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Population structure, growth rates and spatial distribution of two dioecious tree species in a wet forest in Puerto Rico

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Abstract: Dioecious plants often exhibit male-biased sex ratios and sexual differences in life history traits such as plant size, growth rate and frequency of flowering, which arise from the different costs of reproduction for male and female plants. In tropical dioecious species sexual differences in reproductive costs have been demonstrated for several subcanopy species, but few canopy dioecious trees have been studied. We recorded the sexual expression of *c.* 2600 trees of *Cecropia schreberiana* and *Dacryodes excelsa*, two canopy dioecious species, during several censuses over 2 y in a 16-ha plot located in 'subtropical wet forest' in the Luquillo Mountains, Puerto Rico. There were similar numbers of male and female trees of *C. schreberiana* but *D. excelsa* had a female-biased population. *Cecropia schreberiana* showed no differences in male and female diameter distributions or growth rates, suggesting that reproductive maturation and longevity are similar for both sexes. This lack of differences in size and growth rate in *C. schreberiana* may result from mechanisms to compensate for the higher cost of reproduction in females, no resource limitation related to its pioneer life-history, or similar male and female reproductive costs. In contrast, *D. excelsa* males were larger than females, probably because males grow slightly faster than females. This sexual difference in *D. excelsa* may reflect a higher cost of reproduction in females than in males. Spatial segregation of males and females into different habitats is not common in tropical forest and neither *C. schreberiana* nor *D. excelsa* males and females exhibited significant spatial segregation. The contrasting results for these two canopy species reflect their different life history strategies in this hurricane-affected forest.

Key Words: Burseraceae, Cecropiaceae, dioecy, Luquillo Forest Dynamics Plot, sexual dimorphism, sex ratio, size distribution, tropical trees

INTRODUCTION

Dioecious plants may exhibit sex-dependent life-history traits if females allocate a greater proportion of their resources to reproduction and a smaller amount to maintenance and growth than males (Lloyd & Webb 1977, Obeso 2002). Sex differences in reproductive costs arise because the resources required per seed are usually greater than per pollen grain. Differential resource allocation to vegetative versus reproductive processes could produce a male-biased dioecious population if females face a higher risk of mortality than males particularly when resources are limited (Bierzychudeck & Eckhart 1988, Meagher & Antonovics 1982). In addition, females may appear to be underrepresented in a population if they delay flowering and reproduction (Nicotra 1998, Thomas & LaFrankie 1993), or if they flower less frequently than males (Bullock & Bawa 1981, Cipollini & Stiles 1991). Among tropical dioecious trees, male-biased sex ratios have been more frequently observed than equal sex ratios (Thomas & LaFrankie 1993). Female-biased populations have only been reported in the genus *Garcinia* (Clusiaceae) in the Palaeotropics (Thomas 1997) and in two polygonaceous species *Coccoloba caracasana* (Opler & Bawa 1978) and *Triplaris americana* in the Neotropics (Melampy & Howe 1977, Opler & Bawa 1978).

Spatial segregation of the sexes (SSS) at local scales has been associated with an environmental gradient of a limiting resource such as soil water or nutrients (Bierzychudek & Eckhart 1988, Dawson & Ehleringer 1993). This SSS is linked to the differential costs of

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reproduction in dioecious plants and may reflect sexual differences in resources required for growth, reproduction and survival in different habitats, or environmental sex determination (Bierzychudek & Eckhart 1988). In species that exhibit SSS, females predominate in habitats with higher resource levels, while males occupy less favourable sites (Bierzychudek & Eckhart 1988, Freeman *et al.* 1976, Shea *et al.* 1993). Although SSS has been demonstrated in approximately 66% of the species examined (Bierzychudek & Eckhart 1988), there is little evidence of SSS in tropical dioecious tree and shrub species (Queenborough *et al.* 2007).

This study documents the sexual expression of all potentially reproductive individuals of two dioecious canopy species native to Puerto Rico, by conducting several censuses of reproductive behaviour over 2 y in the Luquillo Forest Dynamics Plot (LFDP), a 16-ha permanent forest plot located in the subtropical wet forest of the Luquillo Mountains (Thompson *et al.* 2002). We describe the population structure and compare the growth rates and the spatial distribution of the sexes, using 15 y of LFDP census data. Based upon theoretical considerations of trade-offs between reproduction and other life-history traits we hypothesized that because females face higher costs of reproduction than males: (1) populations will be male-biased; (2) males should be more abundant in small size classes because they start reproduction earlier; (3) males should grow faster than females and become over-represented in large size classes; and (4) populations will exhibit SSS. We infer the latter for our site because of well-studied gradients in nutrients and water associated with soil type and topography (Johnston 1992, Soil Survey Staff 1995, Thompson *et al.* 2002), and variation in the light environment (Queenborough *et al.* 2007) caused by hurricane damage (Brokaw *et al.* 2004).

