Variation in Sexual Expression in *Jacaratia mexicana* (Caricaceae) in Southern Mexico: Frequency and Relative Seed Performance of Fruit-Producing Males

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ABSTRACT

Dioecy, the segregation of male and female structures among individuals, is widespread in tropical plants, encompassing 10–30 percent of species in some sites. In many cases, interindividual sex separation is not complete, as individual plants, although nominally dioecious, may produce both types of reproductive structures. A common form of this sexual variation is the production of female structures in otherwise male individuals, commonly referred to as fruiting males. Here we report the existence of fruiting males in the dioecious tropical tree *Jacaratia mexicana* (Caricaceae). We show that fruiting males can constitute up to 45 percent of all males in some populations of a tropical forest in Southern Mexico. In order to determine the functional significance of fruiting males for the breeding system of *J. mexicana*, we compared the relative performance of male- and female-borne seeds. Our results show that seeds from fruiting males are three times less likely to germinate and survive than seeds from female trees. Based on relative seed fitness data, and sex ratios in natural populations, we estimate that 6–15 percent of the genes contributed by fruiting males to the next generation are transmitted via ovules, meaning that morphological variation in gender is at least partially accompanied by functional gender variation. Finally, our seed fitness estimates for fruiting males suggest that fruiting males will not replace female plants in natural populations.

RESUMEN

El dioicismo, la distribución de estructuras masculinas y femeninas en dos tipos de individuos, es un fenómeno ampliamente distribuido en especies tropicales, llegando a abarcar 10-30 por ciento de las especies en algunos sitios. En muchos casos la separación de los sexos entre individuos no es completa, y un mismo individuo puede producir estructuras reproductivas del sexo opuesto. Una forma común de esta variación en el género es la producción de estructuras femeninas en individuos machos, los que comúnmente se denominan machos fructíferos. En este trabajo describimos la existencia de machos fructíferos en el árbol tropical dioico *Jacaratia mexicana* (Caricaceae). Encontramos que los machos fructíferos pueden constituir hasta el 45 por ciento de todos los árboles macho en algunas poblaciones de un bosque tropical en el Sur de México. Con el objeto de determinar el significado funcional de los machos fructíferos de *J. mexicana*, comparamos el desempeño relativo de semillas originadas en individuos macho y hembra. Nuestros resultados muestran que las semillas provenientes de machos fructíferos germinan y sobreviven con una probabilidad tres veces menor que las semillas provenientes de árboles hembra. Basados en la adecuación relativa de las semillas, así como en las proporciones sexuales en poblaciones naturales, estimamos que 6-15 por ciento de los genes contribuidos por los machos fructíferos a la siguiente generación son transmitidos vía óvulos, lo que significa que al menos parte de la variación en el género a nivel morfológico es acompañada por variación a nivel funcional. Finalmente, nuestras estimaciones de la adecuación de los machos fructíferos, vía semillas, sugieren que éstos no remplazarán a las plantas femeninas en poblaciones naturales.

Key words: breeding systems; dioecy; fruiting males; functional gender; reproductive biology; tropical dry forest.

DIOECY, THE SEPARATE DISTRIBUTION OF MALE AND FEMALE REPRODUCTIVE ORGANS onto two kinds of individuals (the male and female morphs), occurs in approximately six percent of flowering plants, and can be found in 10–30 percent of species in some tropical habitats (Bawa 1980a, Renner & Ricklefs 1995). It is thought that dioecy evolves from hermaphrodite ancestors through suppression of male or female reproductive structures in different individuals. In some cases, however, dioecy is "leaky" in the sense that occasionally individuals of one sex produce sexual structures of the opposite sex. In several of these near-dioecious species, sexual variation occurs in male individuals, while females are constant in sex. Sexual variation in individual male plants may occur by producing perfect (hermaphrodite) flowers in addition to staminate (male) flowers. Perfect flowers in male plants may result in fruit set, and the presence

of fruit-producing males in addition to male and female individuals in one species is generally referred to as subdioecy (Darwin 1877, Yamplosky & Yamplosky 1992, Sakai & Weller 1999).

