INBREEDING DEPRESSION IN ANDRODIOECIOUS POPULATIONS OF DATISCA GLOMERATA (DATISCACEAE)[1]

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Several workers have suggested that the rarity of androdioecy (the presence of males and hermaphrodites in a breeding population) in nature is due to the large fitness gain required by male plants in order to be maintained by selection. As part of an ongoing investigation of this hypothesis, we tested the effects of selfing on fitness in functionally androdioecious populations of Datisca glomerata. We compared progeny from self-fertilizations, cross-fertilizations with pollen from male plants only, cross-fertilizations with pollen from hermaphrodite plants only, and open-pollinated flowers for several measures of progeny fitness including seed weight, germination rate, and seedling weight. Significant inbreeding depression was observed for androdioecious populations of D. glomerata for both seed and seedling weights. However, no significant differences were observed across treatments for seed germination percentages. The observation of significant levels of inbreeding depression in this study, combined with prior evidence of threefold greater pollen production by males, may at least partially account for the large fitness increase required by males to be maintained by selection.

Androdioecy (the presence of males and hermaphrodites in a breeding population) is a rare reproductive system in plants. In fact, Charlesworth (1984) questions whether androdioecy actually exists in nature and notes that most putative androdioecious species are functionally dioecious or subdioecious (e.g., Anderson, Overal, and Henderson, 1988). In other cases, monoecy or andromonoecy has been mistaken for androdioecy (see Charlesworth, 1984). For example, Ricinocarpos pinifolius, although considered androdioecious by Thompson et al. (1989), displays a continuous distribution of floral gender, and would be best categorized as simply monoecious.

The apparent rarity of functional androdioecy is probably due to the large fitness gain required by male plants in order to be maintained by selection (Lloyd, 1975; Charlesworth and Charlesworth, 1978; Charlesworth, 1984). For male fitness to become equal to that of hermaphrodites, male plants must have an increase in male fertility at least double that of hermaphrodites. An even greater advantage is required in partially self-fertilizing populations because fewer ovules will be available for outcrossing. For example, with 50% selfing, male plants require a fourfold increase in male fertility in order to achieve a sufficient fitness gain.

Nonetheless, functional androdioecy has recently been documented in Datisca glomerata (Presl) Baill. (Datiscaceae) (Liston, Rieseberg, and Elias, 1990). Individuals of this species are either male or hermaphrodite. Both male and hermaphrodite flowers have fertile pollen and dehiscent anthers, with males producing approximately 3.2 more pollen than hermaphrodites (Philbrick and Rieseberg, unpublished data). Bagged hermaphrodite flowers produce as many viable seeds as open-pollinated flowers, indicating that the species is self-compatible. In addition, sex ratios are strongly biased toward hermaphrodites, providing further support for the contention that the species is functionally androdioecious. Moreover, observations of plants in numerous populations over the past 5 years have revealed that individual plants are not sexually labile.

Recent phylogenetic studies indicate that the ancestor to D. glomerata was probably a dioecious species (Rieseberg, Hanson, and Philbrick, 1992). All other species in the Datiscaceae besides D. glomerata are dioecious, and D. glomerata is placed in a derived position in a chloroplast DNA-based phylogenetic tree for the family. This is not consistent with traditional models that view androdioecy as an intermediate step in the formation of dioecy from hermaphroditism. However, it is consistent with the theoretical prediction of Charlesworth (1984) that androdioecy is unlikely to evolve in a selfing species as a means of avoiding inbreeding depression, but could evolve in an outcrosser given a sufficient increase in fitness. As a result, Liston, Rieseberg, and Elias (1990) hypothesized that functional androdioecy in Datisca is the result of a breakdown of the dioecious breeding system, possibly due to low population densities and subsequent pollination limitations.

