

FEMALE COMPENSATION THROUGH THE QUANTITY AND QUALITY OF PROGENY IN A GYNODIOECIOUS PLANT, *GERANIUM MACULATUM* (GERANIACEAE)¹

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One of the major evolutionary trends in flowering plants is the evolution of unisexual flowers (male or female) from perfect flowers. This transition has occurred repeatedly in many taxa and has generated a wonderful array of variation in sexual expression among species. Theoretical studies have proposed a number of mechanisms to explain how this level of variation could be maintained in natural systems. One possible mechanism is the female compensation hypothesis, which predicts that female mutants require an increase in their seed fitness in order to invade a hermaphroditic system. Using *Geranium maculatum*, I tested this hypothesis and showed that female mothers produced more and larger seeds than hermaphroditic mothers even though they were indistinguishable in their vegetative traits and the flower production. Seeds from females were also more likely to germinate and produced seedlings with larger above- and belowground biomass. These seedlings were more likely to flower than those from hermaphrodites in at least one of the two populations studied. Combined, these results indicated that females in *G. maculatum* did compensate for their loss of male function by producing more and better seeds than hermaphrodites. This provides a mechanism for the maintenance of female plants in this species.

Key words: female compensation; fitness; Georgia; Geraniaceae; gynodioecy; male sterility; progeny quality; spring ephemeral.

One of the major evolutionary transitions observed in flowering plants is the evolution of unisexual flowers (male or female) from perfect flowers. This transition has occurred more than 100 times in many different taxa (Charlesworth, 2002) and has generated an incredible amount of variation in both the sexual expression and morphology of flowers (Richards, 1997). The variation observed in sexual systems of flowering plants has fascinated biologists since Darwin (1877) in part because of the influence these systems have on the mating patterns of a species. In addition, by affecting mating patterns, the sexual systems of a species can also influence the likelihood of local adaptation, the prevalence of genetic drift and, ultimately, the propensity of a population to evolve. Today, understanding how variation has been generated and maintained in sexual systems remains a central question in plant evolutionary biology (Barrett, 2002).

One sexual system that has proven to be an ideal subject for examining the impact of sexual system on a population is gynodioecy. In gynodioecious systems, a population may contain both hermaphroditic individuals that produce perfect flowers as well as females that produce flowers lacking pollen. Females in gynodioecious species usually arise as the result of a mutation, present either in the nuclear or cytoplasmic genomes, that cause male sterility (Hanson, 1991; Saumitou-Laprade et al., 1994; Schnable and Wise, 1998; Webb, 1999; Budar et al., 2003).

Gynodioecy has received a great deal of attention from

evolutionary biologists in part because of the striking difference in pollen production seen in hermaphrodites (pollen-producing) and females (pollen-lacking) within a population. Significant variation in traits that have a strong effect on fitness, such as pollen production, is unlikely to be maintained in a population for long periods because alleles that convey lower fitness would be quickly eliminated by natural selection (Futuyma, 1998). In the case of gynodioecy, females can only reproduce through ovules, and their average potential for sexual reproduction is half that of their hermaphroditic counterparts, which reproduce through both ovules and pollen. Females, therefore, would not be expected to persist in a population containing hermaphrodites, and gynodioecious populations should occur infrequently. However, far from being rare, gynodioecy is seen in almost 7% of all angiosperms (Richards, 1997). This observation suggests that females in gynodioecious populations possess reproductive advantages that enable them to persist longer than would be expected.

Theoretical studies suggest that one critical requirement for the establishment of gynodioecy is that females need to somehow compensate for their loss of pollen production (Lewis, 1941; Lloyd, 1975, 1976; Charlesworth and Charlesworth, 1978, 1979; Charlesworth, 1980, 1981, 1992; Schultz, 1994; de Hann et al., 1997). One possible mechanism for such compensation would be through increasing seed fitness, often referred to as female compensation (Darwin, 1877). The amount of female compensation can determine whether female plants can successfully invade a hermaphroditic population (Lewis, 1941; Lloyd, 1975; Charlesworth and Charlesworth, 1978; Charlesworth, 1981). In addition, the magnitude of female compensation could also influence the frequency that females could reach in a population (Lloyd, 1974; Jacobs and Wade, 2003). Therefore, characterizing whether and how female compensation occurs is important in understanding the maintenance of females in a gynodioecious system.