METHODS

Study site

The 16-ha Luquillo Forest Dynamics Plot (LFDP) is located in the El Verde Research Area (18°20′ N, 65°49′ W) in the Luquillo Experimental Forest, Puerto Rico (Thompson *et al.* 2002, Zimmerman *et al.* 1994). It is part of the Luquillo Long-Term Ecological Research (LTER) Program and the Center for Tropical Forest Science (CTFS) network of forest plots (Losos & Leigh 2004, Zimmerman *et al.* 2008). The LFDP is in the *Dacryodes excelsa* Vahl forest zone (below 600 m in the Luquillo Mountains; Ewel & Whitmore 1973). Rainfall at El Verde averages 3500 mm y^{-1}. March and April tend to have less rainfall, but all months have ≥ 200 mm. Daily average maximum air temperature is 25.2 °C, minimum is 20.5 °C, and the yearly average is 22.8 °C (Brown *et al.* 1983). This forest is classified as 'subtropical wet forest' in the Holdridge System (Ewel & Whitmore 1973). The plot topography has north-west-running drainages forming steep north-east- and south-west-facing slopes. Elevation ranges from 333 m at the northern end of the LFDP to 428 m at the south (Thompson *et al.* 2002). The soils are clays formed from volcaniclastic sandstone (Soil Survey Staff 1995) that vary from well-drained soils on the ridges to less well-drained soils on some slopes and valleys (Johnston 1992, Soil Survey Staff 1995). The present tree species composition and distribution on the LFDP strongly reflects the impact of past human disturbances in the 1920s, '30s and '40s that affected approximately 11 ha, leaving about 5 ha relatively free from human disturbance (Thompson *et al.* 2002). The Luquillo forest has a long history of hurricane disturbance as well. The plot was established in 1990, a year after Hurricane Hugo impacted the area, and Hurricane Georges struck the forest in 1998.

Every 5 y all self-supporting woody stems ≥ 1.0 cm dbh (diameter at 1.3 m from the ground) are tagged, identified, mapped and measured to assess growth, mortality and recruitment of new individuals (Thompson *et al.* 2002, 2004). We used 15 y of inventory data from censuses conducted in 1990, 1995, 2000 and 2005 to describe the population structure, growth rates and spatial distributions of the sexes of two dioecious trees in the LFDP, *Cecropia schreberiana* Miq. and *Dacryodes excelsa*.

Species

Cecropia schreberiana (Cecropiaceae) is a pioneer species of medium size (up to 21 m tall) found in the humid forest of Puerto Rico between 50 and 1300 m asl (Silander & Lugo 2000) that is currently abundant in the Luquillo Mountain forests because of recent hurricanes (Brokaw 1998). In the LFDP it is distributed relatively uniformly throughout the plot, but is somewhat more frequent in the more human-disturbed portion of the plot (Thompson *et al.* 2002). Most of the individuals recruited following Hurricane Hugo in 1990 (Zimmerman *et al.* 1994). *Cecropia schreberiana* flowers from November to May with a peak in February, and drops fruits from November to June, with a peak in April (Zimmerman *et al.* 2007). It is pollinated by wind and dispersed by birds and bats (Brokaw 1998, Silander & Lugo 2000).

Dacryodes excelsa (Burseraceae) is a large tree (30–35 m tall) dominant in the Luquillo Mountains between 200–900 m asl (Lugo & Wadsworth 2000). This species prefers ridges and upper slopes (Basnet 1992, Lugo & Wadsworth 2000). In the LFDP it is most often found in the southern portion that was relatively free of human disturbance, with scattered individuals throughout the remainder of the plot (Thompson *et al.* 2002). *Dacryodes excelsa* flowers from July to November, with the fruits maturing throughout the year and falling mainly during January to July (Estrada Pinto 1970, Zimmerman *et al.* 2007). It is likely pollinated by small insects, and the seeds dispersed by large birds and bats (J. Forero-Montaña pers. obs. 2006).

Flowering censuses

We conducted several censuses during the reproductive period of both species in 2006 and 2007. Censuses of *C. schreberiana* were conducted in June and October 2006 and in February and April 2007 corresponding to a single reproductive event. *Dacryodes excelsa* was censused in June and November 2006, and in May, August and October 2007 representing two consecutive reproductive events. In order to include all the potentially reproductive individuals, all stems $\geq$ 5 cm dbh for *C. schreberiana* and all stems $\geq$ 10 cm dbh for *D. excelsa* were censused.

Sexual expression

We identified the sexual expression of individual trees by examining the presence of fruits and flowers in tree crowns using binoculars. There are relatively few lianas in the forest (Rice *et al.* 2004) such that they did not severely limit our view. Males and females of *C. schreberiana* can be clearly distinguished by sight in the forest as the inflorescences are large and dimorphic. In contrast, flowers of *D. excelsa* are minute (approximately 4 mm across), and morphological differences between staminate (male) and pistillate (female) flowers are impossible to see in the tree crowns. It was also not possible to determine the sexual expression of individuals by collecting abscised flowers in plots or baskets located beneath the crown of each *D. excelsa* individual (Queenborough *et al.* 2007), as trees are abundant in the LFDP (64.8 stems $\text{ha}^{-1} \geq 10$ cm, Thompson *et al.* 2002) and their crowns are highly overlapping. Thus, we categorized the sexual expression of *D. excelsa* individuals based upon careful observations of patterns of flowering and fruiting during the 2 years of censuses ('reproductive category' hereafter). Trees that produced only flowers in both years and never fruits were considered 'males', and trees that produced fruits in both years were considered 'females'. Trees that were reproductive in a single year and produced abundant fruits were considered 'potential females' and trees that produced only flowers in a single year but no fruits as 'potential males'. Trees that produced abundant flowers in a single year but bore only a few fruits (< 10) were considered 'inconsistent males', and those trees that produced many fruits in one year, but only flowers in the other year were considered 'inconsistent females'.