Although we have established the existence and evolutionary polarity of androdioecy in Datisca, evolutionary factors that influence the stability and long-term maintenance of this reproductive system have not been studied in detail. Thus, it is not clear whether androdioecy is evolutionarily stable or whether it simply represents a transient condition in the breakdown of dioecy to hermaphroditism as suggested by Liston, Rieseberg, and Elias (1990). Fitness parameters that need to be studied in detail include selfing rates, the effects of selfing on fitness, pollen production, the relative pollen contribution of males and hermaphrodites to the next generation, and survival rates of males. In this paper we present the results from a study of one of these parameters: i.e., what are the effects of

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selfing on progeny fitness in androdioecious populations of *D. glomerata*? To accomplish this goal, progeny from self-fertilizations, cross-fertilizations with pollen from male plants only, cross-fertilizations with pollen from hermaphrodite plants only, and open-pollinated flowers were compared to assess several measures of progeny fitness including seed weight, germination rate, and seedling weight. The two different cross-pollination treatments were used to determine whether there were significant fitness differences between male and hermaphrodite pollen.

MATERIALS AND METHODS

Study species—*Datisca glomerata* is a long-lived, tall (1–2.5 m) perennial herb occurring in riparian habitats from Baja California, Mexico to northern California. In winter, the plants are dormant and the aboveground parts die back. In spring, the herbaceous shoots grow rapidly above the rootstock. Flowering and fruiting occur throughout the summer months. A mature male or hermaphrodite plant may produce over 1,000 flowers in a season. The floral morphology of male and hermaphrodite flowers is relatively simple, characteristic of an anemophilous pollination system. Flowers are apetalous, calyx lobes are short and inconspicuous, and nectaries are absent. Male flowers display a greater number of anthers ($\bar{X} = 11.3 \pm 2.4$; $N = 97$) than hermaphrodite flowers ($\bar{X} = 3.0 \pm 0.6$; $N = 100$) (Liston, Rieseberg, and Elias, 1990). Hermaphrodite flowers are protogynous with three linear, branched styles. The fruit is a small (1 cm) capsule that produces 100–300 tiny (approximately 1-mm-long) seeds. The capsules dehisce at the apex, and seed dispersal is probably via a "censer mechanism" as known from *Papaver* (van der Pijl, 1982).

Pollination treatments—A total of 25 mature hermaphrodite individuals from three natural populations (Alder Creek, Baughman Spring, and Mt. Islip I; locality data in Liston, Rieseberg, and Elias, 1990) was selected arbitrarily for experimental manipulations. On each individual, four branches with a minimum of 20 flowers were randomly chosen for pollination treatments. All flowers on each branch received the same pollination treatment in order to minimize position effects (nonrandom fruit production with respect to flower position). On each plant, flowers on one branch were bagged to prevent the introduction of wind-borne pollen and allowed to self-pollinate (hereafter referred to as the self-pollen treatment); hand-selfing was not considered necessary because preliminary data showed high seed set from bagged flowers. Flowers on a second branch were emasculated with small forceps at least 1 week prior to pollination and then cross-pollinated with pollen from hermaphrodite plants (hereafter referred to as the hermaphrodite-pollen treatment). Flowers on a third branch were also emasculated at least 1 week prior to pollination and then cross-pollinated with pollen from male plants (hereafter referred to as the male-pollen treatment). Flowers on the fourth branch were not bagged and were allowed to open-pollinate (hereafter referred to as the open-pollen treatment). For cross-pollinations, anthers from 20–30 male individuals and hermaphrodite individuals were collected and

placed under incandescent light bulbs until they dehisced. The pooled male pollen and pooled hermaphrodite pollen were then carefully applied to the styles with small paintbrushes. This approach ensured that as many male or hermaphrodite individuals as possible were used as pollen parents for the cross-pollination treatments. After the pollination treatments, the flowers (branches) were again bagged to exclude further pollination during the period of stigma receptivity.

Progeny fitness measures—Capsules from each treatment were collected approximately 3 weeks after pollination. For all 25 plants, a minimum of ten seeds from each of four capsules per successful treatment (160 seeds from each of the 25 maternal families) were weighed on a Cahn Analytical Microbalance. Approximately 100 seeds from each treatment were then placed on wet filter paper and exposed to light. Seeds were considered germinated when the radical broke through the outer seed coat. After 3 weeks on filter paper in a growth chamber, all germinated seedlings from each treatment were harvested, dried, and weighed on a Cahn Analytical Microbalance.

Statistics—Data analysis was carried out with the PC versions of SAS (SAS Institute, Inc., 1989) and Biostat (Pimental and Smith, 1985). Post hoc, pairwise, multiple comparisons of Kruskal-Wallis test results were calculated using the procedures of Dunn (1964).