Although the production of fruit in males is a widespread phenomenon (Darwin 1877, Ross 1982, Lloyd & Bawa 1984), we know relatively little about the consequences of this sexual variation for the ecology and evolution of near-dioecious species. The ecological and evolutionary role of fruit-producing males (hereafter FM) depends, in part, on the quality of the seeds produced by FM relative to females (Lewis 1941; Lloyd 1974a, 1976; Charlesworth & Charlesworth 1978; Ross 1978, 1982). Both quality and quantity of seed set determine the fitness achieved via ovule production, *i.e.,* ovule fitness. In turn, ovule fitness affects the ecological and evolutionary role of FM by influencing: (1) the extent to which morphological gender variation (*i.e.,* the production of perfect flowers in FM) translates into functional gender variation (*i.e.,* the ratio of genes transmitted to the next generation via ovules vs. pollen by FM); and (2) whether FM can evolutionary replace females, thus potentially causing nearly dioecious species to revert back to cosexuality.

Relative (FM/female) ovule fitness can be used to estimate the gender of FM on a functional basis. Throughout this paper we use *gender* to describe the quantitative variation in sex expression, following Lloyd (1980a). The functional gender of individual plants or groups of plants cannot be accurately assessed based on morphology alone. Previous studies show that, in sexually dimorphic species, morphologically hermaphrodite individuals may fail to reproduce via seeds, thus being functionally males (*e.g.,* Darwin 1877, Kalin Arroyo & Raven 1975). In order to complement morphological descriptions of gender, Lloyd has proposed the concept of functional gender (Lloyd 1974b, 1976, 1980a). Functional gender (G) is defined, for an individual or a set of individuals, as the ratio of genes contributed via ovules (*i.e.,* ovule fitness) to those contributed via pollen (Lloyd 1980a). Assessment of G in morphologically subdioecious taxa may allow distinguishing between subdioecy and dioecy on a functional basis. For instance, if FM contribute genes to the next generation exclusively through pollen ($G = 0$), then one may conclude that they are functionally male and that the population is functionally dioecious. On the contrary, if FM contribute genes through both ovules and pollen ($G > 0$) then the population may be better described as functionally subdioecious.

In addition, relative ovule fitness (*i.e.,* genes contributed via female gametes) can inform us about the evolutionary stability of near-dioecious breeding systems. Females can be evolutionarily maintained if relative ovule fitness is below a threshold value given by the type of sex determination (Lewis 1941). Under nuclear sex determination, relative ovule fitness below 0.5 is sufficient for the maintenance of females in the population (Lewis 1941; Charlesworth & Charlesworth 1978; Ross 1978, 1982).

In the present study we document morphological and functional gender variation in males of the tropical tree *J. mexicana* (Caricaceae), a species previously described as strictly dioecious in some localities (Bullock 1992). As a first step in understanding the ecological and evolutionary consequences of sexual variation in *J. mexicana*, we estimated a proxy of ovule fitness—relative quality of seeds from FM and females—and the population sex ratios. We discuss: (1) to what extent the production of perfect flowers in male plants (morphological gender variation) translates into male reproduction via ovules (functional variation in gender); and (2) whether FM in *J. mexicana* are likely to evolutionarily replace females.

METHODS

STUDY SPECIES.—The genus *Jacaratia* (Caricaceae) comprises six dioecious species of trees generally occurring in seasonally dry tropical forests from Mexico to northern Argentina (Badillo 1971, Olson 2000). *Jacaratia mexicana* A. DC. is a tree up to 25 m tall, with a trunk reaching up to 1 m diameter at breast height. It is distributed in Mexico and Central America at elevations up to 1500 m above sea level. Flowering in *J. mexicana* occurs during the dry season when trees have lost all their foliage (Bullock 1992). In Southern Mexico flowering takes place between November and February. This species has been previously described as dioecious with staminate and pistillate flowers produced in separate individuals (Baker 1976, Pennington & Sarukhán 1988, Bullock 1992). *Jacaratia mexicana* is sexually dimorphic for flower size and number. Sexual dimorphism occurs in other dioecious species in the Caricaceae including *Carica papaya* and *J. dolichaula* (Bawa 1980b). There are important morphological differences between male and female flowers of *J. mexicana*. In particular, female flowers have a length about three times as large as that of male flowers. This is reflected in the contrast in mass between them (pistillate flowers: mean dry mass = 265 mg; staminate flowers: mean dry mass = 15 mg). In addition, pistillate flowers are borne solitarily, while staminate flowers form small panicles (Bullock 1992) (Fig. 1). Staminate flowers of *J. mexicana* produce small amounts of nectar (*ca* 1.9 ml) with high amino acid content (Bullock 2002). Pistillate flowers do not produce nectar, although in *J. dolichaula* they secrete a stigmatic exudate that could attract pollinators. As in other species in the genus (*e.g.,* *J. dolichaula*), female flowers have fragrances similar to those of male flowers. Anthesis is nocturnal, and the main visitors are sphingid moths (Sphingidae), which visit both flower types (Bullock 2002; A. Aguirre, pers. obs.), and nocturnal bees (*Megalopta* spp., Halictidae), which visit mainly staminate flowers. The fleshy fruits grow from January to April; they are green when mature and have numerous seeds (ranging 47–676 seeds per fruit) (Pennington & Sarukhán 1988, Bullock 1992).