Previous studies have largely attempted to estimate female

¹ Manuscript received 19 August 2005; revision accepted 18 November 2005.

The author thanks N. Armstrong, C. Caruso, L. Donovan, M. Olson and the Donovan lab group for their help to improve an earlier version of the manuscript and L. Chaffin, A. Good, H. Hamilton, S. Held, E. Lafèvre and J. Patel for their technical help in the greenhouse and in the field. Funding for this study was provided by the University of Georgia Research Foundation.

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compensation by examining the number of seeds produced by females and hermaphrodites grown under natural conditions. Results from these studies suggest that females generally produce more seeds than hermaphrodites (e.g., Gouyon and Couvet, 1987; Kohn, 1989; Olson, 2001; Ramsey and Vaughton, 2002; Schultz, 2003, but see exceptions in del Castillo, 1993; Dinnetz and Jerling, 1997; Medrano et al., 2005), but the magnitude of this difference depends on many biotic and abiotic factors (e.g., Wolfe and Shmida, 1997; McCauley and Brock, 1998; Delph and Carroll, 2001; Marshall and Ganders, 2001; Ramula and Mutikainen, 2003; Ashman et al., 2004; Asikainen and Mutikainen, 2005a, b; Rosas et al., 2005). The number of seeds produced by a plant, however, is only a partial measurement of fitness. Other factors, such as the quality of the seeds produced and their ability to germinate and produce healthy seedlings, can also have a significant impact on an individual's reproductive success.

A few studies have examined differences in progeny quality between females and hermaphrodites in gynodioecious species (e.g., Eckhart, 1992; del Castillo, 1993; Jordano, 1993; Puterbaugh et al., 1997; Sakai et al., 1997; Delph et al., 1999; Alonso and Herrera, 2001; Weller and Sakai, 2005). These studies have largely used the mass of the seeds produced as a surrogate measurement to estimate progeny quality, and the results are in conflict. Puterbaugh et al. (1997) found a significant difference in the mass of seeds produced by females and hermaphrodites. However, no differences were found in other studies (e.g., Kohn, 1988; Eckhart, 1992; Sakai et al., 1997; Delph et al., 1999; Alonso and Herrera, 2001; Ramula and Mutikainen, 2003; Weller and Sakai, 2005). Interpretation of results from such studies is further complicated by the fact that seed mass does not always correlate with early seedling performance in gynodioecious plants. For example, hermaphrodites and females produce seeds of similar mass in *Sidalcea oregana* (Ashman, 1992), *Silene acaulis* (Delph et al., 1999; Delph and Carroll, 2001), and *Schiedea salicaria* (Weller and Sakai, 2005), but germination was higher for seeds produced by females. These findings suggest that seed mass may not accurately reflect progeny quality. A small number of studies had examined progeny quality directly, but measurements were limited to very early life stages such as germination and early plant size (Eckhart, 1992; Puterbaugh et al., 1997; Wolfe and Shmida, 1997; Alonso and Herrera, 2001; Delph and Mutikainen, 2003; Weller and Sakai, 2005). Thus far, there are only a handful of studies that examined progeny fitness beyond an early stage of seedling growth (Ashman, 1992; Avila-Sakar and Dominguez, 2000; Ramsey and Vaughton, 2002; Delph and Mutikainen, 2003). Therefore, the extent to which overall progeny performance may contribute to female compensation remains an area that requires more empirical data.

