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## Sex ratio variation and spatial distribution of *Siparuna grandiflora*, a tropical dioecious shrub

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**Abstract** Populations of dioecious plant species often exhibit biased sex ratios. Such biases may arise as a result of sex-based differences in life history traits, or as a result of spatial segregation of the sexes. Of these, sex-based differentiation in life history traits is likely to be the most common cause of bias. In dioecious species, selection can act upon the sexes in a somewhat independent way, leading to differentiation and evolution toward sex-specific ecological optima. I examined sex ratio variation and spatial distribution of the tropical dioecious shrub *Siparuna grandiflora* to determine whether populations exhibited a biased sex ratio, and if so, whether the bias could be explained in terms of non-random spatial distribution or sex-based differentiation in life history traits. Sex ratio bias was tested using contingency tables, a logistic regression approach was utilized to examine variation in life history traits, and spatial distributions were analyzed using Ripley's  $K$ , a second-order neighborhood analysis. I found that although populations of *S. grandiflora* have a male-biased sex ratio within and among years, there was no evidence of spatial segregation of the sexes. Rather, the sex ratio bias was shown to result primarily from sex-based differentiation in life history traits; males reproduce at a smaller size and more frequently than females. The sexes also differ in the relationship between plant size and reproductive frequency. Light availability was shown to affect reproductive activity in both sexes, though among infrequently flowering plants, females require higher light levels than males to flower. The results of this study demonstrate that ecologically significant sex-based differentiation has evolved in *S. grandiflora*.

**Key words** Dioecy · Sex ratio · Spatial segregation · *Siparuna* · Sexual dimorphism

### Introduction

Populations of dioecious plant species frequently exhibit biased sex ratios among reproductive individuals. These biases generally favor males (e.g., Opler and Bawa 1978; Anderson and Levine 1982; Garcia and Antor 1995), though female biases also occur (e.g., Alliende and Harper 1989; Purrington 1993). Sex ratio biases may result from sex-based differences in life history traits. These differences can evolve in dioecious species in concert with the evolution of sexual dimorphisms (Meagher and Antonovics 1982). Spatial segregation of the sexes (SSS), the non-random distribution of the sexes with regard to physical space and availability of a limiting resource, also causes sex ratio bias at local scales in some species of dioecious plants (see review in Bierzychudek and Eckhart 1988). The dioecious tropical understory shrub *Siparuna grandiflora* has a male biased apparent sex ratio, but the role of ecological differentiation between the sexes in the establishment of this pattern is unknown. I examined the pattern of sex ratio bias in *S. grandiflora* to determine whether it could be related to spatial segregation or to differences in life history characteristics.

It is important to examine SSS in any analysis of sex ratio bias in a dioecious species, if only to demonstrate that segregation does not occur. SSS is generally regarded as a relatively uncommon cause of sex ratio bias (Bierzychudek and Eckhart 1988). To demonstrate SSS, a *reciprocal* sex ratio bias must be demonstrated. In other words, the reaction norms of male and female fitness must cross along the environmental gradient which the species naturally occupies (Houssard et al. 1994). If the sexes differ only in sensitivity to resource limitation, and a sex ratio bias is apparent only at one end of the environmental range, SSS is not demonstrated. In those species that do exhibit SSS, females

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generally prevail under high resource conditions, while males dominate in less favorable sites (e.g., Freeman et al. 1976; Lloyd and Webb 1977; Grant and Mitton 1979; Onyekwelu and Harper 1979; Fox and Harrison 1981; Vitale and Freeman 1986; Shea et al. 1993). However, in itself SSS may not be indicative of an overall population level sex ratio bias, and it is unlikely to be of adaptive significance in all observed cases.

In contrast to SSS, sex specific differences in life history traits are likely to be common causes of sex ratio biases (Meagher and Antonovics 1982). Precocial reproduction of one sex (often the males) has been shown to yield a bias in reproductive sex ratio that is most pronounced in the youngest or smallest size classes (Allen and Antos 1993; Garcia and Antor 1995). Therefore, prevalence of males in small size classes is often cited as evidence of male precociality (Opler and Bawa 1978; Bullock and Bawa 1981; Armstrong and Irvine 1989; Thomas and LaFrankie 1993). Different frequency of reproduction for the sexes may also result in an apparent sex ratio bias, as females of many dioecious species flower less frequently than males (e.g., Bullock and Bawa 1981; Bullock 1982; Meagher and Antonovics 1982; Bullock et al. 1983; Ågren 1988a; Oyama 1990; Cipollini and Stiles 1991; Ataroff and Schwarzkopf 1992; Ibarra-Manriquez and Oyama 1992; Thomas and LaFrankie 1993; Garcia and Antor 1995). In general, females of dioecious plant species face higher costs of reproduction than males (e.g., Putwain and Harper 1972; Wallace and Rundel 1979; Gross and Soule 1981; Meagher and Antonovics 1982; Lovett Doust et al. 1987; Ågren 1988b; Allen and Antos 1988, Popp and Reinartz 1988, Armstrong and Irvine 1989, Cipollini and Stiles 1991; Korpelainen 1992; Gehring and Linhart 1993; Cipollini and Whigham 1994; Garcia and Antor 1995). The stress imposed by relatively greater reproductive investment may lead to higher mortality rates among females, and may constitute another cause of a male-biased sex ratio – one that is most pronounced in larger or older size classes (e.g., Ågren 1988b; Bierzychudek and Eckhart 1988; Lovett Doust and Lovett Doust 1988; Allen and Antos 1993). Likewise, precociality and greater frequency of reproduction in males are likely to be related to the lower cost of reproduction for males.

Plants may incur a cost of reproduction because resources allocated to reproduction are not available for allocation elsewhere in the plant. As such, expression of differences in life history traits between the sexes may be affected by resource limitation. I examined the relationship between light availability and spatial distribution, and between light availability and sex-based differences in life history traits. I focused on the affects of light availability in particular, as plants generally decrease flowering frequency, delay reproduction and experience higher rates of mortality at low light. Light limitation is often severe in tropical rainforest understory (Chazdon and Fetcher 1984), and previous work indicates that at the study site, light limitation is more

important than soil resource limitation (Denslow et al. 1987). I expected that light mediated effects would be more acute in females, due to higher costs of reproduction (e.g., Hoffman and Allende 1984; Ågren 1988b; Houssard et al. 1994), and that females would require higher light levels to reproduce. However, given the level of spatial and temporal variation of light in forest understories, I did not expect differential effects of light limitation to result in spatial segregation of the sexes.

