). Reproductive females are easily recognized throughout the year by fruit peduncles that remain attached to branches after fruit fall (Ortiz-Pulido and Rico-Gray 2006). These peduncles can remain on the plant for 2 or 3 years. Outside of the flowering period, using field plant signals, it is almost impossible to tell

whether an individual without peduncles is a male or a nonreproductive individual (see Parthasarathi and Angavi 1984 for an alternative way to determine this in other *Bursera* species). To the best of our knowledge, there are no data for this species, nor for other *Bursera* taxa, on individual change in sex over time.

### Field work

Field work was conducted between January and May, 1995 and December, 2005. We marked all the plants in the population, but in this study, we did not measure individuals that were located 10 m or less from the hill top, to avoid confusion between which environmental condition (of the two different aspects) was affecting an individual. Climatic characterization of the eastern and western facing slopes of each hill is reported elsewhere for measurements conducted during 1997 (Ortiz-Pulido and Rico-Gray 2006; Table 1). The climate data used here (light, air temperature, soil temperature, air moisture, and soil moisture) were averaged to obtain a single measurement per aspect (mean + 1 S.E.). In 1995, all the individuals of *B. fagaroides* taller than 10 cm were marked and sexed as soon as they bore flowers and fruit peduncles ( $n = 346$  individuals). In each individual, the following size variables were measured: diameter at base of the trunk (10 cm from the ground), total height (from ground to highest branch, using a telescopic pole) and cover (the area covered by the projection of the crown on the ground). In December 2005, individuals of *B. fagaroides* were measured and sexed again. For each aspect, we recorded the individuals that had died of the 346 that were measured in 1995 (i.e., those which fell down or dried; sensu Matelson et al. 1995).

### Statistical analysis

In order to determine whether the sex ratio of the whole population and that of each aspect differed from 1:1, a chi-square test was applied to the 1995 data. The same test was used to determine, for each slope, whether there was any difference in mortality rates between sexes. We did not test sex proportion for the 2005 data, as these data represented a subsample of the original population.

ANOVA was performed to determine whether there were differences in diameter at base of the trunk, total height, and cover between dead and live individuals over the 10 years. Plant size (diameter at base of the trunk, total height, and cover) was analyzed using repeated measures ANOVA, with sex and aspect as factors over the two sampling periods (1995, 2005). The use of model 1 from the ANOVA is not appropriate in this case because it fails to model the correlation between the repeated measures in the data, and thus violates the assumption of independence (von Ende 2001). When the ANOVA revealed significant differences, we used a Tukey test to determine which treatments were significant. All the variables were square-root transformed to achieve a normal distribution (in all the cases  $\chi^2 < 5.9$ ,  $P > 0.102$ ). For the analysis, we eliminated the data corresponding to the 43 individuals that disappeared between 1995 and 2005, 79 individuals whose sex could not be assigned in 2005 (due to lack of peduncles or flowers, or because we diagnosed a different sex than in the 1995 data), and 107 individuals which were not measured in 2005 (due to time and budget limitations). We did not take into account individuals that apparently changed sex, because their change must be demonstrated with complete certainty, and it added a difficult variable to interpret to our study. This left only 117 individuals of the 346 marked in 1995. On the eastern aspect, there were 37 females and 44 males, and on the western aspect, there were 17 females and 19 males. This unbalanced sample represents natural differences in individual abundance of the plant species in our study site. *Bursera fagaroides* individuals are naturally more abundant on the east-facing slope, perhaps, because the west-facing slope has limited space for growth, as other plant species are more abundant.

## Results

The sex ratio on the west-facing slope did not differ significantly from a 1:1 proportion (72 males : 78 females;  $\chi^2 = 0.24$ ,  $df = 1$ ,  $P > 0.6$ ), but it did on the east-facing slope, where there was a significant trend favoring males (113 males : 83 females;  $\chi^2 = 4.59$ ,  $df = 1$ ,  $P < 0.05$ ).