Sex ratio

Deviations of a sex ratio (male/female) from 1:1 were tested using the G-test for goodness of fit (Sokal & Rohlf 1995). For *D. excelsa*, we conducted three separate analyses for each of the different reproductive categories, beginning, first, with only trees that showed consistent patterns of flowering and fruiting in both years of observation (males vs. females). Second, we added potential males and potential females to the first analysis and finally, in the third analysis, we added inconsistent males and inconsistent females to the previous two groups.

Size distributions

The size distributions of each sex (*C. schreberiana*) or reproductive category (*D. excelsa*) within species were described using the dbh recorded in the most recent census of the LFDP (2005–2006; Thompson *et al.*, unpubl. data). Differences in cumulative size distributions between males and females of *C. schreberiana* were tested using the Kolmogorov–Smirnov two-sample test (Sokal & Rohlf 1995). Differences among the reproductive categories of *D. excelsa* were examined using a one-way test, a procedure that is equivalent to a one-way ANOVA but does not require equal variances for all groups (Dalgaard 2002). Specific comparisons between groups were performed using a pairwise t-test (Crawley 2007, Dalgaard 2002). To correct for multiple comparisons we used Holm, which is a less conservative variant of the Bonferroni correction method (Crawley 2007, Dalgaard 2002).

Growth rates

Growth rates were calculated for each separate 5-y census period, from LFDP censuses starting in 1990, 1995 and 2000 and also over 15 y from 1990 to 2005. Annual growth rates were calculated as $((\text{dbh}_2 - \text{dbh}_1/\text{date}_2 - \text{date}_1) \times 365))$, where subscripts refer to consecutive censuses and time was measured in days. Differences in growth rates between males and females of *C. schreberiana* and among reproductive categories of *D. excelsa* were compared using ANCOVA (Quinn & Keough 2002). The response variable in each analysis was diameter growth rate with dbh as the covariate, and the explanatory factor was sex for *C. schreberiana* or reproductive category for *D. excelsa*. Before the analysis we checked homogeneity of variances in growth rates and dbh between male and female trees of *C. schreberiana* and among reproductive categories of *D. excelsa,* and used the homogeneity of variances in growth rates to test the hypothesis that one sex experienced greater habitat variability than the other.

To identify the best covariate, we examined the correlation between growth rate, and both initial and final dbh. The models for *C. schreberiana* were best fitted with final dbh, while the models for *D. excelsa* were best fitted with initial dbh. The ANCOVA models tested the effect of sex and size separately, in addition to their interaction. We compared a full model with an interaction term, and a reduced model without an interaction, and retained the interaction term when it was significant. A significant interaction term means that, for trees of a similar diameter range, the relationship between growth and dbh was different for each sex. To investigate differences among reproductive categories of *D. excelsa*, we simplified the model for the entire growth period 1990–2005 by combining groups with similar intercepts to find the model with the best fit. All models were compared with ANOVA (Crawley 2007). The growth rate and size data for *D. excelsa* were log-transformed to improve normality of the residuals. The P values of all the analyses were adjusted with the sequential Bonferroni test to reduce Type I error of multiple comparisons (Rice 1989).

Spatial segregation

Spatial segregation between male and female trees of *C. schreberiana*, and among the six reproductive categories of *D. excelsa*, were tested using interpoint distance methods based on Ripley's K (Ripley 1981) and Distance to Neighbour functions (Diggle 1983) following the methods of Barot *et al.* (1999). The spatial pattern analyses involved three complementary functions based on the following measurements: (1) the distance from each tree to its nearest conspecific neighbour (Diggle's G function); (2) the distance from a randomly chosen point to the nearest tree of the test species (Diggle's F function); and (3) the average number of conspecific trees located within a given distance of each sampled tree (Ripley's K function, Barot *et al.* 1999). Each function has a different sensitivity to a specific type of spatial distribution, therefore we compared the result of the three functions and if a conflict in the results occurred we selected the test with the highest power (for more details see Barot *et al.* 1999).

Tests to describe the spatial pattern and tests to infer spatial associations between two types of events (trees) were conducted separately using univariate and bivariate methods. The univariate methods test whether a group of trees exhibits a regular, random or aggregated pattern, and the bivariate methods test whether the relationship between two types of trees suggests association (trees growing in the same habitat), repulsion (trees growing in different habitats) or independence (no relationship to habitat). For *D. excelsa*, spatial pattern analyses were conducted for each reproductive category separately, then the spatial association between each of the reproductive categories was tested by conducting separate bivariate analyses for each pair of associations. The bivariate analyses of spatial association between two types of trees used versions of Diggle's G nearest neighbour and Ripley's K functions where the distances are calculated between trees of two groups (1 and 2), instead of trees within the same group. The nearest-neighbour relationship is not reciprocal (Barot *et al.* 1999), therefore G_{1-2} and G_{2-1} were evaluated separately for each pair of associations. This allows us to detect asymmetric relationships. For example, females could be spatially associated with males, but the spatial distribution of males could be independent from that of females. On the other hand, the bivariate K function is symmetrical and K_{1-2} and K_{2-1} are equivalent (Barot *et al.* 1999). Therefore, only one K test was performed for each pair of association. The spatial analyses were performed using Spatstat, a statistical package of the software R (Baddeley & Turner 2005, www.spatstat.org). Edge-effect bias corrections were performed for all spatial tests (Baddeley & Turner 2005). The test significance was evaluated using Monte Carlo procedures with 500 simulations to calculate rejection limits. The null hypothesis was rejected if the estimated function values lay outside the rejection limits. For Diggle's G function and Ripley's K function positive departures indicate a tendency towards aggregation/association, while negative departures indicate a tendency towards regularity/segregation (Baddeley & Turner 2005). For Diggle's F function the interpretation is the opposite, positive deviations indicate regularity/segregation, while negative deviations indicate aggregation-association (Baddeley & Turner 2005).