STUDY SITE.—The study site is located in the state of Morelos in South-Central Mexico, between 18°20′ N and 19°07′ N, and 98°37′ W and 99°30′ W. The state of Morelos comprises part of the Balsas river basin, and is considered to be one of the most important centers of endemism in Mexico (Rzedowski 1991). Seasonally tropical dry forest covers the majority of the state's area (60%) or about 2843 km^2 (Trejo & Dirzo 2000). The climate is warm-subhumid (mean annual temperature 22–26°C, and annual rainfall 800–1000 mm) (García 1988). The landscape is characterized by a series of alternating valleys and mountain ranges (Trejo & Dirzo 2000) (Fig. 2).
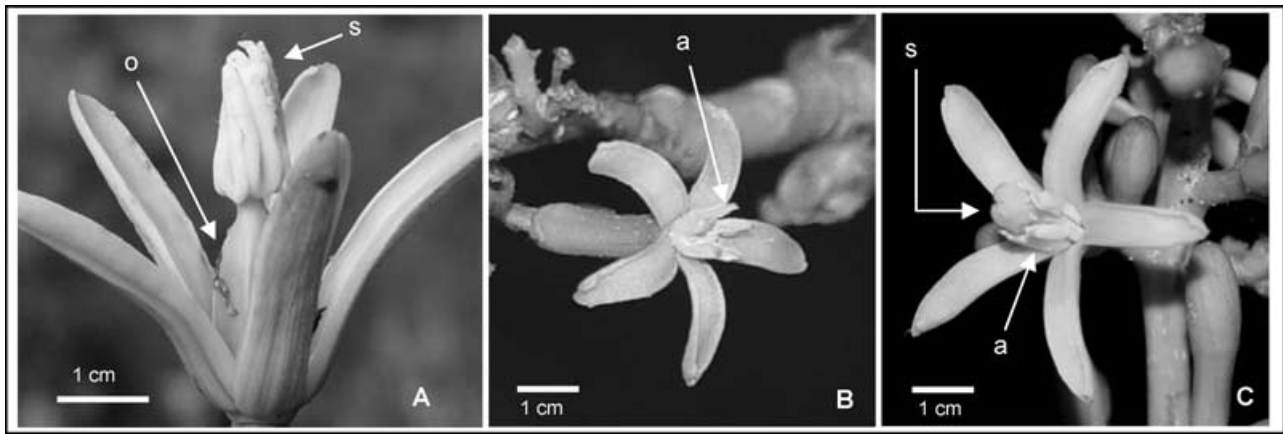
FIGURE 1. Morphology of the three sexual flower types in *J. mexicana*. (A) Female flower, (B) male flower , and (C) perfect (hermaphroditic) flower. Only female flowers occur in female trees, but both male and perfect flowers can occur in fruiting male (FM) individuals. The main sexual structures are marked in lower case: *o*, ovary; *s*, stigma, *a*: anthers.

VARIATION IN GENDER.—Preliminary observations of populations of *J. mexicana* in Central Mexico had uncovered the existence of perfect flowers in some male individuals (FM). In order to quantitatively document the occurrence of FM, four populations were surveyed on March 2005 by determining the presence/absence of perfect flowers and/or developing fruits. In addition to the number of FM per population, the number of females and males was recorded.

