

SHORT COMMUNICATION

Sex ratio, size distribution and nitrogen resorption in the dioecious tree species *Bursera morelensis* (Burseraceae)

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(Accepted 21 May 2008)

Key Words: deciduous forest, Metztlán, nitrogen, leaves

Dioecious plant populations have generally been considered to maintain sex ratios of 1:1 (Allen & Antos 1993, Carroll & Mulcahy 1993, Charnov 1982). The sex ratio does, however, change if the plants are growing in a stressful environment, often being male-biased under these conditions (Ortiz *et al.* 1998, 2002). This pattern has been explained by differences in how the sexes resolve their respective energy requirements (Obeso *et al.* 1998). Females generally assign more resources to reproduction in comparison to growth and maintenance than do males, and they are smaller and longer-lived (Allen & Antos 1993, Nicotra 1999, Obeso *et al.* 1998, Willson 1983). Thus their higher reproductive costs take a toll on females, modifying the population sex ratio in favour of males (Allen & Antos 1993, Lovett-Doust & Lovett-Doust 1988). However, in order to determine the reproductive cost it is necessary to consider the compensatory mechanisms (Obeso 2002). These reduce the reproductive cost and include plastic response in terms of plant architecture and plant physiology. For example, nutrient resorption is a process that may help decrease dependence on nutrient intake, thereby constituting an important nutrient economy mechanism that can also reduce the reproductive cost if a significant proportion of the nutrients had been reassigned to reproduction (Killingbeck 1986, Obeso 2002).

For the above-mentioned, we postulate the following hypothesis: dioecious plant populations in a stressful environment maintain their sex ratio 1:1, provided that the compensatory mechanisms are significantly more efficient in the females than males. We test this prediction in *Bursera morelensis* (Burseraceae), a dioecious deciduous trees which dominates a tropical dry forest in a

semiarid region in the state of Hidalgo, Mexico. Sex ratio, physiognomy and nitrogen resorption were measured in a population of *B. morelensis* located within the Barranca de Metztlán Biosphere Reserve in the central eastern part of the state of Hidalgo, Mexico (98°23'00''–98°57'08''W, 20°14'15''–20°45'26''N; elevation 1000–2300 m). The average annual precipitation of study area ranges from 500–700 mm, and average annual temperature from 18–22 °C.

Bursera morelensis is the dominant species of the tropical deciduous forest. Within ravines and steep valleys, it grows mainly on the south-facing slope. It grows in regosol soil, poor in nutrients (24.7 kg ha⁻¹ nitrate), with less than 50 cm of depth (Puig 1991). Soil analyses showed neutral pH (6.8–7.3) with low organic matter content (1.0–2.5%) and low carbon content (0.58–1.45%). These values suggest a nitrogen deficiency, which was corroborated by the direct nitrogen content value measured at 0.2%.

Fieldwork was carried out in April and May 2006 at two tropical deciduous forest sites located 1 km apart. At each site, three transects were laid out perpendicular to the slope, each one consisting of 12 contiguous 5 × 5-m squares. The sex of *B. morelensis* individuals in each square was determined based on observations of flowers and fruit peduncles. Height and trunk diameter at 0.5 m above ground level were measured for each individual. If branching occurred below this height, the sum of the branch diameters was used. Ten males and 10 females which showed no damage from pests or disease were selected at random. In order to estimate the age of individuals, a sample of wood up to the heartwood was removed from the trunk at 0.5 m above ground level using a 12-mm Pressler borer. The growth rings were examined under the microscope, and were counted by a specialist (Dr José Goche Télles of the Forest Research Center, UAEH).

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In order to measure leaf nitrogen concentration, samples of leaves were taken from each selected individual during 2006 (July, September, October and December) and 2007 (September and November). Each sample consisted of leaves picked from different heights in the tree canopies. In July 2006 and September 2007, the leaves were green, while by October–November they had turned red. By the first week of December 2006 trees had partly defoliated, and only reddish-brown leaves showing signs of abscission were collected. In November 2007, leaves of selected trees showed signs of abscission, and were beginning to change to reddish yellow, although the colour of the sampled leaves was not homogeneous. In December the trees had defoliated completely. The samples were dried at 80 °C for 4 d. They were then ground and the powder analysed for total nitrogen using a PerkinElmer 2400 CHNS/O Elemental Analyser.