RESULTS

Seed weights—The seed weight data from all 25 plants did not meet ANOVA assumptions even after transformations. This was due, in part, to a heavily unbalanced model that resulted when some pollination treatments were not successful on some plants (e.g., bags were dislodged from some branches). As a result, nonparametric analyses were employed. In order to avoid an inflated value for the degree of freedom, seed weights for each treatment were averaged for each plant. A Kruskal-Wallis test indicated that differences in median seed weights among treatments (Table 1; Fig. 1) were significant (Kruskal-Wallis $H = 14.5$, $N = 70$, df = 3, $P < 0.005$). Post hoc, pairwise, multiple comparison test results show that the median weights of seeds derived from self-pollinated flowers were significantly lower than median seed weights from any other pollination treatment (experimentwise $P < 0.01$). Mean seed weights among the other three treatments were not significantly different.

Although the seeds derived from self-pollinated flowers were significantly lower in weight than seeds from other treatments when data from all plants were averaged and pooled with other plants, variation in this pattern was observed in individual plants. To investigate this, 12 plants with which comparisons were possible between selfed and outcrossed treatments were individually analyzed. In five of the plants, weights of seeds from self-pollinated flowers were significantly lower than seed weights for the other three pollination treatments (plants 1, 3–5, 8; Table 2). In three other plants, seed weights from self-pollinated flowers were significantly lower than seed weights from at least one other treatment, with the remaining comparisons not available or not significant (plants 10–12).

TABLE 1. *Means and standard errors of seed weights (in µg) of average values from each plant. N for seed numbers indicates total number of seeds examined within each treatment before plant averaging. N for plants is the number of plants represented for each treatment (not all treatments were successful on all 25 plants)*

	Hermpahrodite	Male	Open	Self
N (seeds)	610	625	880	505
N (plants)	16	17	22	15
Mean	62.2	62.5	63.3	52.5
SE	1.9	1.9	1.4	2.8

Selfed seeds from plant 6 weighed significantly less than seeds from male- and open-pollinated treatments, but significantly more than seeds sired by hermaphrodite pollen. In contrast to seed weight data from all other plants, selfed seeds from plant 9 weighed significantly more than seeds from the other three treatments.

Seedling weights—These analyses were based on seed from eight parental individuals at the Alder Creek site only. Seedling data from Mt. Islip and Baughman Spring were not included because sample sizes were either too small or highly unbalanced among treatments. Data were common log transformed to meet ANOVA assumptions.

The data were analyzed with a two-way, fixed ANOVA design. Since seeds available for this part of the experiment were restricted to seeds produced by the first part of the experiment and to only those seeds that germinated, plants were not treated as a random factor. The mean weights of seedlings originating from flowers pollinated by different methods were significantly different (Table 3; Fig. 2). Post hoc analyses further indicated that weights of seedlings from self-pollinated flowers were significantly lower than seedling weights from open- or male-pollinated flowers ($P < 0.001$; Table 4).
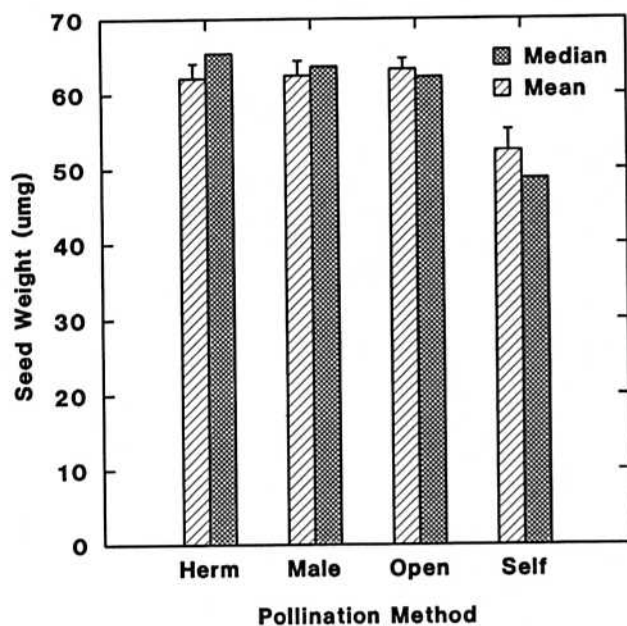

Fig. 1. Means and medians of seed weights (μm; $N = 2,620$) of average values from each plant ($N = 25$) by pollination treatment. Error bars indicate standard error.