To determine differences among female and fruiting male individuals in relative fruit/seed size, seed germination, and seedling performance, flowering plants of both sexes were located and marked in December 2003. At the end of the fruiting season (April 2004), three ripe fruits were collected from each individual. In most cases, the three fruits collected per individual represented 20–30 percent of total fruit production per tree. Fruits were sampled from a total of 26 (13 FM and 13 female) individuals from four different and independent populations (Fig. 2). Populations were separated by a minimum distance of 1.84 km (Pop1–Pop2). Populations were comparable in that they were within the same vegetation type and at a similar elevation (900 m a.s.l. to 1211 m a.s.l.) and climatic conditions. Estimated population sizes are given in Figure 3. Fruit size (length) and weight, and number of seeds per fruit were estimated for each fruit. Viability was estimated by a flotation technique, consisting of placing the seeds in a water-filled container. Viable seeds sunk while inviable or damaged seeds floated and were discarded. A subset of 25 viable seeds per fruit was used for germination in the greenhouse. Germination proportion was evaluated 61 d after sowing the seeds, approximately a month after the emergence of the first seedling. Seedling survival was assessed 11 mo after planting as the ratio of surviving plants to germinated seeds.

Throughout this paper we use the term ovule fitness to refer to the rate of gene transmission to the next generation via female gametes. Relative performance of seeds, *i.e.*, germination and seedling survival, is one of the components that constitute ovule fitness. The calculations described below assume that relative seed performance can be used as a proxy of ovule fitness. This assumption implies that both FM and females produce equivalent numbers of seeds. To date

there is no quantitative data on total seed number among genders of *J. mexicana*. In the Discussion we briefly examine to what extent relaxing this assumption may affect our estimate of ovule fitness.

To calculate the functional gender of FM, we used Lloyd's (1976) estimates of the genetic contributions via ovules and pollen. Lloyd's calculation of genetic contributions uses information on both relative ovule fitness and population sex ratios to estimate the number of genes transmitted via either ovules or pollen by each sex type. We slightly modified Lloyd's (1976) approach because the original derivation averages seed set across males, and thus does not distinguish between fruiting and nonfruiting males. We found useful to calculate functional gender separately for pure males ($G_M = 0$) and for FM because we are interested in whether perfect-flower production is translated into transmission of genes via ovules. Pooling together fruiting and nonfruiting males into a single category would have biased our estimate of the extent in which morphological variation in gender represents functional variation. For subdioecious species functional gender of FM can be defined as the ratio of genes transmitted via ovules over those transmitted via pollen

$$G_{FM} = \frac{\bar{C}r}{(\bar{C}r + p) * {}^r\!/_{r + q}},$$

where $\bar{C}$ represent the average ovule fitness of FM relative to females, and p, q, and r the frequency of females, nonfruiting males, and FM, respectively ($p + q + r = 1$). The above derivation assumes random outcrossing and that all males, both fruiting and nonfruiting, contribute equally to the pollen pool.

RESULTS

DESCRIPTION OF PERFECT FLOWERS IN MALE TREES.—Both perfect and staminate (male) flowers are found in the inflorescences of some male trees. Perfect flowers are approximately the same size as staminate flowers (~1.2 cm long; Fig. 1). Perfect and staminate flowers
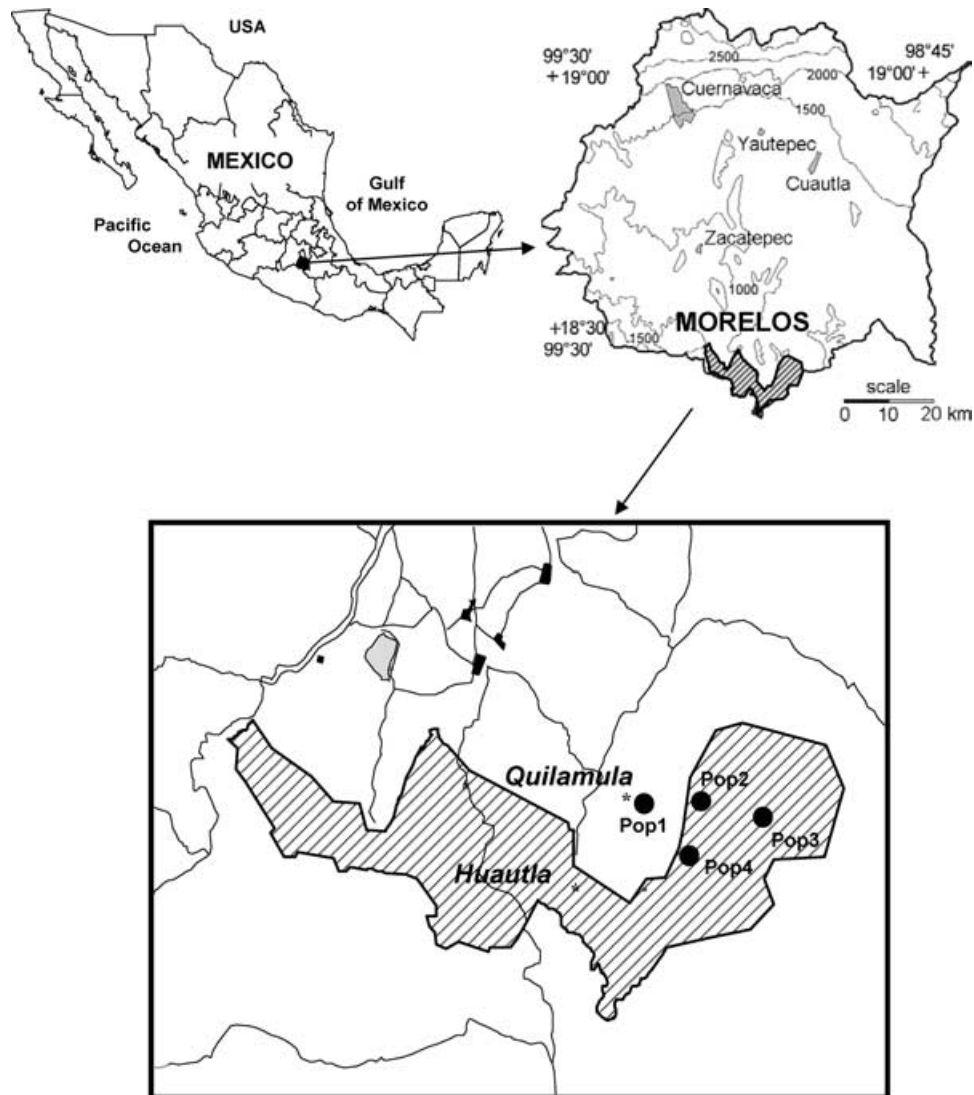
FIGURE 2.   Study area. Black circles indicate the populations of *J. mexicana* included in the present study (Pop 1–4). The dashed area in the inset marks the location of the Huautla Biosphere Reserve (Map modified from Trejo & Dirzo 2000).