Over the 10-year study period, 12.4% of the marked individuals died. Seven males and seven females died on the eastern aspect, and 13 males and

16 females died on the western aspect. There was no difference between sexes in the proportion of deaths between the slopes ( $\chi^2 = 0.00$ ,  $df = 1$ ,  $P > 0.05$ ). Mortality in the 10-year period did not explain the trend in sex ratio favoring males on the eastern aspect. However, taking into account the proportion of deaths for each slope, there was higher mortality on the western aspect (15.4%) than on the eastern aspect slope (9.3%). Mortality was related to size; dead individuals were larger than surviving individuals in terms of total height ( $F = 11.86$ ,  $df = 1$ , 343,  $P = 0.003$ ) and diameter at base of the trunk ( $F = 5.67$ ,  $df = 1$ , 342,  $P = 0.018$ ), but not in cover ( $F = 1.4$ ,  $df = 1$ , 343,  $P = 0.22$ ). We observed from our field maps and in situ observations that the dead individuals were not spatially aggregated.

Plants grew significantly during the 10 year period; using ANOVA, we found that within subjects, there was a significant effect of time on the three measurements (diameter at base of the trunk, total height, and cover; Table 2). However, growth was not related to the sex/slope interaction over time; within subjects, there were no interactions that were significant (Table 2). Between subjects, total height showed significant differences between sex, slope, and the interaction of both factors; diameter at base of the trunk and cover only showed significant differences by the sex–slope interaction (Table 2). In both 1995 and 2005, females on the west-facing aspect were taller than males on the same slope or than females and males of the eastern aspect slope (Tukey test dif.  $< -0.302$ ,  $P < 0.01$ , for all the cases). These results allow us to conclude that the differences in height were present in 1995 and persisted in 2005. For diameter at base of the trunk and cover, there was no clear pattern to explain the few differences detected between treatments.

## Discussion

Our results indicate that slope aspect is related to sex ratio, as reported for other plant species (Shea et al. 1993). Climate variation between slope aspects has been suggested as one of the primary determinants for epiphyte (e.g., *Tillandsia recurvata*; Pavón 2002), tree (e.g., *Pinus silvestres*; Erefur et al. 2008), and grass (Amezaga et al. 2004) establishment; and it appears that climate variation influences height and

**Table 2** Two-way ANOVA (sex and aspect) on three plant parameters (diameter at base of the trunk, height, and cover) of *B. fagaroides* inhabiting coastal hills in Veracruz, Mexico

Source	Diameter at base of trunk		Height		Cover	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Between subjects						
Sex	1.283	0.260	5.674	0.019	0.355	0.552
Aspect	0.052	0.819	23.658	0.000	1.387	0.241
Sex × Aspect	8.993	0.003	9.869	0.002	13.338	0.000
Within subjects						
Time	6.523	0.012	30.735	0.000	26.538	0.000
Time × Sex	0.002	0.967	1.010	0.317	0.107	0.744
Time × Aspect	0.732	0.394	0.847	0.359	0.496	0.483
Time × Sex × Aspect	0.612	0.436	1.001	0.319	0.030	0.863

The factor “Time” was considered for two periods (1995 and 2005)

cover in several deciduous forest species (Chmura 2008), leaf size of some shrubs (e.g., *Pistacia lentiscusson*; Auslander et al. 2003), and biologic interactions (Flores-Palacios and Ortiz-Pulido 2005).

In our study, sex ratio showed a trend toward males in harsh environmental conditions (east-facing slope) and females were taller in less harsh conditions (west-facing slope; lower air and ground temperature and less light in the dry season). These results support the hypothesis that environmental variation, caused by the effect of slope orientation, directly affects population parameters, which, in our case, are sexual expression and size distribution of plants. In other plants, such as *Juniperus*, a similar pattern was observed; males were more abundant in harsh environments (i.e., locations with scarce water supplies; Ortiz et al. 1998, 2002). Our results suggest that a similar pattern exists for *B. fagaroides*. The tendency toward males was stronger on the aspect with harsher conditions, and this finding cannot be explained by mortality and growth patterns over 10 years.