TABLE 2. *Individual plant comparisons of mean weights (in µg) of seeds from self-pollinated flowers to mean seed weights from other pollination treatments. Plants 1 and 2 are from Mt Islip, 3–10 are from Alder Creek, and 11 and 12 are from Baughman Spring. P values for significance levels between self-pollinated and indicated pollination treatment are post hoc Tukey HSD values for ANOVA tests or values (experimentwise error rate) obtained using Dunn's method for Kruskal-Wallis tests, whichever was appropriate. Required transformations of seed weights for ANOVA tests are indicated with the post hoc procedure. Number of seeds for each treatment is 40 except plant 1, male (N = 22); plant 4, self (N = 24); plant 7, self (N = 24); and plant 12, hermaphrodite (N = 10)*

Plant no.	Self	Hermaphrodite	Male	Open	Post hoc method
1	57.5	65.1***	76.3****	64.1**	Tukey (log)
2	65.5	68.6	60.3**	66.4	Tukey (log)
3	48.7	59.4***	68.9****	65.0****	Dunn
4	38.8	67.0****	69.6****	68.5****	Dunn
5	48.4	65.9****	65.3****	78.6****	Tukey
6	55.5	49.6**	68.5****	73.6****	Tukey
7	55.0	na	52.8	59.8	Dunnn
8	46.5	68.5****	63.6****	61.4****	Tukey
9	78.8	53.3****	65.5***	74.9	Dunn
10	59.0	63.7	72.9****	64.4*	Dunn
11	47.2	48.6	50.1	59.3****	Tukey
12	43.8	50.4**	na	52.4***	Tukey (log)

$* = P < 0.05$, $** = P < 0.01$, $*** = P < 0.001$, $**** = P = 0.0001$; na = data not available.

The two-way ANOVA also indicated a significant difference in mean seedling weights among parent plants and a significant interaction between parents and pollination method (Table 3). These results reveal that not only do seedling weights vary significantly with pollination method, but that seedling weights from individual plants differ significantly from other plants, and that plants respond to pollination treatments differently.

Seed germination—Percentages of seed germination were quite low, ranging from approximately 26% for open-pollinated progenies to over 40% for progenies sired by hermaphrodites (Fig. 3). A repeated-measures ANOVA indicated that there were no significant differences in mean germination percentage among seeds from different pollination treatments ($F = 0.70$, df = 3,44).

DISCUSSION

Significant inbreeding depression was observed for functionally androdioecious populations of *D. glomerata* for two of the three fitness measures. Self-pollination reduced mean seed weight by about 16% when compared to outcrossed seed sired by pollen from either hermaphrodite or male plants. Likewise, self-pollination reduced mean seedling weight by 17% when compared to outcrossed seedlings fostered by pollen from staminate plants. However, outcrossed seedlings sired by pollen from hermaphrodite plants were not significantly heavier than seedlings from the self-pollination treatment. Levels of inbreeding depression observed for different parental plants were highly variable, with only 50% of the parental plants exhibiting significant levels of inbreeding depression for both outcrossed pollen treatments. Reasons for the observed variation in inbreeding depression are not

TABLE 3. *Two-way ANOVA of seedling weights. Significance levels as in Table 2*

Source	df	SS	MS	F	P
Model	26	9.17	0.35	14.3	****
Pollination treatment	3	1.13	0.38	15.3	****
Plant	7	1.66	0.24	9.6	****
Pollination × plant	16	5.16	0.32	13.1	****
Error	730	17.99	0.02		
Total	756	27.16			

clear, although similar patterns of variation have been reported for other plant species (e.g., Schoen, 1983; Sakai, Karoly, and Weller, 1989; Dudash, 1990; Schmitt and Ernhardt, 1990).