RESULTS

General patterns of reproduction

The *C. schreberiana* population included 1566 individuals, and although the censuses covered only one reproductive event, we are confident that our estimation of the reproductive pattern is robust because 75% of the trees flowered during the censuses, and 89% of the non-reproductive individuals were trees smaller than 15 cm dbh (Figure 1). The population of *D. excelsa* was composed of 1038 individuals. The majority of the trees (74%) were reproductive over the 2 y of observations; among those trees 74% flowered in both years, while 26% flowered in only 1 y. Within the reproductive categories, 46% were females (produced fruit over 2 y of observations), 24% were males (produced only flowers over 2 y), 6% produced fruits in only 1 y (potential females), 19% produced only flowers in 1 y (potential males), 3% produced many fruits in 1 y but in the next year were observed only with flowers

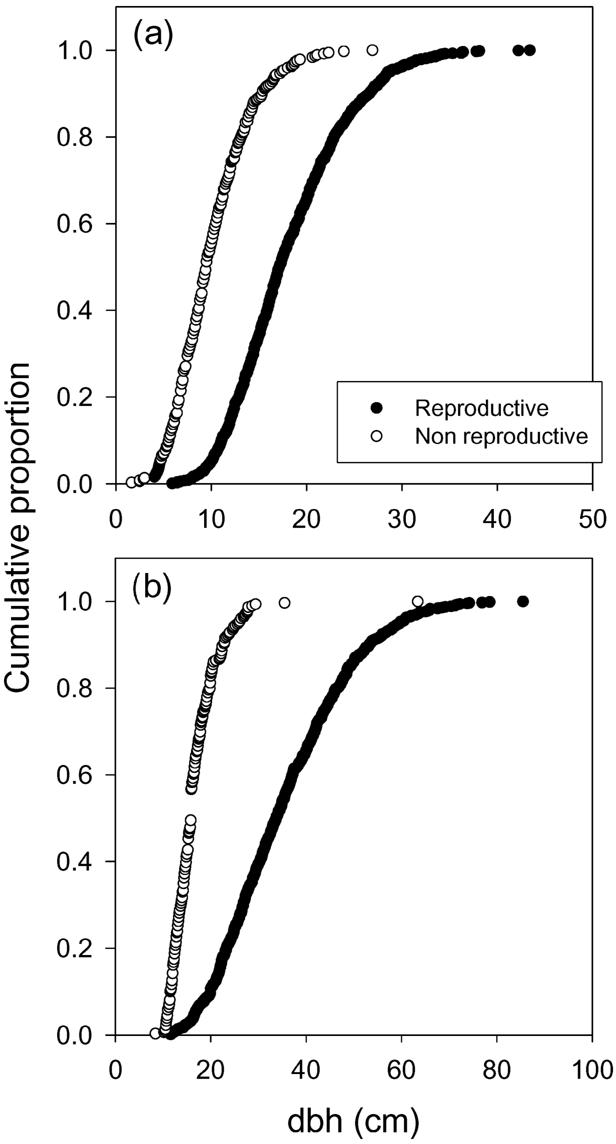

Figure 1. Cumulative distributions of stem diameter (dbh) for reproductive and non-reproductive trees in the LFDP. *Cecropia schreberiana*, trees ≥ 5 cm dbh (a), and *Dacyodes excelsa*, trees ≥10 cm dbh (b). Note different scales for the *x*-axes.

Table 1. Number of male and female trees and cumulative sex ratios (male/female) for *Cecropia schreberiana* and *Dacryodes excelsa* in the LFDP, Puerto Rico. G-test statistic and significance tests are shown. For *D. excelsa* we conducted three tests: (a) only individuals that consistently produced flowers or fruits over 2 y (males and females); (b) individuals that were reproductive in 1 or 2 y, (individuals in (a) plus potential males and potential females); and (c) all individuals that were reproductive at some time (individuals in (a) and (b) plus inconsistent males and inconsistent females).

Species	Male	Female	Sex ratio	G	P
C. schreberiana	660	595	1.11	3.37	> 0.05
D. excelsa[a]	180	310	0.58	34.9	< 0.001
D. excelsa[b]	315	372	0.84	4.73	< 0.05
D. excelsa[c]	355	417	0.85	4.98	< 0.05

(inconsistent females), and 2% produced mainly flowers, but in at least one of the censuses were observed with a few fruits (inconsistent males). Most of the non-reproductive individuals (80%) were trees smaller than 20 cm dbh (Figure 1).

Sex ratios

The cumulative sex ratio of *C. schreberiana* was not different from unity. In contrast, the cumulative sex ratio of *D. excelsa* was significantly female-biased and this biased sex ratio was significant for all three sex-ratio analyses, including the following: (1) only the trees that consistently produced flowers and fruits over the 2 y; (2) trees that were reproductive in 1 or 2 y and showed consistent sexual expression in both years; or (3) when all the reproductive trees were included using the criteria established in the methods. As more individuals were included in the analyses the sex ratio became less female-biased, but it was always significantly female-biased (Table 1).