We did not find any significant differences in mortality between sexes with respect to slope orientation. Sex ratio differences were detected on the east-facing slope, although mortality was higher (15.4%) on the west-facing slope than on the east-facing slope (9.3%). The causes of higher mortality on the west-facing slope remain untested, but they do not appear to be related to ratio differences. We believe that higher mortality could occur on the west-facing slope when *B. fagaroides* individuals are

shadowed by the canopies of other plants. This did not occur on the east-facing slope, where environmental conditions are harsher and plant abundance is lower in comparison to the west-facing slope.

We found differences in height between males and females (as reported previously by Ortiz-Pulido and Rico-Gray 2006), but they were present from the start of our study (1995) and persisted at the end (2005). Therefore, the differences do not appear to have determined the sex ratio differences observed between sexes. It had been proposed that growth in adult individuals as well as other factors cause this difference in sex ratio (Bierzychudek and Eckhart 1988; Allen and Antos 1993; Cipollini and Stiles 1991; Vasiliauskas and Aarssen 1992; Dawson and Ehleringer 1993). We did not find field evidence to support that this is occurring in the *B. fagaroides* populations studied.

An alternative possibility, to be tested in the field in future studies, is that the factors affecting sex ratio at population levels may have an effect on other stages of the life history of *B. fagaroides*. This possibility is supported by indirect evidence; several phases of the *B. fagaroides* life cycle show environmental plasticity, and environmental conditions varied between slopes. Individuals of *B. fagaroides* showed plasticity with respect to the environment (Rzedowski and Kruse 1979; Ortiz-Pulido and Rico-Gray 2000, 2006), and this could mean that the sex ratio observed in this study could have been produced in some earlier stage of life (e.g., seeds or seedlings). In the same study area, it was found that seeds of

*B. fagaroides* germinated differently in three microhabitats (i.e., below the same species, below the second-most abundant species [*C. barbadensis*], and in bare sand); and that fruit production was higher on the east-facing slope, while the probability of fruit removal was higher on the west-facing slope (Ortiz-Pulido and Rico-Gray 2006). It is necessary to study other stages (e.g., seeds, seedling) or phenological periods (e.g., fruit production period) of the plant to find out whether there are further factors influencing the sex proportion pattern observed here. All the climate variables (light, air temperature, soil temperature, air moisture, and soil moisture) varied significantly between the two slopes (Ortiz-Pulido and Rico-Gray 2006); in other words, the variability in habitat conditions between the study areas seems to be strong enough to affect some stages of life history in *B. fagaroides* individuals. It is also possible that a selective environmental factor affects the individuals of this species before reproduction. It has been observed that the first reproductive event can cause energy stress in some plant species (Geber et al. 1999). It is known that males of several species reach reproductive maturity after the females (Falinski 1980; Allen and Antos 1993) and that in some dioecious species, females grow slower than males, perhaps, as a consequence of reproductive energy demands (Obeso 1997). In our case, we estimated plant size and recorded significant differences between sexes, but it cannot explain the sex ratio difference between slopes.

It is possible that plant size differences between sexes could be determined by reproductive stress. *Bursera fagaroides* females had more fruits (i.e., higher reproductive effort) and had lower height (i.e., lower growth) on east-facing than on west-facing slopes. It could be that in stressed environments, adult female individuals use their energy mainly for reproduction, leaving any residual energy for growth. This view appears to be supported by field studies with other plant species. It was found that females of *Austrocedrus chilensis* invest more in reproduction than males, and it was found that males grew 100% more per year than females in stressed environments (Nuñez et al. 2008). In another study, young *Juniperus thurifera* females were found to be more sensitive to summer water stress, which, in turn, caused lower tree ring growth in females than in males (Rozas et al. 2009). It remains to be determined whether the

growth–reproduction relationship affects mortality differentially by sex in *B. fagaroides*.

In our study, the sex ratio of *B. fagaroides* populations was related to slope orientation, and not explained by mortality and growth during the 10 study years. However, the possibility is not ruled out that both variables, over time scales longer than a decade, could have created the sex ratio bias.

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