Clearly, the inbreeding effects observed in this study represent an underestimate of inbreeding depression. First, only progeny fitness parameters were measured in this study, and it is well known that inbreeding depression can act at later stages of the life cycle (Schoen, 1983; Sakai, Karoly, and Weller, 1989; Dudash, 1990; Holtsford and Ellstrand, 1990). Second, not all progeny fitness parameters were measured due to experimental constraints. For example, the significance of abortion of initiated seeds, a potentially important measure of inbreeding depression, was not assessed herein. Third, the inbreeding effects shown here would undoubtedly be much greater if the experiments were conducted entirely under field conditions where environmental variation and competition would be much greater than under greenhouse conditions (e.g., Schoen, 1983; Dudash, 1990; Schmitt and Gamble, 1990).

Nonetheless, the evidence of inbreeding depression in *D. glomerata* presented here has a number of interesting implications regarding the evolutionary stability of androdioecy. First, inbreeding depression will increase male fitness because all progeny sired by males are outcrossed, whereas a significant proportion of hermaphrodite progeny are inbred (selfing rates range from 8% to 35% in *D. glomerata*; Fritsch and Rieseberg, 1992). Thus, inbreeding depression is likely to favor the maintenance of males in androdioecious populations and potentially limit the spread of hermaphrodites. A second interesting implication is that inbreeding depression, if sufficiently high, could actually favor dioecy (where all progeny result from outbreeding) rather than either androdioecy or hermaphroditism. However, it is doubtful whether the effects of inbreeding are strong enough to overcome the advantages afforded by selfing such as the increased probability of pollination and lowered energetic costs of fertilization. Indeed, the evolution of androdioecy from dioecy was probably promoted by such advantages in the first place (Liston, Rieseberg, and Elias, 1990). It should also be

TABLE 4. *Post hoc analysis of two-way ANOVA for the effect of pollination treatment on seedling weight. Significance levels as in Table 2*

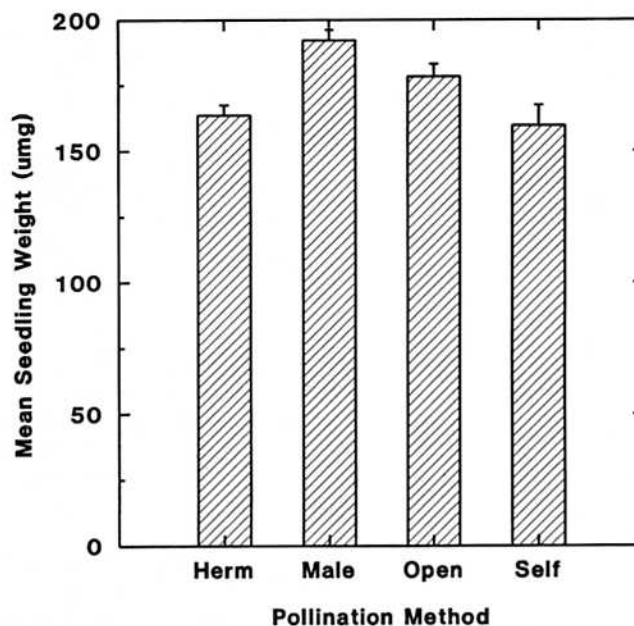|	Mean weight	N	Hermaph-rodite	Male	Open
Hermaphrodite	163.5	274			
Male	192.2	203	***		
Open	178.3	179	*	*	*
Self	159.5	101	ns	***	***

Fig. 2. Mean seedling weights (μg) from all plants at the Alder Creek study site (757 seedlings, eight plants) by pollination treatment. Error bars indicate standard error.

pointed out that these advantages are likely to be most critical in populations that are small in number and where individual plants are widely scattered—a condition common in *D. glomerata*.