Differences in cumulative size distributions

Cecropia schreberiana did not show significant sexual differences in size, as the cumulative distributions of male and female diameters were almost identical ($D = 0.126$, $P > 0.05$; Figure 2). In contrast, *D. excelsa* exhibited significant differences in size distributions among reproductive categories ($F = 44.4$, $P < 0.0001$). Pairwise comparisons indicated that males had the largest average diameter among all reproductive categories (mean dbh = 43.8 ± 14 cm). Inconsistent females (mean dbh = 38.4 ± 11.6 cm), females (mean dbh = 35.6 ± 11.2 cm) and inconsistent males (mean dbh = 32.7 ± 9.8 cm) formed the second group with the largest diameter. Size of inconsistent males, however, was significantly similar to potential males (mean dbh = 27.8 ± 10.7 cm) that formed a third group, the smallest, with potential females (mean dbh = 23.0 ± 9.1 cm).

Growth rates

Variances in growth rates between the sexes of *C. schreberiana* were not significantly different ($F = 1.014$, $P > 0.05$), but the reproductive categories of *D. excelsa* exhibited significant heterogeneity of variances in all census periods ($F = 0.711$, $P < 0.05$). Variances in growth rates of *D. excelsa* tended to be greater for male (mostly non-fruiting) categories than for female categories over all the census periods (not shown).

Table 2. Results for the ANCOVAs comparing differences in growth rates between male and female trees of *Cecropia schreberiana* and reproductive categories of *Dacryodes excelsa*. Bold P values indicate significant results after the sequential Bonferroni correction (Rice 1989) was applied.

	1990–1995			1995–2000			2000–2005			1990–2005		
	df	SS	P	df	SS	P	df	SS	P	df	SS	P
Cecropia schreberiana												
Sex	1	0.04	> 0.05	1	0.07	> 0.05	1	0.74	> 0.05	1	0.01	> 0.05
dbh	1	96.1	< **0.001**	1	56.9	< **0.001**	1	43.9	< **0.001**	1	98.2	< **0.001**
Residuals	1127	148		1140	141		1239	275		1127	50.5	
Dacryodes excelsa												
Group	5	0.21	< **0.001**	5	0.219	< **0.001**	5	0.375	< **0.001**	5	0.244	< **0.001**
dbh	1	0.785	< **0.001**	1	0.235	< **0.001**	1	0.301	< **0.001**	1	0.635	< **0.001**
Group × dbh	5	0.125	< **0.01**									
Residuals	748	7.84		765	5.07		755	6.08		753	4.08	

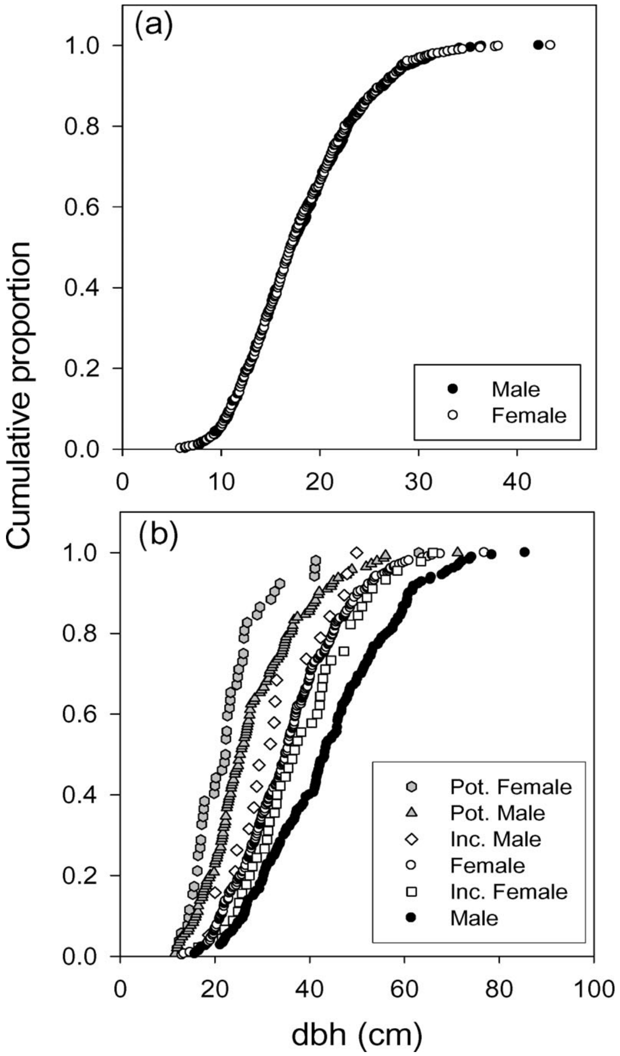

Figure 2. Cumulative distributions of stem diameter (dbh) for male and female trees in the LFDP. *Cecropia schreberiana*, trees ≥ 5 cm dbh (a), and *Dacyodes excelsa*, trees ≥ 10 cm dbh (b). Potential females (Pot. Females), potential males (Pot. Males), inconsistent females (Inc. Female) and inconsistent males (Inc. Male). Note different scales of the *x*- and *y*-axes.

Growth rates of *C. schreberiana* showed no significant differences between the sexes (Table 2). The best-fitting model had regression lines with identical slopes for male and female trees and explained more than 65% of the variation in growth ($F = 1096$, $R^2 = 0.66$, $P < 0.001$). (Table 2, Figure 3). For this species, however, there was a significant effect of diameter, with growth rates tending to increase with tree size (Figure 3).