The chi-square test was used to determine whether the proportion of males and females was significantly different from the expected proportion of 1:1. Differences in trunk diameter and height between sexes were analysed by t-tests. The data were transformed before analysis by taking the natural logarithm in order to meet assumptions of normality and homogeneity of variance assumptions (Zar 1999). The relationship between number of growth rings, and height and trunk base diameter was analysed using the Pearson correlation with the Bonferroni correction.

For the 2006 data, total N concentration in the leaves was analysed by sampling date and by sex using an analysis of variance with repeated measures. The differences in nitrogen values between senescent leaves sampled in December 2006 and November 2007 was tested by the t-test (Zar 1999). Resorption efficiency (RE) was calculated using the equation proposed by Killingbeck & Costigan (1988):

$$\text{RE}(\%) = \frac{[(N_{\text{mature leaves}} - N_{\text{senescent leaves}})]}{(N_{\text{mature leaves}})} \times 100.$$

Nitrogen concentration in mature leaves collected in late July was used to estimate 2006 RE, as values were highest in July. Concentrations were lowest in senescent leaves from November. For 2007, nitrogen concentrations were obtained from mature September leaves and senescent November leaves. Per cent RE values were standardized using an arcsine transformation, and differences between sexes and years were tested by a two-way analysis of variance (Zar 1999). All analyses were carried out using the Systat 12 statistical package.

At neither study site did the number of males and females significantly differ from 1:1 ($\chi^2 = 0.01$, $P < 0.05$ for site 1; $\chi^2 = 0.6$, $P < 0.05$ for site 2). For the remainder of the analysis, data from both sites were

therefore pooled. The *B. morelensis* population maintains a sex ratio of 1:1 ($\chi^2 = 0.376$, $P = 0.47$) as would be expected under the influence of natural selection and the absence of environmental variation (Allen & Antos 1993, Carroll & Mulcahy 1993, Charnov 1982). Many studies show that this proportion is actually rare due to the influence of a variety of environmental factors on survival of females (Allen & Antos 1993, Bierzychudek & Eckhart 1988, Cipollini & Stiles 1991, Dawson & Ehleringer 1993, Vasiliauskas & Aarssen 1992). This suggests that *B. morelensis* is adapted to the conditions of scarce precipitation and soil nutrient deficit that are typical of the regions where it grows.

On average, males were significantly taller than females ($t = 3.02$, $P = 0.003$). There was no significant correlation between height and the number of growth rings in either sex ($r = 0.36$ and $r = 0.51$, for males and females respectively), so age of individuals cannot be considered to account for differences in height. In both sexes, trunk diameter was significantly correlated with the number of growth rings ($r = 0.94$, $P < 0.05$ in females; $r = 0.86$, $P = 0.003$ in males), but trunk diameter did not differ significantly by sex ($t = 0.721$, $P = 0.472$). The lower heights of female individuals as reported here cannot be considered a factor that would cause a survival disadvantage; rather they may be due to the fact that females of dioecious species generally assign proportionately more of their resources to reproduction than to growth and maintenance when compared to males (Obeso 2002, Obeso *et al.* 1998, Willson 1983). Females have been reported to grow more slowly than males for some dioecious species, perhaps as a result of the greater toll reproduction takes on females (Obeso 1997).

The N concentration of the leaves was significantly different for 2006 sampling dates ($F = 195$, $P < 0.001$) (Figure 1). For females no significant differences were found between values for senescent leaves from December 2006 and November 2007 ($t = 1.19$, $P = 0.19$) (Figure 1). Average RE was $82.4\% \pm 0.642\%$ for 2006 and $53.2\% \pm 6.05\%$ for 2007, a significant difference ($F = 23.6$, $P < 0.01$). In 2006, the highest nitrogen concentration values for the year were recorded in July. In 2007, it was not possible to take a sample in that month, for that reason we used September values to estimate 2007 RE. It is possible that June or July of 2007 had the highest values of nitrogen concentration in that year and RE of 2007 could have been as high as that of 2006. On the other hand, in tropical deciduous forests and arid tropical scrub, RE may vary considerably from year to year according to the availability of water (Pavón *et al.* 2005, Rentería *et al.* 2005). The values obtained in this study could reflect that RE had an inverse relationship with rainfall. The lowest value in RE was obtained in 2007, that year was extraordinarily wet with a precipitation of 693.8 mm, while in 2006 was 457.3 mm.