I examined patterns of sex ratio variation in *Siparuna grandiflora* over 3 years. By incorporating multiple years of data, I minimized the impact of annual variation in flowering on overall sex ratio of reproductive individuals. A spatially explicit study design was used to detect spatial segregation. To examine relationships between resource availability and sex-specific differences in life history traits, a logistic regression analysis was utilized. This novel combination of approaches allowed a rigorous examination of relative importance of factors underlying sex ratio variation. The specific objectives of the study were: (1) to determine whether the observed male sex ratio bias was representative of a significant deviation from 1:1, and whether the bias was consistent among sites and years; (2) to determine whether the bias was indicative of spatial segregation; or (3) arose as a result of light limitation, independent of spatial pattern; and (4) to determine whether precocial reproduction, differences in frequency of reproduction, or differences in mortality were mechanisms leading to sex ratio bias.

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## Methods

### Study site and species description

The study was conducted at the Organization for Tropical Studies La Selva Biological Station in Costa Rican lowland wet tropical forest (for detailed site description see McDade et al. 1994). *Siparuna grandiflora* (Kunth in Hub. & Bonpl., A. DC., syn *S. tonduziana*, Siparunaceae; S. Renner, unpublished work) is a common understory shrub in secondary forests of the Sarapiquí region of Costa Rica. Plants of both sexes flower at just over 1 m in stem length, and can reach over 5 m in height. In the absence of flowers, it is not possible to sex the plants, so sex cannot be determined for pre-reproductive individuals. At La Selva, flowering occurs primarily between January and May. The flowers are borne cauliflorously, and are 2–4 mm in diameter. Staminate flowers (male) do not bear vestigial pistillate structures, nor do pistillate flowers (female) bear any male structures. Although other *Siparuna* species are reported to be pollinated by Cecidomyid midges (Feil 1992), pollinators in *S. grandiflora* have not been observed. Fruits mature between June and December, and are dehiscent along irregular lines (Antonio 1983). The seeds are bird-dispersed (B. Loiselle, personal communication). There are no records of *S. grandiflora* or any other *Siparuna*, switching sex (S. Renner, personal communication; Antonio 1983, Feil 1992), nor did any individual change sex during the course of this study.

### Field methods

*S. grandiflora* is patchily distributed, and common only in secondary forests on residual soils. Prior to selecting sites for my study plots, I surveyed all such stands at La Selva Biological Station and

the nearby Selva Verde Ecologe. Plots were established only after I had determined that *S. grandiflora* individuals were present at sufficient numbers and density to allow spatial analysis. *A priori*, I decided that at least 50 individuals must occur in a given area for a plot to be established. Plots were approximately  $50 \times 50 \text{ m}^2$  (0.25 ha). One stand (LOC2) abutted an abandoned pasture and was too narrow to fit a square plot, so a  $30 \times 80 \text{ m}^2$  rectangle was used instead. In another stand (SSA2), plants were too widely spaced to get 50 individuals in the  $50 \times 50 \text{ m}^2$  plot, so the plot was extended to  $50 \times 75 \text{ m}^2$ . In all cases, plot boundaries were established before plants were mapped or sexed. All plots were located more than 10 m from established trails, and more than 85 m from the closest neighboring plot; the intervening areas were forest and/or abandoned pasture. In January 1994, three plots were established in secondary forest at La Selva Biological Station (Table 1). A fourth plot (the SV plot) was established at the Selva Verde Ecologe less than 10 km away. In 1995, two additional plots were set up at La Selva (Table 1). In total, data were collected from three of the sites (LOC1, LOC2, and SV) in all three study years. The SSA1 plot was excluded from data collection after the 1994 season, as it was the site of a destructive harvest in late 1994. Data were collected from the SSA2 and SJA plots in 1995 and 1996.

In each plot, all *S. grandiflora* individuals greater than 100 cm in stem length (hereafter called "mature-sized") were mapped using a hand-held compass to determine bearing and a meter tape to determine horizontal distance (to nearest 10 cm). Only flowering plants could be sexed, so plants were classified as male, female, or non-reproductive. Frequently, *S. grandiflora* branches from the stem at ground level, but as rhizomes do not occur it is possible to identify individual genets. All plants were identified and sexed again during the 1995 and 1996 flowering seasons. New mature-sized recruits were added to the study, and all deaths were noted. As plants could resprout from nearly total dieback, only those plants with completely dead stems and no sign of regrowth were classified as dead. In 1994, hemispheric canopy photographs were taken above the crown of each plant in the four plots. Photographs were taken again in five plots in 1995 (SSA1 was excluded). Photographs were analyzed digitally using the Solarcalc canopy photograph analysis package (Chazdon and Field 1987). The weighted canopy openness values calculated by Solarcalc were used as an index of total light availability. Total stem length was measured for each plant in 1995 as an indicator of plant size. Total stem length is preferable to height, basal diameter, or diameter at breast height in this species because of the prevalence of branches at and near ground level, and because stems are rarely vertical. As these tropical shrubs cannot be aged in the same way a temperate shrub might be, size is used as a surrogate for effective age.

In two of the plots, LOC1 and LOC2, individuals were censused weekly between January and June 1994. This census encompassed the flowering season, and therefore allowed the timing and duration of flowering to be determined on an individual basis. The other census method recorded only whether or not an individual flowered in a given year. The weekly census data were used to contrast flowering phenology for the sexes, and to examine variation in reproductive sex ratio within a single flowering season. In all years of this study flowering was nearly simultaneous in all sites.

## Analysis

### Sex ratio

Sex ratio of reproductively active individuals was analyzed on a site-by-site basis for each study year. Any plant that flowered during a given season was considered reproductively active in that year. As not all individuals flower in all years, sex ratio was also analyzed on a comprehensive basis, whereby any individual that flowered in at least one of the three years was included. The comprehensive approach provides a more conservative assessment of sex ratio bias, as it partially accounts for temporal variation. If sex ratio is assessed based upon a single flowering season, any propensity of females to flower less frequently than males could artificially accentuate a reproductive sex ratio bias (Bullock and Bawa 1981; Meagher 1981; Clark and Clark 1987; Cipollini 1991; Thomas and LaFrankie 1993).