An unexpected result from this study was the relatively high seed weights observed for open-pollinated progenies. Because open-pollinated progenies result from both cross- and self-fertilizations (Fritsch and Rieseberg, 1992), seed
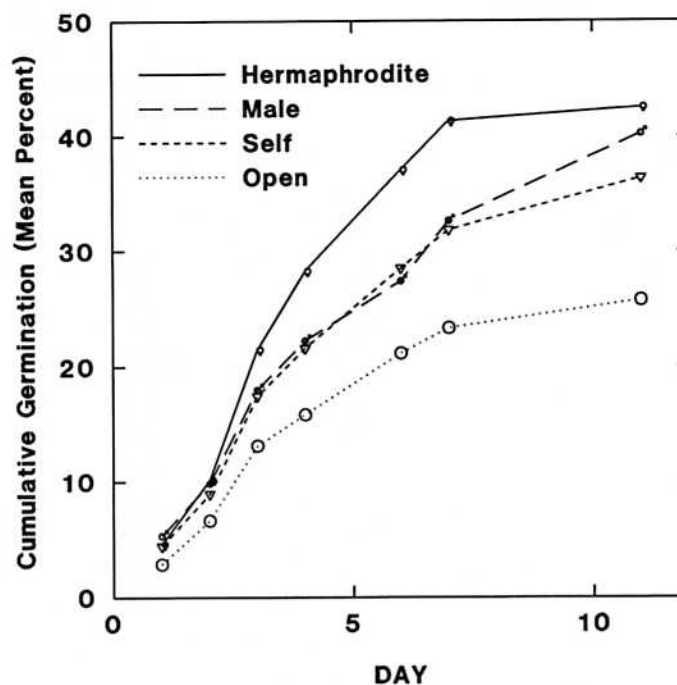

Fig. 3. Cumulative percentages of seed germination by pollination treatment at successive sampling times.

weights were expected to be intermediate between those observed for the selfed and outcrossed progenies. Instead, when all seeds were pooled, open-pollinated seeds were not significantly different in weight when compared to progenies sired by either male or hermaphrodite pollen. A possible explanation for this result is that the branches used in the outcrossed and selfed treatments were bagged for several weeks to eliminate any possibility of pollen contamination. In contrast, the open-pollinated treatments were not bagged. The presence of the bag may have reduced the amount of local photosynthate available to a particular fruit, possibly resulting in decreased seed weight in bagged fruits. Thus, the general observation that seed weight is related to the proximity of the resource supply may apply here (see Haig and Westoby, 1988). It is also important to recognize that pollen grain loads differed among treatments; pollen load may be related to the total number of seeds per fruit and thus possibly indirectly to the variation in seed weight observed.

Another unanticipated result was the significant difference between the two classes of outcrossed progenies for seedling weights; seedling weights of male sired progeny were greater than those of hermaphrodite progeny. A similar difference was observed for seed weights if the seed weight data were restricted to the same progenies used for the seedling weight comparisons. One possible explanation for the differences in progeny fitness between the two outcrossed treatments is that quantities of male and hermaphrodite pollen were not equally applied to outcrossed flowers. Unequal pollen application could result in differences in seed quality since numerous studies have demonstrated a positive correlation between pollen load and progeny fitness (e.g., Bertin, 1988, 1990 and references therein; Marshall and Whittaker, 1989). Explanations for this correlation include the possibility that faster-growing pollen tubes produce more vigorous offspring, or that larger pollen loads may induce the parental plant to allocate more resources to certain fruits (reviewed in Walsh and Charlesworth, 1992). This seems unlikely in *Datisca*, however, since every attempt was made to completely coat styles of both outcrossing treatments with their respective pollen. An alternative explanation for the fitness differences observed between the outcrossed progenies is that gene(s) for female sterility or linked genes confer some type of progeny fitness advantage or that there are differences in pollen viability over time between the two sources. These hypotheses are currently being tested by comparing relative rates of pollen germination and pollen tube growth between male and hermaphrodite pollen (Philbrick, unpublished data). Obviously, the possibility of a fitness difference between male and hermaphrodite pollen would have important implications regarding the maintenance of androdioecy in *D. glomerata*.

The observation of significant levels of inbreeding depression in this study, combined with prior evidence of a greater than threefold pollen production by males (Liston, Rieseberg, and Elias, 1990), may at least partially account for the large fitness increase required by males to be maintained in androdioecious populations. Nonetheless, a great deal of additional information is required to determine whether androdioecy is evolutionarily stable in *D. glomerata*. This includes studies of inbreeding depression in later life history stages, selfing rates, the relative pollen contribution of males and hermaphrodites to the next generation, and the survival rates of males vs. hermaphrodites. Recent studies of outcrossing rates using random amplified polymorphic DNA markers (Fritsch and Rieseberg, 1992) indicate high levels of outcrossing (65%–92%), a condition that would also contribute to the large fitness increase required by males to be maintained by selection.

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