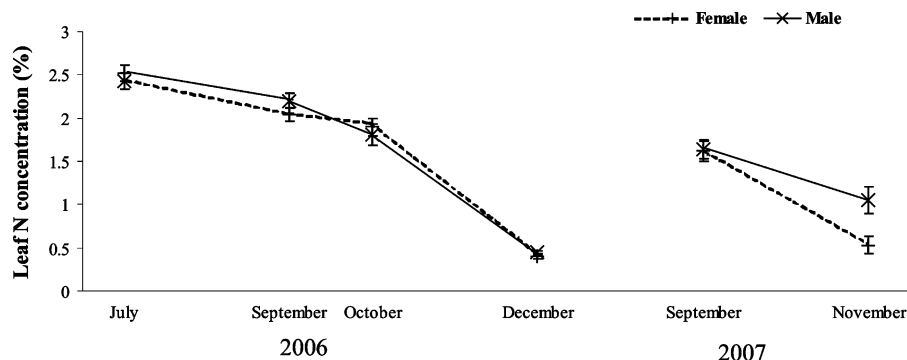


Figure 1 Foliar nitrogen percentage (average \pm SE) of mature leaves of female and male individuals of *Bursera morelensis* during two growth season (2006 and 2007) in a deciduous tropical forest in central Mexico.

Nitrogen resorption efficiency in the population of *B. morelensis* was found to be between 53.2% and 82.4%, higher values than the average of 50% reported in the review by Aerts (1996). In other tropical deciduous forest species, RE is less than 60% (Rentería *et al.* 2005). In these ecosystems, lower RE values have been reported in nitrogen-fixing trees such as *Lysiloma microphyllum*, where RE ranged from 16% to 42% (Cardenas & Campo 2007). In another ecosystem, tropical montane rain forest, under more favourable environmental conditions, RE values are lower; the average RE of 14 tree species was 49.2% and the maximum was 71.5% for *Alseodaphne petiolaris* (Cai & Bongers 2007).

Females of *B. morelensis* had significantly higher RE values for both years ($F = 6.19$, $P = 0.018$). In 2006, RE for females was $84.0\% \pm 0.65\%$ and $80.8\% \pm 0.8\%$ for males, whereas in 2007 females were $67.9\% \pm 5.4\%$ and $40.0\% \pm 9.6\%$ for males. Although, the interaction was not significant ($F = 4.00$, $P = 0.06$), the difference between sexes was more evident in 2007. These results support the hypothesis that dioecious plant population in a stressful environment maintain their sex ratio 1:1, provided that the compensatory mechanisms are significantly more efficient in the females than males. It is likely that greater resorption efficiency compensates part of the greater reproductive cost in females in comparison with males (Obeso 2002). The absence of an estimate of reproductive costs in *B. morelensis* limits us in defining the biological importance of a minimum difference between sexes in the efficiency of nitrogen resorption (3%), as a compensatory mechanism for reproductive costs. However, it is likely that other compensatory mechanisms (Obeso 2002) are working simultaneously and as a whole they could compensate the higher reproductive costs in females. A similar result was reported for other dioecious species growing in high-quality environments (e.g. deep, well-drained soils), as they can readily maintain a balance between energy resources taken in and consumed in such areas (Dawson & Ehleringer 1993, Freeman

et al. 1993, Ramadan *et al.* 1994). However, in stressful environments this pattern is scarcely known, but our results suggest that it could happen at *Bursera morelensis* inside the study area.

ACKNOWLEDGEMENTS

The manuscript was improved by the helpful comments of Raul Ortiz-Pulido. We thank José Rodolfo Goche Télles for the growth-ring analysis, Yolanda Marmolejo Santillán for the chemical analysis and Margaret Schroeder for English revision. This paper was funded by Universidad Autónoma del Estado de Hidalgo (PAI 06/02).

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