Replicated *G*-tests were used to test for significant deviation from a 1:1 reproductive sex ratio within and among sites, for both the single year and 3-year cumulative data sets. Sites were used as replicates. The analysis yields a *G*-heterogeneity term which, like the interaction term of an ANOVA, can indicate whether bias is consistent among sites (Sokal and Rohlf 1981). To assess sex ratio variation within a single flowering season (1994), sex ratio bias was tested using individual *G*-tests for data from each weekly census. Sites were pooled for these analyses, but because weekly sex ratio data are repeated measures of the same plants, weeks were not pooled.

### Spatial distribution

Spatial distribution of individuals was analyzed using Ripley's *K*, a second-order neighborhood analysis that allows non-random spatial distribution to be examined as a function of scale (Ripley 1981; Diggle 1983; Mouer 1993). Ripley's *K* analysis is an extension of standard nearest-neighbor analysis, in that it utilizes a distribution based upon the distances among all possible pairs of plants rather than among *nearest*-neighbor pairs. This approach identifies the scales over which a non-random distribution is occurring, and can be used to develop hypotheses about spatial processes at specific scales. Furthermore, distributions of different classes of points – e.g., the distribution of males with regard to females – can be contrasted. The Ripley's *K* analysis has been used to examine distributions of trees and for intertype analysis of tree classes in a variety of forest types (Sternner et al. 1986; Getis and Franklin 1987; Kenkel 1988; Mouer 1993), but to my knowledge, this is the first application of Ripley's *K* to the analysis of spatial distribution of a dioecious species.

The software utilized for the Ripley's *K* analysis outputs *L*(*d*) (the Ripley's *K* statistic) as well as a 95% confidence envelope for each distance analyzed (Mouer 1993). The confidence envelope is generated using 100 Monte Carlo simulations of random distributions based upon plot-specific numbers of points and site dimensions. Each study plot was analyzed for distances up to half the length of the shortest side. When *L*(*d*) and the confidence envelope

**Table 1** Study plot dimensions, years included in study, and total number of mature-sized individuals found over course of study (*n*)

Name	Location	Length (m)	Width (m)	Area (m <sup>2</sup> )	Years in Study			<i>n</i>
					1994	1995	1996	
LOC1	La Selva	52	55	2860	√	√	√	70
LOC2	La Selva	30	82	2460	√	√	√	102
SV	Selva Verde	46	56	2576	√	√	√	58
SSA1 <sup>a</sup>	La Selva	51	50	2550	√			59
SSA2 <sup>b</sup>	La Selva	51	75	3825		√	√	68
SJA <sup>b</sup>	La Selva	45	54	2430		√	√	123

<sup>a</sup> Site included only in 1994, site of destructive harvest

<sup>b</sup> Site added in 1995

are plotted on the same axes, patterns of clumping and regularity become apparent. If  $L(d)$  exceeds the upper confidence interval for any distance class, those points are relatively closer together than expected, indicating clustering or clumping at those scales. If  $L(d)$  falls below the lower confidence interval for a distance class, the points are relatively further from one another than expected under a random distribution indicating regularity, repulsion or over-dispersal of points. Values of  $L(d)$  within the confidence envelope indicate random distribution of points at those scales.

Each population was first analyzed using the univariate approach, which included all individuals of reproductive size, and examined whether the population as a whole was randomly distributed in habitat space. All plants that flowered in at least 1 of the 3 years could be classified as male or female, all other plants were designated as non-reproductive for these analyses. The bivariate, or intertype analyses, were done for males relative to females and females relative to males. Only results from the analysis of male distribution relative to female are presented here, because the bivariate analysis of females relative to males produced an identical pattern. If *S. grandiflora* is spatially segregated, the Ripley's  $K$  analysis would indicate that males are further from females than expected at random, and the  $L(d)$  statistic would fall below the lower confidence interval over some range of the distances considered, indicating repulsion.

#### Logistic regressions

To examine relationships between resource availability and gender specific differences in life history traits, logistic regression analysis was utilized. This approach can be used to identify which of a set of hypothesized factors and mechanisms play a significant role in creating the sex ratio bias. Two models were employed to assess the effects of size and light on sex and reproductive activity. Total stem length was used as the measure of plant size. Preliminary analyses demonstrated that light availability in the current year was not the most important measure of light availability, rather, light availability (weighted canopy openness) from the preceding year was consistently more important, and thus was used as the measure of light in the models. All plants included in the analyses were reproductive in at least one year, and so could be identified as male or female. Because data for only 1 year were available for the SSA1 site, it was excluded from both models. A site factor was also included in both models.

The first model was designed to examine the effects of light availability, stem length, and frequency of reproduction on sex, as differences between the sexes in any of these factors could strongly influence sex ratio. The model 1 data set included all plants that were present in both 1995 and 1996, and flowered in at least 1 of the 2 years. Frequency of reproduction was classified as "1" if a plant flowered in both years, and as "0" if it did not.

The second model examined the effects of light availability, stem length, sex, and the past year's reproductive state on current reproductive state, where reproductive state is defined as either flowering or non-flowering. The model therefore allowed a detailed examination of factors affecting flowering frequency. Model 2 included all plants that were present for 2 consecutive years, and that flowered in at least one of the three years. To increase sample size in the second regression model, the data were collapsed to a 2-year set. Thus, "past and current" years can refer to either 1994 and 1995, or 1995 and 1996. Collapsing the data increases sample size, but also leads to representation of any plant that was present in all 3 years as two data points. Therefore, year was considered as a factor in the analysis of model 2.

Each model was analyzed first with all main effects and all interactions hypothesized to be of biological importance. This version of model 1 included terms for site, light, stem length, and some of the possible interaction terms (see results). Model 2 included terms for site, year, light, stem length, sex, and past reproductive activity, and interactions among these terms (see results). In order to arrive at the best fitting model with the fewest terms, non-significant interactions were removed from the models, beginning with the highest order terms. Those terms that explained

the least amount of the variance were removed first. Non-significant terms were removed until further removal compromised the fit of the model. A model was judged to have a good fit so long as the likelihood ratio chi-square was not significant at the 0.05 level. Analyses were conducted in SAS (PROC CATMOD, SAS Institute 1985).