release a similar fragrance, and anthesis of both types is nocturnal. Stamens of perfect flowers are colored similarly as staminate flowers. Perfect flowers do not produce nectar but they do produce abundant pollen. The ovary of perfect flowers is slightly swollen (approximately 7 mm in length). The 1-mm long style ends in three small stigmas. Sex of a particular flower in a FM cannot be easily determined at the bud stage since both perfect and staminate buds are of equivalent color, shape, and size.

FREQUENCY OF FRUITING MALES.—Sex ratios for each population were calculated as the proportion of male trees (both fruiting and nonfruiting) relative to the total number of individuals. Sex ratios in the four populations studied here were statistically indistinguishable from equality ($\chi^2 = 18.1$, df $= 3$, $P = 0.99$), meaning that females consistently represent 50 percent of reproductive trees

(Fig. 3). In contrast, the number of FM varied widely (Fig. 3). In two populations, approximately 40 percent of male trees (25% of all trees) had hermaphroditic flowers, while in the other populations FM were either rare (Pop4: <10% of male trees, <6% of all trees) or completely absent (Pop3) (Fig. 3). The frequency of FM when all populations are pooled together is 17 percent.

RELATIVE PERFORMANCE OF FRUITS AND SEEDS PRODUCED BY FEMALE AND FRUITING MALE TREES.—Fruits produced by pistillate flowers in female plants were significantly larger than those produced by perfect flowers in male plants (19.5 and 13.3 cm for pistillate and perfect flowers respectively; $t = 9.33$, df $= 74$, $P = 0.001$). Pistillate flowers produced 590.8 ± 27.8 (mean $\pm$ SE) seeds per fruit, while perfect flowers produced 232.6 ± 20.5. The weight of both fruits and seeds developed from pistillate flowers was consistently larger
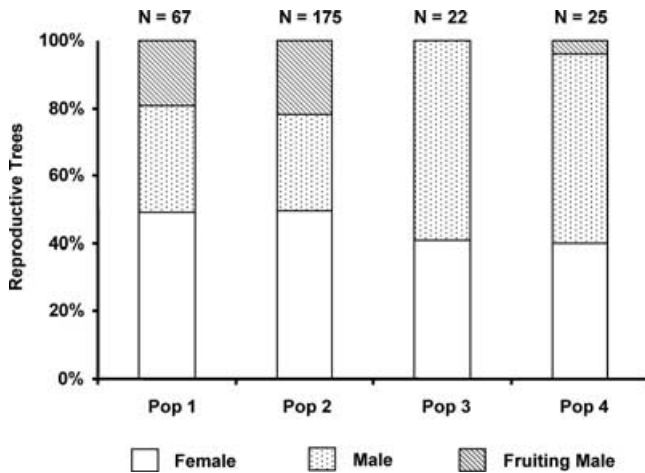
FIGURE 3. Proportion of sexual morphs observed in natural populations of *J. mexicana* (Pop 1–4). The number of individuals present in each population is shown above the bar.