Growth rates (log-transformed) of *D. excelsa* among reproductive categories were significantly different over all census periods. Mean annual growth of male groups exceeded female groups in all the census periods by more than 0.1 cm y^{-1}. For *D. excelsa* the effect of the covariate (log-transformed dbh) was significant, but in contrast to *C. schreberiana*, the slope of the regression between dbh and growth rate was small and negative (Figure 3), and explained only a small proportion of the variance in growth rates ($R^2 = 4$–11% among periods). For the first period (1990–1995) the best-fitting model included the interaction term between groups and size, while for the other periods, including the entire period of 1990–2005, an additive model was the best-fit model (Table 2).

The best-fitting model ($F = 39.35$, $R^2 = 0.168$, $P = 0.001$) indicated that males and inconsistent males exhibited similar growth rates and grew slightly faster than all other reproductive categories. Males were followed by inconsistent females, then by potential males and females, which formed a third statistical group, and lastly, by potential females, the group with the lowest growth rate (Table 3, Figure 3).

Spatial segregation between the sexes

There was no evidence for either species that trees of different sexes or belonging to different reproductive categories exhibited significant spatial segregation. Males and females of *C. schreberiana* exhibited significant aggregation and symmetrical associations, at all spatial scales (Figure 4). Similarly, there was a tendency towards aggregation and association for all *D. excelsa* reproductive categories. When the relationship between

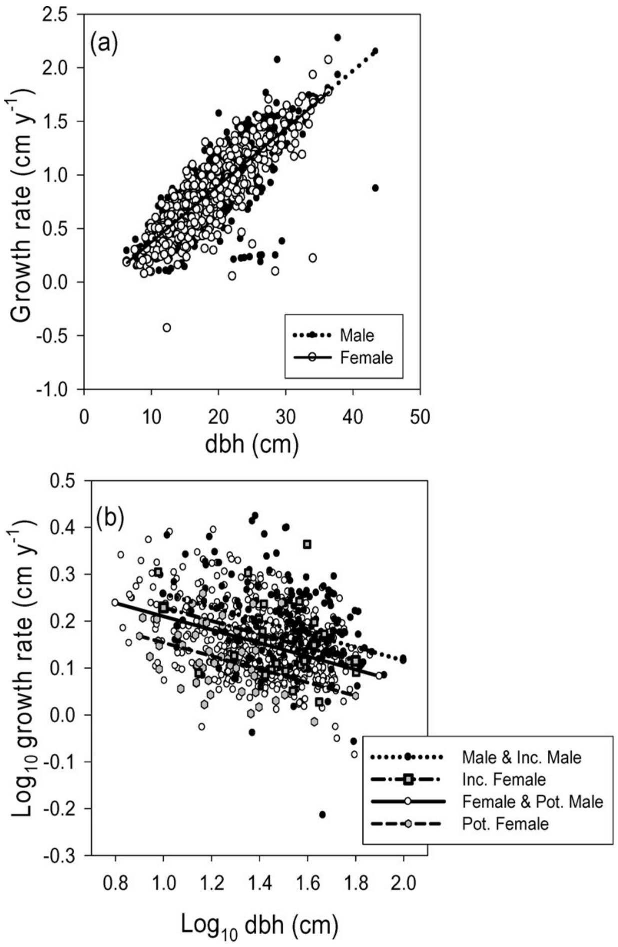

Figure 3. Growth rates of male and female trees for (a) *Cecropia schreberiana* and (b) reproductive categories (male, female, potential females, potential males, inconsistent females and inconsistent males) of *Dacryodes excelsa* in the LFDP from 1990–2005. Similar results were found for the other periods (not shown). Note different scales of the *x*- and *y*-axes for each species.

Table 3. Coefficients and significance test for the ANCOVA comparing differences in growth rates between male and female trees of *Cecropia schreberiana* and among reproductive categories of *Dacryodes excelsa* for the entire period (1990–2005).

Intercept	Estimate	SE	t value	P
Cecropia schreberiana				
Female	−0.159	0.024	−9.86	< 0.001
Male	0.011	0.014	0.795	> 0.05
dbh (Slope)	0.053	0.001	44.2	< 0.001
Dacryodes excelsa				
Female and potential male	0.352	0.019	18.6	< 0.001
Potential female	−0.056	0.011	−4.98	< 0.001
Inconsistent female	0.019	0.015	1.17	> 0.05
Male and inconsistent male	0.047	0.006	7.37	< 0.001
dbh (Slope)	−0.142	0.13	−10.7	< 0.001

males and females alone was tested it was significant and symmetrical at all spatial scales, but the relationships among each of the other reproductive categories were not significant nor symmetrical at all spatial scales, in part because these groups had small sample sizes. Because there was no evidence that males and females had repulsed distributions for either species, which would be consistent with the hypothesis of SSS, we did not investigate the habitat associations of the two sexes any further.

DISCUSSION

This study was conducted to understand the ecological implications and significance of dioecy for two canopy tree species, *C. schreberiana* and *D. excelsa*, that have different life-history strategies, and potential sex differences in size, growth rate and spatial distributions. Sex ratios of tropical dioecious trees frequently differ from equality, with male bias more frequently reported than female bias (Thomas & LaFrankie 1993). In our study *C. schreberiana* had similar numbers of male and female trees, while the sex ratio of *D. excelsa* was significantly female-biased. Although we were not able to directly identify the sex of *D. excelsa* trees, we conducted a sensitivity analysis of the sex ratio that took into account the limitations of our ability to determine tree gender. Our results for *D. excelsa* consistently indicated a female-biased sex ratio in the population.