## Results

### Sex ratio

The sex ratio of reproductive individuals in the six *S. grandiflora* populations was male-biased within each year as well as cumulatively (Table 2). The proportion of males among reproductives varied from 0.51 (not significantly different from 1:1) to 0.79 (a highly significant deviation), depending upon the site or year considered. The only site to show no significant sex ratio bias in any year was SSA2, even though cumulatively nearly 60% of the reproductives were male. SJA and LOC1 had male sex ratio biases in all 3 years, but the bias was significant in just 1 year; SV was significantly biased in 2 of the 3 study years; and LOC2 showed a significant bias in all 3 years. Based on the cumulative data set, LOC2, SV and SSA1 showed a significant male sex ratio bias. When all sites are pooled, for each year or cumulatively, the bias is highly significant. Because the  $G$ -heterogeneity statistic was not significant in any of the analysis, and because the direction of bias in every site and every year is the same, the sites are pooled in the following examinations of sex ratio. Site effects are, however, considered in the logistic regression analysis (see below).

Out of the total 480 plants in the study, 119 did not flower during any of the study years. Using the cumulative data set, the proportion of mature-sized non-reproductives (plants that did not flower in any study year) was positively correlated with the proportion of males among reproductives ( $n = 6$  plots,  $r = 0.8$ ,  $P = 0.054$ , data not shown), indicating that plots with more strongly male-biased sex ratios also had correspondingly greater numbers of non-reproductives (Ågren 1988b). Such a pattern may suggest that females are over represented among non-reproductives, and that they flower less frequently than males.

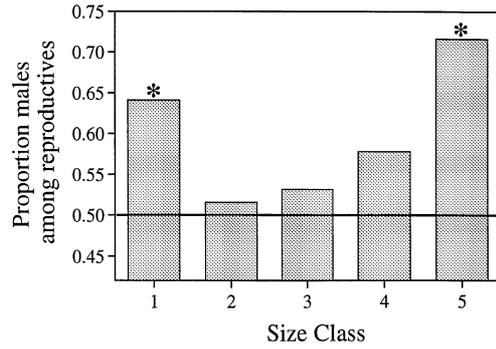
Examination of the reproductive sex ratio bias in the cumulative data set by size class revealed that the bias was significant in the extreme size classes – the smallest or largest plants – but not in the intermediate classes (Fig. 1). The bias in the smallest class suggests that males are precocial relative to females. The bias in the largest class may indicate either that females are on average smaller than males or that they face higher mortality upon or before reaching the largest size classes. The even sex ratio in intermediate size classes may serve as evidence of a 1:1 seed sex ratio for the species.

Too few individuals died during the course of the study to effectively examine patterns of mortality. There

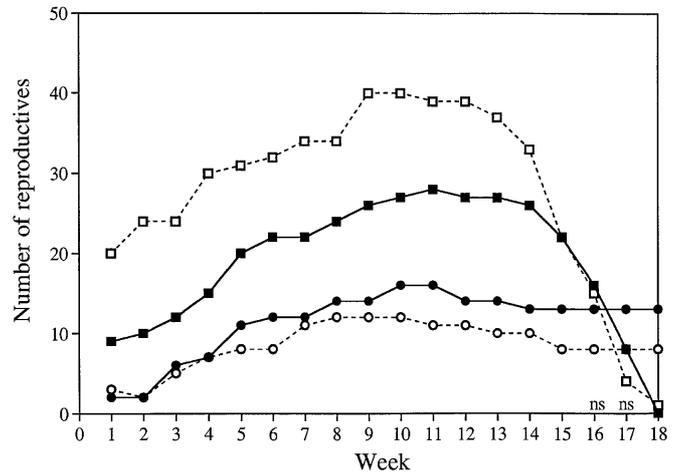
**Table 2** Sex ratios of reproductive individuals in each site in 1994, 1995, 1996, and cumulatively across years. The cumulative analysis includes all individuals that flowered in at least one year. The total number of reproductive individuals, for each year or cumulatively, is included (*n*) for reference

Site	1994				1995				1996				Cumulative				
	Proportion male	<i>n</i>	<i>G</i>	<i>P</i>	Proportion male	<i>n</i>	<i>G</i>	<i>P</i>	Proportion male	<i>n</i>	<i>G</i>	<i>P</i>	Proportion male	<i>n</i>	<i>G</i>	<i>P</i>	
LOC1	0.62	50	2.91	ns	0.70	44	1	7.58	**	0.63	40	1	2.53	59	1	2.89	ns
LOC2	0.72	57	11.35	***	0.75	44	1	11.51	***	0.74	46	1	10.96	67	1	8.06	**
SV	0.71	28	5.31	**	0.68	25	1	3.31	ns	0.79	14	1	4.86	36	1	5.59	*
SSA1	0.75	40	10.47	**	NA	45	1	1.81	ns	NA	44	1	1.46	40	1	10.47	**
SSA2	NA				0.60	101	1	0.49	ns	0.59	67	1	8.06	52	1	1.24	ns
SJA	NA				0.53				ns	0.67				108	1	0.01	ns
<i>G</i> -Total								24.7	***							27.87	***
<i>G</i> -Pooled								16.48	***							24.36	***
<i>G</i> -Heterogeneity								8.22	ns							3.51	ns

\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$



**Fig. 1** Sex ratio (proportion males among reproductives) of *Siparuna grandiflora*, by size class. Populations were pooled for this analysis. Each size class contains equivalent numbers of plants. Asterisks denote significant deviations from the expectation of a 1:1 sex ratio (*G*-test)



**Fig. 2** Number of reproductive male (squares) and female (circles) *S. grandiflora* in the LOC1 (solid symbols) and LOC2 (open symbols) sites over the course of a single flowering season (1994). Census began in January and ended with the end of the flowering season in May. All sex ratio biases are significant for the two sites combined, except for weeks 16 and 17 (marked *ns* on graph)

were 21 deaths out of a total 321 plants for which sex was known and that were present for more than one year of the study (excluding SSA1). More than half of these deaths were due to falling trees and branches. Of the 21 deaths, females accounted for 9, males 12, thus the pattern of mortality provides no evidence that females suffer higher mortality than males ( $P > 0.05$ , chi-square). This result is not affected by counting only deaths that were not associated with tree-falls.