DISCUSSION

MORPHOLOGICAL VARIATION IN GENDER.—In this study we have shown that some male plants of *J. mexicana* produce perfect flowers capable of setting viable seeds. In addition to these FM, both pure female and pure male individuals are also observed in natural populations, so we conclude that the morphological breeding system of this species is subdioecious rather than dioecious (*sensu* Sakai & Weller 1999). Moreover the presence of FM seems to be common, and their frequency in some populations reaches up to 45 percent of all male trees. Although FM are relatively common in *J. mexicana* we found that they may be completely absent from some populations. Presently we are unable to establish whether this wide variation in FM frequency is due to ecological differences between populations favoring different levels of gender variation (Barrett 1992, Delph & Wolf 2005) or to other factors including genetic drift. However, the relatively constant frequency of females across populations suggests that, in addition to genetic drift, other factors, perhaps ecological, may be affecting variation of FM (Case & Barrett 2001). Elucidation of the underlying reasons for such variation in the incidence of male plants with female flowers among populations is an important aspect that warrants further study. Work on this is in progress and will be reported elsewhere.

Sexual variation in dioecious species, despite being common among flowering plants in general (Ross 1978, Lloyd & Bawa 1984, Webb 1999), is rare within *Jacaratia* (Badillo 1971, Bullock & Bawa 1981, Piratelli *et al.* 1998). Badillo (1971) reports sporadic cases of ovary development in males of two of the six dioecious species in the genus *J. spinosa* (Aubl.) A. DC. and *J. digitata* (Poepp. et Endl.) Solms. In the case of *J. digitata*, male-borne flowers displaying ovary development have shorter and wider corolla tubes, and lack styles and stigmas (Badillo 1971). In contrast, a detailed study by Bullock and Bawa (1981) reported consistent expression of gender in the dioecious *J. dolichaula* (D. Smith) Woodson in Costa Rica. These authors followed numerous individual trees of *J. dolichaula* up to four consecutive years to detect gender variation within or between flowering seasons. Their study did not detect any changes in gender in either male or female trees, despite registering wide variation in flower and fruit production between years.

RELATIVE PERFORMANCE OF MALE- VERSUS FEMALE-BORNE SEEDS.— Despite the production of viable seeds in males of *J. mexicana*, our data show that male-borne seeds perform significantly worse than seeds from female plants. Differences in the relative performance of seeds from male and female individuals may arise from (1) inbreeding depression, (2) sex allocation trade-offs, or (3) floral sexual interference. First, because FM produce both ovule and pollen on the same individual, they have the potential to self-fertilize. Self-fertilized seeds may be of lower genetic quality due to the effects of inbreeding depression. Inbreeding depression is expected to be high in species with high rates of outcrossing due to their reduced ability to purge recessive deleterious alleles (Lande & Schemske 1985). The existence of pure females in *J. mexicana* indicates that outcrossing rates in this species are likely to be high. These high outcrossing rates should, in turn, facilitate the accumulation of

than for fruits derived from perfect flowers (mean fruit weight $F = 604.8$ g, FM $= 159.7$ g, $t = 13.60$, df $= 81$, $P = 0.001$; mean seed weight $F = 1.25$ g, FM $= 0.74$ g, $t = 10.85$, df $= 94$, $P = 0.001$; Fig. 4a). Seed size from pistillate flowers was almost double with respect to the seeds from perfect flowers (Fig. 4b). The proportion of vain seeds (an indirect measure of aborted seeds) was significantly lower among seeds from pistillate flowers (mean $F = 0.02$; mean FM $= 0.15$, $t = 5.13$, df $= 75$, $P = 0.0001$; t-test with square root transformed data).