Female-biased sex ratios in plants are uncommon and have been linked to the presence of heteromorphic sexual chromosomes, gametic selection (Stehlik *et al.* 2007) and apomixis (Thomas 1997). In the tropics, female-biased sex ratios have only been previously reported in three studies (Melampy & Howe 1977, Opler & Bawa 1978, Thomas 1997). In a lowland rain forest in Malaysia, a population of *Garcinia scortechinii* that consists entirely of pistillate individuals has the most extremely female-biased sex ratio reported in the tropics, and perhaps among all flowering plants (Thomas 1997). Embryological evidence suggested that female-biased sex ratios in *Garcinia* may result from apomixis (Thomas 1997). Apomitic plants are able to produce seeds without fertilization via adventive embryony that usually results in more than one seedling per seed (Thomas 1997). Although two seedlings per seed have been observed in *D. excelsa*, apomixis is not the likely explanation for the female-biased sex ratio detected here because this phenomenon occurs in < 1% of the seedlings in the LFDP (J. K. Zimmerman, per. obs.).

In tropical dioecious species, it has been frequently observed that males begin flowering at smaller sizes than females (Queenborough *et al.* 2007, Thomas & LaFrankie 1993). We found no differences in the size distributions of male and female *C. schreberiana*, but trees of *D. excelsa*, when grouped by pattern of fruit and flower production, showed significant differences in diameter, indicating

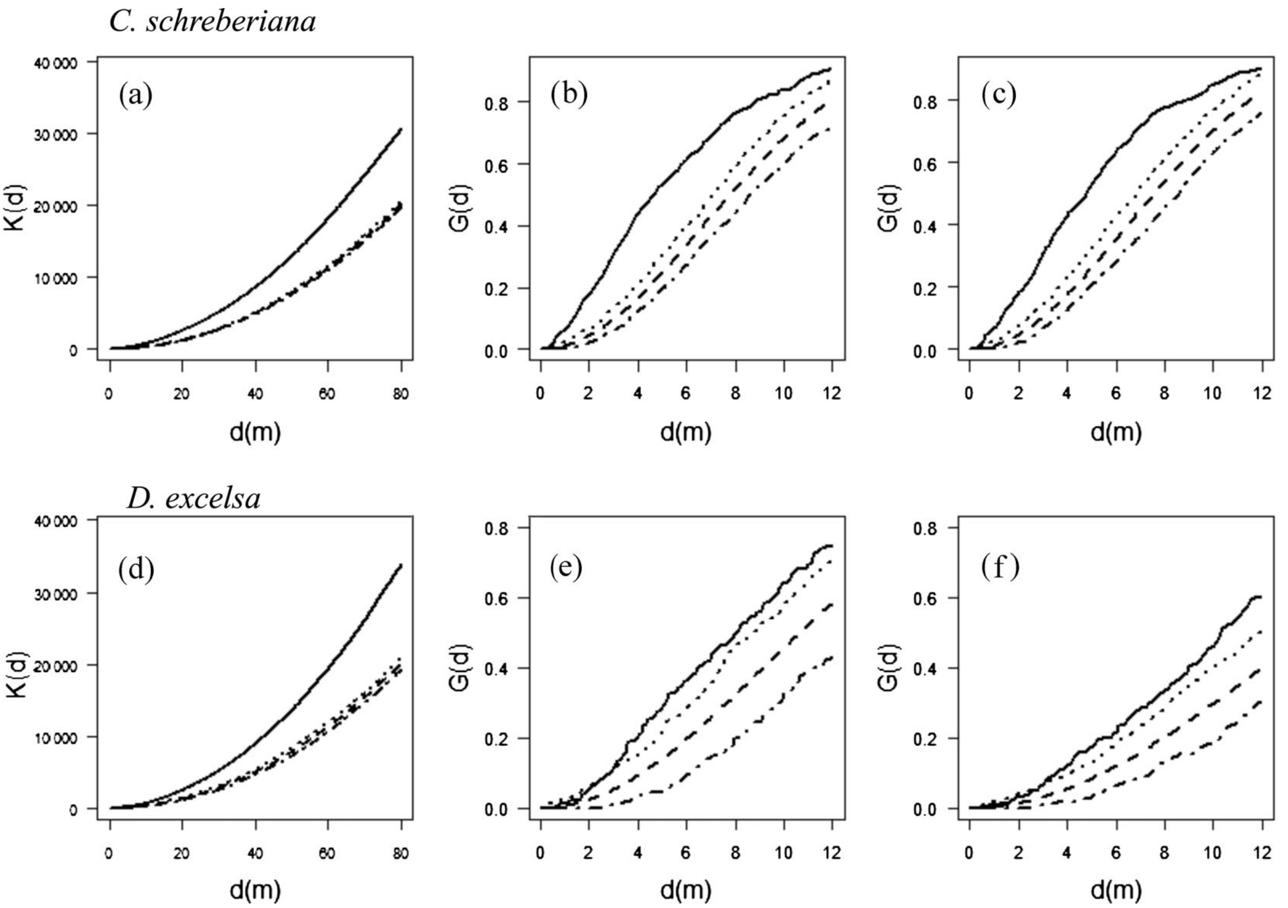

Figure 4. Spatial association between male and female trees of *Cecropia schreberiana* (above) and *Dacryodes excelsa* (below) in the LFDP, showing (a and d) bivariate Ripley's K analysis, (b and e) bivariate G function for males to females, and (c and f) bivariate G function for females to males. For *D. excelsa* only trees that exhibited consistency in the sexual expression over 2 years of observations are shown. Solid lines show test statistic, dashed lines show the theoretical function for an independent pattern (middle curve) and 99% confidence envelopes. Note different scales of the *x*- and *y*-axes for each species.

that size is an important factor determining reproductive activity. In a number of tropical dioecious trees larger individuals tend to flower more frequently than smaller trees (Bullock & Bawa 1981, Clark & Clark 1987, Nicotra 1998, Queenborough *et al.* 2007, Thomas & LaFrankie 1993). Similarly, in *D. excelsa*, trees that consistently produced flowers or fruits over the 2 y of observation were larger than trees that were reproductive only in a single year.