The sex ratio among flowering individuals within a flowering season was significantly male-biased for all but the 16th and 17th weeks of the flowering season (Fig. 2). The bias is proportionally stable throughout the season, demonstrating that the phenology of the sexes is the same. The change in sex ratio bias during the last weeks of the flowering season results because males stop flowering while females begin maturing fruits. Thus, by

week 18, the sex ratio of reproductives was significantly female-biased. The data provide no evidence of differences between the sexes in duration of flowering activity (median duration of flowering was 14 weeks for females, 12.5 weeks for males,  $P > 0.05$ , Mann-Whitney  $U$ -test).

### Spatial analyses

A visual examination of the site maps suggests that within each population individuals are clumped in space (Fig. 3). The univariate Ripley's  $K$  spatial analysis supports this impression, demonstrating that *S. grandiflora* individuals are significantly more clustered in their habitat than would be expected at random (Fig. 4). For each site, the  $L(d)$  statistic falls well above the upper confidence interval for most if not all of the distances considered. The consistency of this pattern among plots suggests that plot sizes were adequate to describe the distribution of the species within its habitat.

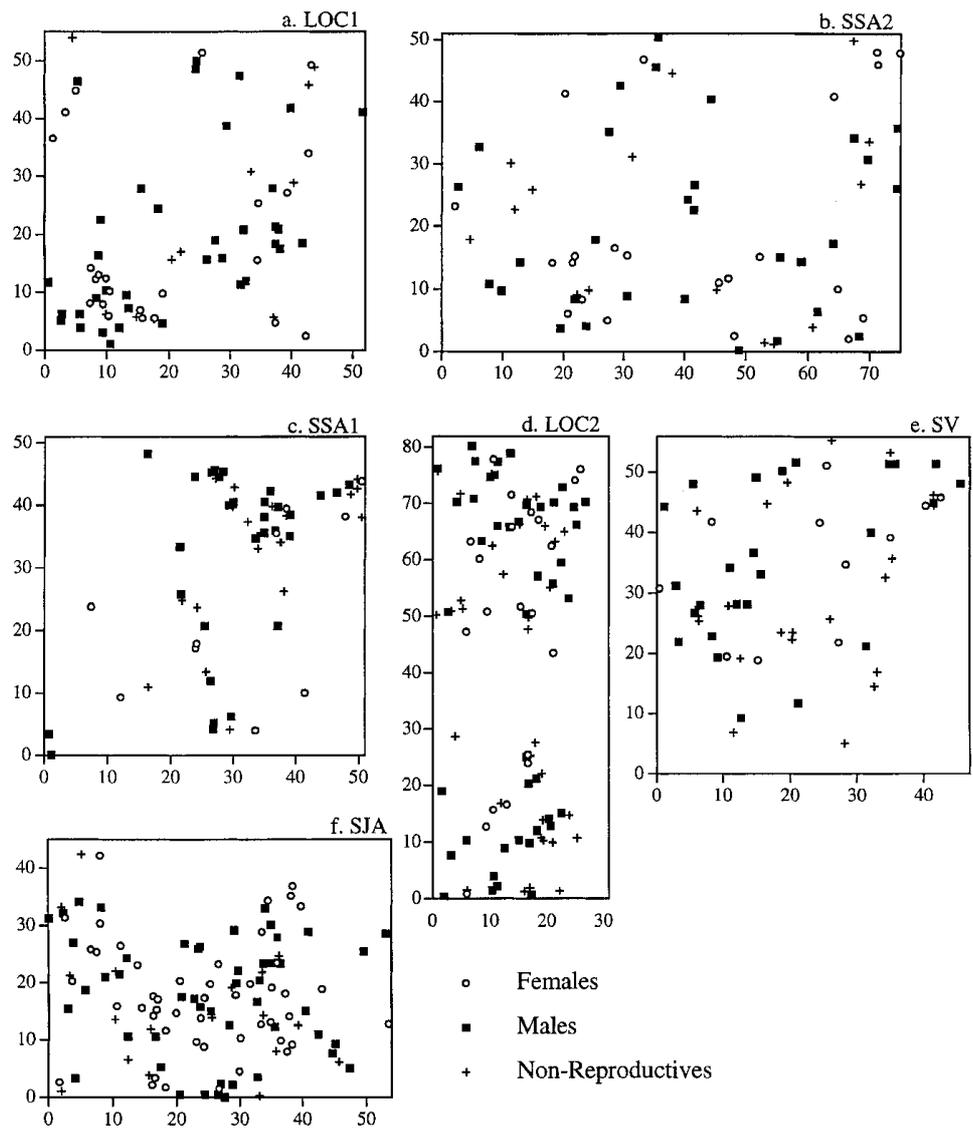
The bivariate analysis of the distribution of males with regard to females provided no indication of spatial segregation (Fig. 4). The sexes were not significantly over-dispersed or regularly distributed at any scale. Instead, the significant clumping demonstrated by the univariate analysis is reflected to a lesser degree in each of the bivariate analyses.