The goal of the present study was to obtain a more thorough estimate of female compensation over multiple life history stages in the wild geranium, *Geranium maculatum*. This project builds on a previous study by Ågren and Willson (1991) who investigated differences between females and hermaphrodites in *G. maculatum* using a natural population in Illinois, USA. Ågren and Willson found that females produced more seeds than hermaphrodites, but they did not detect any difference in the size of seeds produced nor did they examine subsequent seedling performance. In this study, I measured the number and size of seeds produced as well as progeny performance in two populations of *G. maculatum* over two

seasons. A second objective of the current study was to examine the potential impact of population sex ratios on female compensation by comparing results from this study to Ågren and Willson's study (1991). The frequency of females in a population can potentially influence seed production in females (pollen availability) and therefore overall female fitness (McCauley and Brock, 1998; Graff, 1999; Ashman and Diefenderfer, 2001; Ramula and Mutikainen, 2003; Rosas et al., 2005). The population studied by Ågren and Willson had a low frequency of females (9.4%), while I examined female compensation in populations with much higher female frequencies (35% and 50%). If pollen availability is one of the factors contributing to the reproductive success in female plants, the female compensation observed in this study should be lower than that was observed by Ågren and Willson (1991).

The specific questions addressed in this study are (1) Do females in mixed populations in *Geranium maculatum* compensate for their loss of male function by producing more and/or heavier seeds than hermaphrodites? (2) Do progeny from female plants perform better in seedling and adult (reproductive) stages than progeny from hermaphrodites? (3) Are the levels of female compensation lower in populations with higher frequencies of female plants? The first question was addressed using seeds collected from two field populations over 2 years, the second by growing the field-collected seeds in a greenhouse for two seasons, and the third by comparing results from this study to the earlier estimate by Ågren and Willson (1991).

MATERIALS AND METHODS

Study organism—*Geranium maculatum* is a common spring ephemeral species that is often found in alluvial woods and coves. It is widely distributed in eastern North America; north to Newfoundland and Manitoba in Canada, south to Georgia, and west to Kansas and the Dakotas in the U.S.A. (Radford et al., 1968). *Geranium maculatum* is a perennial species with a thin rhizome ca. 1 cm in cross-section diameter. In my northern Georgia (GA) study sites, ramets emerge in late February and flowers appear within the following month. Individual plants may flower for 2–3 weeks, but the flowering season of the population usually lasts until early June with the peak in mid April. Each ramet is an annual structure that dies back in August and individuals overwinter as dormant rhizomes.

Flowers of *G. maculatum* are pink to lavender with diameters ranging from 1.5 to 3.0 cm. The most commonly observed insect visitors in GA include bumblebees, honeybees, halictid bees, and butterflies. Flowers are protandrous, where anthers dehisce soon after the petals open, but the five stigmatic lobes remain tightly pressed together and are nonreceptive until 1–2 days later. In natural populations, the nearly non-overlapping sexual phases within a flower make autogamous selfing a rare event (S.-M. Chang, unpublished data). However, plants often have more than one open flower at a given time, allowing for the possibility of selfing between flowers of the same plant (geitonogamy).

Among natural populations surveyed in northern GA, half (7/16) of them contained some female plants. The sex ratios for mixed populations ranged from 0.1 to 50% females (this study and Ågren and Willson, 1991). In this study, I focused on two populations, MP and OT, in Clarke County, GA, that have about 1800 and 1200 reproductive plants and about 35 and 50% of female plants, respectively.

Adult morphological traits—To determine if adult female and hermaphroditic plants in natural populations differed from each other in their morphological traits, plants were measured in their natural environment. Two 1-m wide transects through the main portion of the two study populations were examined in April 2003, and the following traits of all reproductive plants within the transects were measured: (1) three vegetative traits (number of rosette leaves, length of the largest rosette leaf, and length of the largest cauline leaf) and (2) two reproductive traits (height of the inflorescence and size of one petal randomly selected from one open flower).

Gender-specific success in seed production—Progeny quantity—To compare reproductive success through seed production between females and hermaphrodites, the number and the size of seeds they produced in the two study populations were measured for 2 years. In 2003, 50 (25 female [F] + 25 hermaphrodite [H]) plants were originally sampled in both populations, but the sample size was reduced to 28 (10F + 18H) and 31 (15F + 16H) for MP and OT, respectively, due to deer browsing. In 2004, a deer fence was assembled to prevent deer damage and a total of 289 (112F + 177H) and 117 (59F + 58H) plants were sampled from MP and OT. In both years, I counted the total number of flower buds on the determinant inflorescence for each plant sampled. In late May after all target plants had finished flowering and fruits had started to develop, entire inflorescences of the sampled plants were bagged using fine-mesh bridal veil. This procedure was necessary to collect mature seeds because fruits of *G. maculatum* have an automatic seed dispersal mechanism that forcefully throws seeds to as far as 3 m from the maternal plants (Stamp and Lucas, 1983). Plants were examined every week in May and June to record the number of fruits produced and to collect the mature seeds. Fruits were collected and stored in paper envelopes until they were processed later in the laboratory. The total number of seeds produced by each plant was counted to compare the quantity of seeds produced by females and hermaphrodites.