Seed germination occurred between 18 and 33 days after the seeds were sown. The proportion of seed germination, and seedling survival was lower for seeds derived from perfect flowers than for seeds from pistillate flowers (seed germination, $t = 4.07$, df $= 31$, $P = 0.0001$; seed survival, $t = 1.95$, df $= 30$, $P = 0.01$, data were square root transformed; Figs. 4C and 4D). Among the surviving plants there were no significant differences in plant height, stem diameter, or leaf production between seeds originated from perfect or pistillate flowers (results not shown).

The relative performance of male-borne seeds ($\bar{C}$) was calculated by multiplying the mean values of seed germination and survival, and dividing it by the corresponding value for female-borne seeds. Seeds from FM were found to perform 30.4 percent as well as those from females. Thus, male-borne seeds are approximately three times less likely to germinate and survive than their female-borne counterparts.

FUNCTIONAL GENDER.—We used our approximation of ovule fitness ($\bar{C}$) based on relative seed quality to calculate separate estimates of the functional gender (G_{FM}) for each of the three individual populations with FM. Functional gender in the population with the fewest FM ($r = 6\%$) was only $G_{FM} = 0.067$, while in populations where FM are more abundant ($r = 20\%$) functional gender reached higher values $G_{FM} = 0.15$.
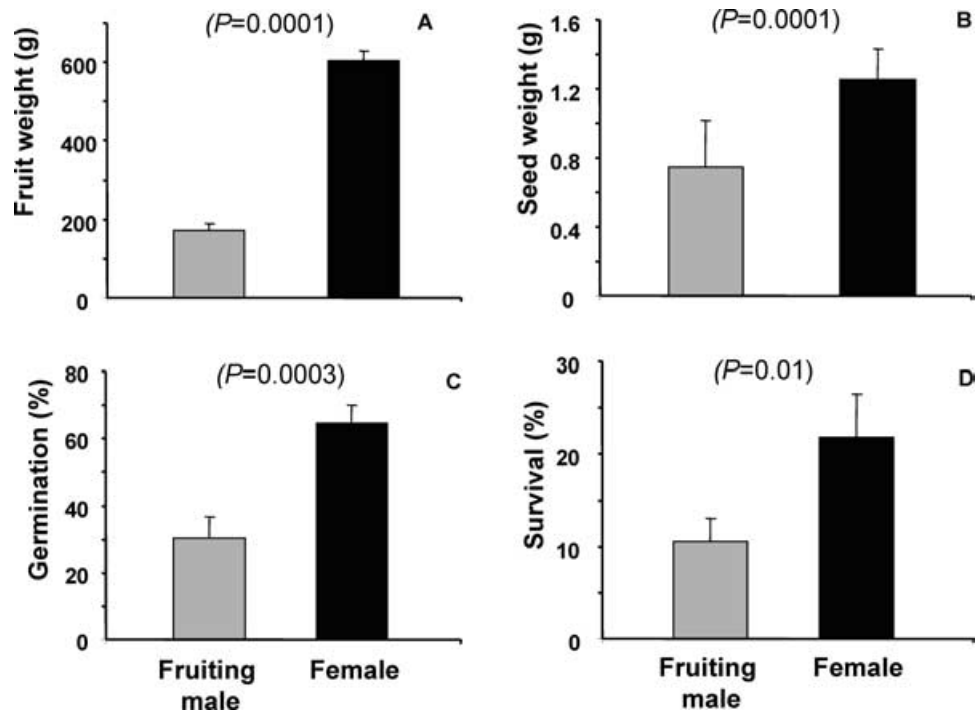
FIGURE 4. Differences in fruit weight (A), seed weight (B), percent germination (C), and percent survival (D) for fruits/seeds borne in male (*i.e.*, FM) or female trees.

inbreeding depression, *e.g.*, by reduced purging of recessive deleterious alleles occurring in a heterozygous state. A second mechanism for reduced seed performance in males is a trade-off between resources allocated to pollen, and those allocated to ovules and fruits (Darwin 1877). In *J. mexicana* pistillate, flowers are borne singly while perfect flowers are usually found in inflorescences among several other staminate flowers. Moreover, at the individual level male trees produce many more flowers than female trees. Resources allocated in males to large floral displays, at both the inflorescence and single-flower levels, may limit the resources availability for fruit and seed maturation thus reducing overall seed quality. Finally, a third mechanism is floral sexual interference (Bawa & Opler 1975, Webb & Lloyd 1986, Barrett 2002). Sexual interference may occur if male structures in perfect flowers limit the physical space for ovary development, and/or interfere with the process of pollen deposition. Sexual interference may be particularly acute in *J. mexicana* because pistillate and staminate flowers differ in both size and production of pollinator rewards. The intermediate morphology of perfect flowers may be suboptimal for fruit maturation and/or for the attraction of pollinators and the receiving of pollen. Further manipulative studies are needed to establish whether the disadvantage of male-borne seeds in *J. mexicana* derives from inbreeding depression, resource competition, floral sexual interference, or a combination of these mechanisms.