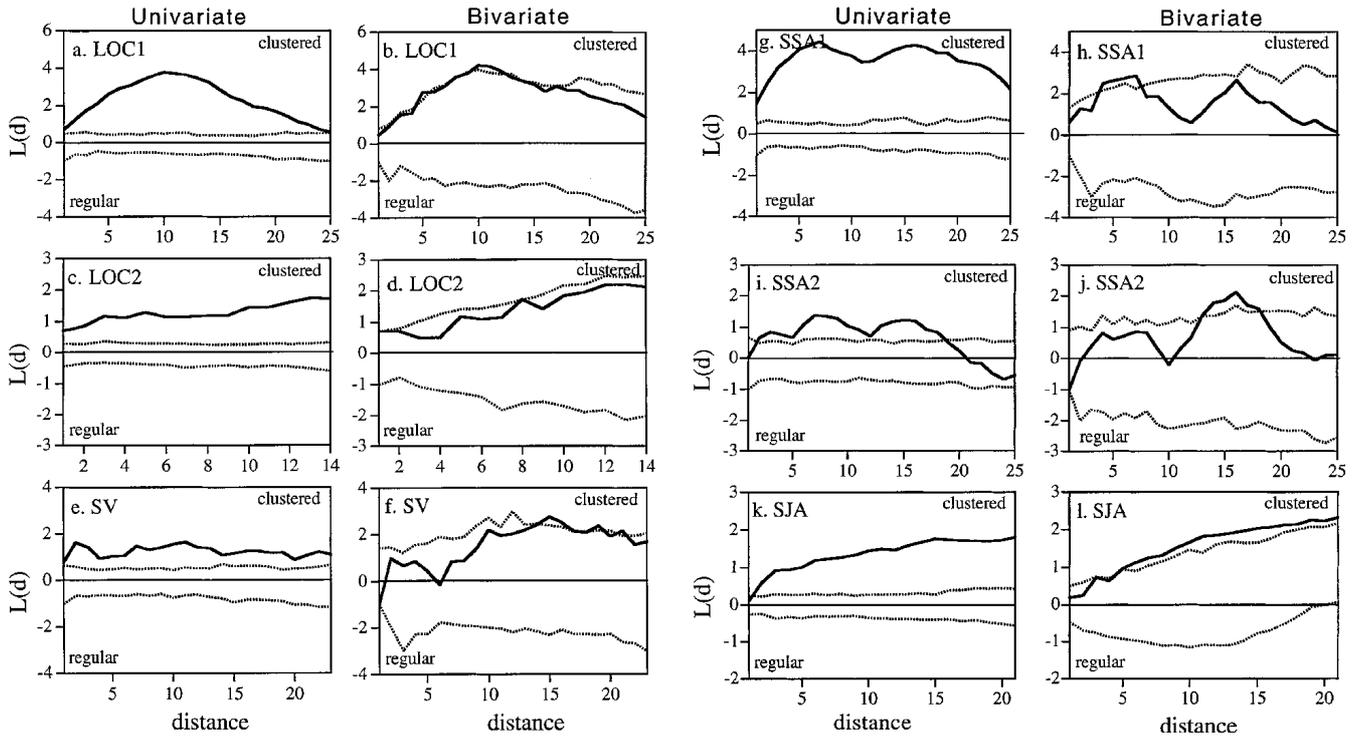
### Logistic regressions

Model 1 examined the relationship between light availability, stem length, flowering frequency, and sex of individuals (Table 3a). The best fitting model included terms for site, light availability, stem length, and flowering frequency, as well as the following interaction terms: site  $\times$  light; site  $\times$  stem length; site  $\times$  frequency; frequency  $\times$  stem length; and frequency  $\times$  light.

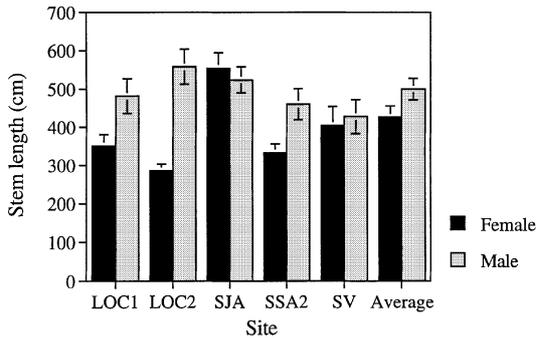
There was no significant relationship between sex and light; thus, the analysis provides no indication that the

**Fig. 3a–f** Maps of the six study plots. Axes are in meters. Position of graphics in figure does not represent location in forest





**Fig. 4a–l** Results of Ripley’s *K* analyses for each study plot. The *dark line* depicts the Ripley’s *K* statistic [*L*(*d*)], and the *stippled lines* are the 95% confidence interval generated by Monte Carlo simulation of randomly distributed points. The univariate analysis addressed the distribution of all mature-sized individuals, regardless of sex or reproductive status, at each site. The bivariate analysis examined the distribution of males relative to females. Note that any distance at which the *L*(*d*) statistic falls above the confidence envelope denotes clumping, and any distance at which it falls below the envelope denotes over-dispersal



**Fig. 5** Mean ( $\pm$  SE) stem length of male and female *S. grandiflora* plants by site

sexes are segregated with regard to light. The significant site  $\times$  stem length interaction indicates that males are on average larger than females, though the size difference varies among sites (Fig. 5). The significant site  $\times$  frequency interaction demonstrates that males were more likely to flower in both 1995 and 1996 than females, though again, this depended upon site. Overall, 72% of the males and only 39% of the females included

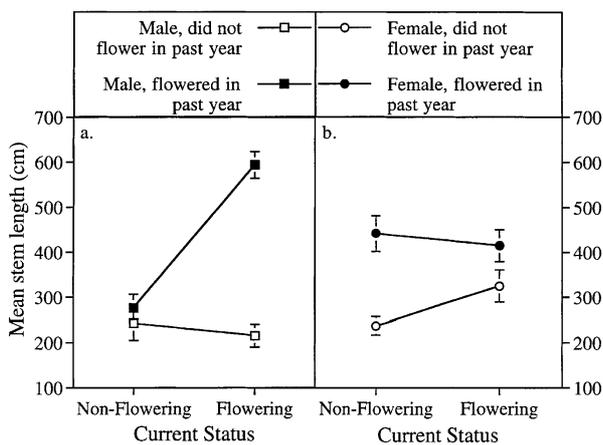
in the model 1 analysis flowered in both years. The significant frequency  $\times$  stem length interaction was primarily the result of a size difference between males that reproduced in both years ( $580 \pm 35$  cm), and males that did not ( $297 \pm 35$  cm). Females that reproduced in both years were approximately the same size as females that did not ( $439 \pm 53$  cm and  $417 \pm 34$  cm, respectively), and were of intermediate size relative to the males.

Model 2 investigated effects of light, stem length, sex, and past reproduction on current reproduction (Table 3b). Reproduction is here represented as flowering or non-flowering in a given year. The best fitting model included the main effects of year, site, sex, light, stem length, and past reproduction. Interaction terms for sex  $\times$  light; sex  $\times$  stem length; sex  $\times$  past reproduction and sex  $\times$  past reproduction  $\times$  stem length were included in the final model.