Cecropia schreberiana did not exhibit sexual differences in growth rates. The pattern of similar male–female growth rates in *C. schreberiana* suggests the presence of compensatory mechanisms that counteract the reproductive allocation effects (Nicotra 1999a, 1999b). Theory indicates that greater reproductive allocation by females should result in slower female growth rates. However, greater resource use efficiency and carbon assimilation rates, or more effective resource allocation may help females to compensate for the greater costs of reproduction (Nicotra 1999b). Moreover, the lack of sexual differences in *C. schreberiana* in size distribution and growth rates suggests that the sexes may have similar life expectancies. On the other hand, males of *D. excelsa* tended to grow faster (mean 0.1 cm y^{-1}) than females, representing 20% of the overall mean diameter growth rate of 0.5 cm y^{-1}. This result suggests that there are reproductive constraints that affect female trees more than males (Obeso 2002).

We tested homogeneity in the variances of growth rate of male and female trees of each species not only to verify the assumptions of the statistical analyses we used, but also to determine sexual differences in the variance of growth rate. Sexual differences in variance of growth rate would be expected if the sexes experienced different habitats or site quality. *Cecropia schreberiana* showed no significant sexual differences in the variance of growth rate, but in *D. excelsa* males and potential males exhibited higher variance than females and potential females, suggesting that male categories may experience a greater variation in site quality. Our spatial analyses, however, did not indicate that the sexes of our two study species occurred in spatially segregated habitats, thus SSS does not explain the greater variation in growth rate among male versus female trees of *D. excelsa* and other factors must be involved.

Spatial segregation of the sexes has been reported in plant species growing in heterogeneous environments with steep gradients in water, elevation, light, nutrients, pH or temperature (Bierzychudek & Eckhart 1988), and is more likely to occur in habitats where a critical resource is distributed along an extreme gradient (Nicotra 1998). Although in the Luquillo Experimental Forest the distribution of soil moisture and nutrients are related to slope and elevation (Johnston 1992), we found no evidence that this affected the spatial distribution of the sexes of either species. Most of the analyses indicated the opposite pattern in that the sexes or reproductive categories tend to be spatially aggregated. The absence of SSS among tropical dioecious shrubs has been attributed to the greater spatial and temporal variability of the light regime in the forest understorey (Nicotra 1998, Queenborough *et al.* 2007). Similarly, in the subtropical wet forest of the Luquillo Mountains hurricanes, tropical storms and droughts (Beard *et al.* 2005) may have created such variability in environmental conditions that it may have precluded the evolution of SSS in these canopy dioecious species.

The lack of sexual dimorphisms in size and growth rates reported here for *C. schreberiana* suggests that resources are not strongly limiting for either sex, or they support similar reproductive costs (Obeso 2002). Male-biased sex ratios and associated patterns of sexual dimorphisms in tropical rain forests have been primarily observed among subcanopy species that inhabit strongly light-limited environments (Thomas & LaFrankie 1993). *Cecropia schreberiana* trees are unlikely to become reproductive until they reach a position in the canopy where light becomes less limiting for growth and reproduction. The high population density of *C. schreberiana* in this forest results from post Hurricane Hugo (in 1989) recruitment (Zimmerman *et al*. 1994) and the forest canopy was again heavily damaged by Hurricane Georges (in 1998). Thus, the relatively open forest canopy prevalent during our study may have reduced the competition for light, such that the costs of reproduction for the different sexes were not readily apparent.

While males do not face the costs of provisioning seeds and associated structures, it is still not clear to what extent males and females differ with respect to reproductive costs (Opler & Bawa 1978). In some woody species males allocate more biomass to flowers than females (Bullock & Bawa 1981, Nicotra 1999a, Wheelwright & Bruneau 1992). In tropical rain forests the scarcity of anemophilous species has been attributed to the low effectiveness of this type of pollination system in environments with high humidity and dense vegetation that constrain the free movement of pollen through the air (Turner 2001). *Cecropia schreberiana* is wind-pollinated and males may produce large amounts of pollen to successfully compete for mates (Forero-Montaña & Zimmerman in press). Thus, high levels of pollen production in *C. schreberiana* may impose equivalent male and female reproductive costs.

The lack of sexual dimorphism in *C. schreberiana* may reflect its life-history strategy of rapid growth and early reproduction where any differences in reproductive costs between males and females may be only weakly expressed in the relatively competition-free period that follows hurricane disturbance. Conversely the sexual dimorphism of *D. excelsa* likely reflects the large difference in resources required to grow slowly in the forest understorey until eventually reaching the canopy where relatively few large seeds, when compared with pollen, are produced. The untypical female bias of *D. excelsa* in particular, needs further investigation, and some aspects will be covered by future studies of these and other dioecious species in this forest.

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