Our results suggest that regardless of the particular mechanism reducing the fitness of male-borne seeds, the ovule fitness of FM ($\bar{C}$) is small. However, our estimate of $\bar{C}$ ignores two potential mechanisms that could influence the relative number of genes passed through ovules. First, the larger floral displays observed in males of *J. mexicana* could result in the production of more fruits (Lloyd 1980b). Unfortunately, to date we lack quantitative data on the total number of seeds produced by male and female plants. Nevertheless, previous studies in other subdioecious taxa have demonstrated that fruit set tends to be higher for females than for males, despite the fact that males tend to have more flowers (*e.g.*, Ramsey & Vaughton 2001, but see Feil (1992) for an exceptional example in which fruits from male plants of *Siparuna echinata* produced more seeds than those produced by female plants). If FM of *J. mexicana* indeed produce less fruits than females then their ovule fitness will be lower than our estimate of 30 percent. Second, if seed set in females is limited by the availability of either mates or pollinators, FM could have higher seed production because the co-occurrence of both sexes in perfect flowers facilitates fertilization. Nevertheless, the advantages of reproductive assurance in FM could be diminished if individual plants reproduce asexually (Baker 1955). Piratelli *et al.* (1998) have reported both agamospermy and vegetative propagation in *J. dolichaula*.

FUNCTIONAL GENDER.—Establishing the relative ovule and pollen contribution of FM, *i.e.,* their functional gender (G_{FM}), is equivalent to asking whether *J. mexicana* behaves as functionally dioecious or subdioecious. Our results suggest that FM of *J. mexicana* contribute between 6 percent and 15 percent of their genes via ovules relative to pollen. Thus, our estimates of G_{FM} suggest

that morphological subdioecy in *J. mexicana* represents functional subdioecy.

EVOLUTION OF DIOECY VERSUS COSEXUALITY.—In functionally subdioecious taxa, the ovule fitness of FM can be used to estimate whether FM can replace females (Lloyd 1974a; Charlesworth & Charlesworth 1978; Ross 1978, 1982). If FM have an ovule fitness ≥ 0.5, and assuming that sex determination is nuclear, then selection will drive females to extinction and the species will revert to cosexuality (or to androdioecy, *i.e.*, production of staminate and perfect flowers in different individuals) (Charlesworth & Charlesworth 1978). Our results based on the performance of male- and female-borne seeds show that ovule fitness of FM ($\sim$30%) is below this threshold. This result is in itself sufficient to explain the evolutionary maintenance of females in this species.

EVOLUTION OF SUBDIOECY.—Subdioecy is usually considered a transitional nonadaptive stage in the evolution toward or away from dioecy (Charlesworth & Charlesworth 1978; Ross 1978, 1982). However, at least in some cases subdioecy may constitute an adaptive reproductive strategy. The adaptive explanation for seed set in males is that it allows individuals to take advantage of abundant resources when they become available (Ramsey & Vaughton 2001, Delph & Wolf 2005). According to this hypothesis, individual males growing in resource-limiting conditions benefit from reproducing exclusively through the male pathway, while males in more resource-abundant environments increase their fitness by reproducing through both male and female functions. This scenario assumes that fitness returns through male function switch from linear or accelerating in resource poor environments to decelerating when resources become abundant, and that investment in female structures in males compensates for any losses through male reproduction and survival (Ramsey & Vaughton 2001).

At present, we are unable to determine whether fruit production in males of *J. mexicana* represents a transitional stage or instead represents a stable reproductive strategy. Future studies are necessary to establish the existence of a trade-off in male individuals between seed set and male reproduction, or between seed set and future reproduction and survival. Additionally, surveys of male trees across multiple reproductive seasons could help to determine to what extent fruit production is a plastic trait. Finally, it remains to be tested whether diminishing returns through male function with increasing resources favor a switch from male to female reproduction under favorable environmental conditions as predicted by adaptive hypotheses for the evolutionary maintenance of subdioecy (Ramsey & Vaughton 2001).

ACKNOWLEDGMENTS

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