Model 2 yielded a significant light effect, a significant stem length effect, a marginally significant interaction for sex  $\times$  light, and a significant interaction term for sex  $\times$  past reproduction  $\times$  stem length (Table 3b). Flowering plants were found at higher light levels than non-flowering plants. Weighted canopy openness was  $8.30 \pm 0.2$  for flowering and  $7.54 \pm 0.34$  for non-flowering plants. Flowering plants were also significantly larger than non-flowering plants ( $509.3 \pm 17$  cm vs.  $335.5 \pm 21$  cm). The marginally significant interaction between sex and light resulted from non-flowering males being at lower light levels ( $6.53 \pm 0.41$ ) than flowering males ( $8.17 \pm 0.23$ ) or either class of females ( $8.35 \pm 0.5$  and  $8.59 \pm 0.4$  for non-flowering and flowering females, respectively).

**Table 3a,b** Maximum likelihood analysis of variance tables. **a** Model 1 examined the effect of site, stem length, light availability, and frequency of reproduction on sex of *Siparuna grandiflora* individuals. **b** Model 2 examined the effect of year, site, sex, stem length, light availability and previous reproductive activity on current reproductive activity of *S. grandiflora* individuals. See Results for description of model fitting approach. Terms in *italics* were included in the full model, but excluded from the final model

Source	<i>df</i>	Chi-square	Probability
<b>a Model 1 (dependent variable = sex)</b>			
Intercept	1	3.92	<b>0.048</b>
Site	4	0.95	0.918
Light	1	3.04	0.081
Stem length (cm)	1	0.20	0.656
Frequency	1	0.37	0.542
Site × Light	4	3.03	0.553
Site × Stem length	4	13.25	<b>0.010</b>
Site × Frequency	4	13.64	<b>0.009</b>
Frequency × Light	1	0.07	0.783
Frequency × Stem length	1	9.85	<b>0.002</b>
<i>Site × Frequency × Stem length</i>	—	—	—
<i>Site × Frequency × Light</i>	—	—	—
Likelihood ratio	262	289.92	0.114
<b>b Model 2 (dependent variable = reproductive activity)</b>			
Intercept	1	2.52	0.112
Year	1	0.72	0.398
Site	4	7.19	0.126
Sex	1	0.20	0.656
Light	1	5.89	<b>0.015</b>
Stem length (cm)	1	9.80	<b>0.002</b>
Past reproduction	1	0.73	0.392
Sex × Light	4	3.78	0.052
Sex × Stem length	4	0.51	0.474
Sex × Past reproduction	1	1.20	0.274
<i>Past reproduction × Light</i>	—	—	—
<i>Past reproduction × Stem length</i>	—	—	—
<i>Light × Stem length</i>	—	—	—
<i>Sex × Past reproduction × Light</i>	—	—	—
Sex × Past reproduction × Stem length	1	4.42	<b>0.036</b>
Likelihood ratio	400	412.88	0.318



**Fig. 6a,b** Reaction norm plot representing the significant sex × past reproduction × stem length interaction in logistic regression analysis (model 2) which examined effects on current reproductive activity. Points are mean ( $\pm$  SE) stem length. *Solid points* represent plants that flowered in the past year, *open points* are plants that did not flower in past year. **a** Males, **b** Females

The significant three-way interaction between the effects of sex, past reproduction and stem length in model 2 can be viewed as an elaboration of the frequency effect found in model 1. Males that flowered in both years were clearly larger than males that flowered in neither or only one year. Females that flowered in neither year

were smaller than females that flowered in either or both years (Fig. 6).

## Discussion

*S. grandiflora* populations exhibit a significantly male-biased sex ratio among reproductive individuals that is consistent within and among years, and that cannot be explained in terms of spatial segregation of the sexes. Rather, the results demonstrate that the sex ratio bias is the result of sex-related differences in life history traits, interacting with resource conditions. Such differences in life history traits may be viewed as an indication of the role of ecological differentiation in the evolution and maintenance of dioecy.

The relationship between sex ratio bias and the number of non-reproductives in the population suggested that females may be over-represented among non-reproductives and may reproduce less frequently than males. In conjunction with the relationship between sex ratio bias and the size of reproductive individuals, the data suggested that females flower at a larger size, and face higher mortality rates than males (Allen and Antos 1993). By using a logistic regression approach incorporating 3 years of data I was able to closely examine the mechanisms underlying these patterns, and the role of resource limitation in them.

The logistic regression analysis provided evidence that males reproduce more frequently than females (model 1, Table 3a). Model 1 also demonstrated that males are on average larger than females. This result is consistent with the earlier indication of the highest sex ratio bias in the largest size class (Fig. 1). Finally, model 1 showed that there is an interaction between plant size and reproductive frequency in males, but not females. Females were larger than infrequently reproducing males, and smaller than frequently reproducing males, but only in males was there a significant difference in size between frequently flowering and infrequently flowering plants.

Logistic regression model 2 also demonstrated an effect of size on frequency of reproduction in males (Table 3b). Males that flowered in both years were significantly larger than males that flowered in one year or males that did not flower in either year (Fig. 6). But, unlike model 1, model 2 also showed an effect of size on frequency of reproduction in females. Females that flowered in one or both years do not differ in size, but are on average larger than females that did not flower in either year (Fig. 6). Model 1 did not detect the size effect in females because it only included plants that flowered in at least 1 of 2 years. The sex-based difference in the relationship between size and reproductive frequency provides evidence that males are precocial relative to females and indicates that to flower even infrequently, females must be larger than males of equivalent reproductive frequency.

The logistic regression incorporating multiple years of data also increased my power to examine the influence of light availability on reproductive sex ratio. The analysis provided no evidence for differential distribution of the sexes with regard to light (model 1). Flowering plants of both sexes were, however, at higher light levels than non-flowering plants (model 2). Though only marginally significant, the sex  $\times$  light interaction is of interest, as it implies that flowering females are not at higher light levels than non-flowering females, whereas males exhibit such a difference. Note, however, that all plants included in the logistic regression analysis flowered at least once in the 3 years. Thus, the finding that both flowering and non-flowering females were at higher light levels than non-flowering males (model 2) indicates that to reproduce even once in the 3 years of this study, females required higher light levels than infrequently flowering males.

The study demonstrates that resource availability affects reproductive investment in *S. grandiflora*, but the effects are sex-specific. The sexes differ in the effects of both size and light on flowering frequency. Females have an apparently larger minimum size and higher light requirement for reproduction than males. The greater size and light requirements of females may have evolved to minimize the probability of mortality or loss of growth incurred by reproduction.

The relatively greater significance of the size effects, relative to light effects, may reflect correlations between

plant size and levels of stored reserves. Such stored reserves may be useful in buffering effects of variation in light availability over time. Thus, light effects on flowering may be mediated by impacts on allocation to storage. Using a similar approach, but in controlled experimental conditions, Houssard et al. (1994) did not find an environmental effect on flowering frequency in *Rumex acetosella*, a dioecious perennial herb. Effects of resource limitation may be expected to be more apparent in woody species than herbs, though effects of year to year environmental fluctuations on flowering frequency have been observed in the dioecious herb *Chamaelirium luteum* (Meagher and Antonovics 1982). In general, detecting effects of resource limitation on reproduction may require multiple years of data, and analyses that enable inclusion of multiple factors.

Given the low level of mortality observed in this 3-year study, I can draw no conclusions regarding the potential for differences in mortality between the sexes to result in sex ratio bias. It is conceivable that the under-representation of females in the largest size class could be due to females being innately smaller than males, rather than having higher mortality rates. But, if females were simply smaller than males, or spent more time in lower size classes due to slower growth rates, then they should be over-represented in the intermediate size classes, leading to a female-biased sex ratio at intermediate sizes. That the male bias pervades all size classes suggests instead that females are suffering higher mortality. In some dioecious species, higher mortality rates among females of dioecious species have been documented (Meagher and Antonovics 1982; Ågren 1988a; Bierzychudek and Eckhart 1988; Lovett Doust and Lovett Doust 1988), whereas in others they have not (Lovett Doust and Lovett Doust 1987; Oyama 1990; Bullock 1992; Allen and Antos 1993; Garcia and Antor 1995). Mortality is hard to measure in a perennial shrub such as *S. grandiflora*, because plants are more likely to become non-reproductive than to die, and because mortality rates are low. More frequently, I expect individuals are knocked back in size, perhaps even to ground level, and then resprout. As males can flower at smaller sizes, they might recover from such near death experiences and reach reproductive maturity again more rapidly than females.

An additional factor which could result in a sex ratio bias among reproductive individuals is a biased primary (zygotic) sex ratio (Charnov 1982; Bull and Charnov 1988). Generally, a 1:1 primary sex ratio is predicted for strictly dioecious species (Fisher 1930; Charnov 1975). Because sex cannot be identified for seeds or pre-reproductives in *S. grandiflora*, it is not possible to directly test this prediction. The available data, however, may provide suggestive evidence that the reproductive sex ratio bias in *S. grandiflora* is not the result of a biased primary sex ratio. If there were a primary sex ratio bias, it might be expected to be apparent in all sites, years and size classes or to change consistently with age. However, my data showed that the sex ratio approaches 1:1 in

intermediate size classes, a pattern which is consistent with a zygotic sex ratio of 1:1 (Fig. 1). The sex ratio also varied among sites and years, ranging from significantly to not significantly biased. Thus, the data provide no reason to suspect a primary sex ratio bias.

### Sex ratio and spatial distribution

Although about two-thirds of published studies testing for SSS demonstrate SSS, this frequency most likely reflects a bias toward investigating or reporting interesting patterns (Bierzychudek and Eckhart 1988). In actuality, SSS may occur in a much lower fraction of dioecious species, may be especially rare among those that do not switch sex, and may seldom have adaptive value (Bierzychudek and Eckhart 1988). If it occurs at all, adaptive SSS may be most likely to occur in environments where a critical resource is distributed along a gradient with stable extremes (Bullock 1982; Dawson and Bliss 1989). Perhaps this explains why the species that best demonstrate SSS tend to be riparian (e.g., Freeman et al. 1976; Dawson and Ehleringer 1993; Shea et al. 1993), given that riparian moisture gradients tend to be characterized by extreme but highly predictable environmental conditions. In contrast, forest understory light environments are both spatially and temporally variable (e.g., Chazdon et al. 1996). This may explain why woody understory species like *S. grandiflora* are less likely to demonstrate SSS (e.g., Bawa and Opler 1977; Melampy and Howe 1977; Hancock and Bringham 1980; Bullock 1982; Armstrong and Irvine 1989) (but see Cox 1981 where segregation according to soil nutrient content occurs).

Some studies that have investigated SSS have documented corresponding physiological differences between the sexes (Crawford and Balfour 1983; Dawson and Bliss 1989; Dawson and Ehleringer 1993). A correlation between spatial segregation of habitats and physiological traits which seem specialized to the favored habitat, may argue for adaptive SSS in these species. The results of this study, however, demonstrate that ecological differentiation in dioecious species is not a by-product of SSS, but a characteristic of the dioecious breeding system. The physiological differentiation that has been documented in spatially segregated species is likely to occur in non-segregated species as well, and in non-segregated species, may allow the sexes accomplish different reproductive functions with equivalent resource availability (e.g., Gehring and Linhart 1993; Gehring and Monson 1994; Laporte and Delph 1996).

As a final note on SSS, the Ripley's *K* analysis proved an excellent tool for analyzing distribution of the sexes of a dioecious species. This method may be particularly useful in investigations of SSS in species with clonal growth (e.g., Grant and Mitton 1979; Iglesias and Bell 1989). Because the Ripley's *K* analysis uses all possible pair distances to examine distributions as a function of scale, it is possible to determine the exact scale at which

SSS is occurring. By relating the size of genets to the scale of clumping indicated by a Ripley's *K* analysis, a researcher could determine whether segregation was occurring at scales beyond those explicable by clonality alone.

### Conclusions

The observed sex ratio bias in *S. grandiflora* represents a significant deviation from a 1:1 sex ratio. This bias was shown to be unrelated to patterns of spatial segregation or to non-random distribution with regard to light. However, an explanation of the sex ratio bias may be derived from several sex-based differences in life history characters and resource response characteristics, each of which is likely to be affected by sex-based differences in reproductive costs. In dioecious species, selection can act upon the sexes in a somewhat independent way, leading to differentiation and evolution toward sex-specific ecological optima. The results of this study demonstrate that such patterns have evolved in *S. grandiflora*, thereby raising questions about both the functional mechanisms underlying the observed sex differences, and the adaptive value of these differences. If the patterns illustrated in the present study are representative of characteristics which improve the fitness of the sexes, then selection on differing ecological optima would be important in the evolution and maintenance of dioecy.

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