Progeny quality—Seed mass—To make up for seeds lost to deer browsing, additional seeds from nontarget plants were collected in 2003. Because not all seeds were collected from these plants, they were used to study the quality but not the quantity of the progeny. In total, 792 seeds from 117 (42F + 75H) and 86 (35F + 51H) maternal plants from MP and OT were collected and weighed in 2003. In 2004, the sample size was increased to 2909 seeds from 184 (97F + 87H) and 134 (71F + 63H) individuals from MP and OT, respectively. Seeds collected in both years were weighed individually using a digital balance with the precision of 0.01 mg.

Seedling performance—To evaluate the quality of progeny beyond seed mass, I planted most of the seeds collected in 2003 and followed them throughout their first two growing seasons. A total of 436 seeds from MP (41F + 75H maternal plants) and 305 seeds from OT (35F + 51H maternal plants) were planted. Prior to planting, seeds were first scarified by nicking the seed coat with a sharp razorblade and then soaking them in water for 14 days in a cold room (5°C). *Geranium maculatum* seeds are notoriously difficult to germinate, and an earlier study by Martin (1965) showed that germination occurred slowly and over a long period of time when planted without scarification. To facilitate the uniformity of germination, I removed the seed coat carefully without damaging the cotyledons and embryos inside after the seed coat was softened by soaking in water for 3 days. This method has been shown in a pilot study to be effective in breaking the physical dormancy of the seeds.

Two weeks later, seeds were removed from the cold room and planted individually into 2-inch pots containing Faford 3B mix (Conrad Faford, Awawam, Massachusetts, USA). For the following 7 days, these pots were kept on a greenhouse bench with misting spray every 10 min and indirect sunlight before being moved into a regular greenhouse bench. Limited by the space available and the low number of seeds in many families, seeds from the two populations were planted in separate temporal blocks to maximize the power of detecting sex differences within a population. This design, unfortunately, sacrificed the ability to detect any difference between populations.

Seedling size was measured as the total leaf area produced at 1 mo (early size) and 4 mo (late size) after they were moved into the greenhouse. I used leaf width as a simple and nondestructive way to measure leaf area. A very strong relationship was found between leaf areas and leaf widths ($\text{area} = 1.03[\text{width}] + 0.32[\text{width}]^2$; $R^2 = 0.99$) using 100 leaves from nonexperimental plants at the same developmental stages. This equation was used to convert the measurements of leaf width into leaf areas for all of the study plants.

After 4 mo of growth, a length of time similar to the growing period in the field for the first growing season, ramets had distinct signs of senescence: the leaves turned brown or red. The amount of water given to the plants was then gradually reduced over the course of 2 wk, and all the wilted plant material above ground was removed at the end of the drying period.

To obtain the belowground biomass, soil was carefully washed away from the roots and the rhizomes. All experimental plants were processed on the same day, and were air dried on a lab bench for 24 h before being weighed. Because these plants would be studied through the next growing season, the rhizomes' wet mass was measured, instead of killing plants to measure dry mass. After weighing, the rhizomes were wrapped in moist sphagnum mosses and kept in unsealed plastic bags for 1 mo in a 5°C cold room before they were planted back into soil at room temperature (approximately 25°C). This method has been

previously tested and shown to be effective to stimulate *G. maculatum* rhizomes to continue regular growth in the greenhouse.

Most plants resumed growth within 1 wk after the rhizomes were brought back to the ambient temperature in the greenhouse. Two months after new ramets emerged, I again measured the total leaf area using the method described. Some inflorescences also started to grow within 2 wk after emergence, but the first flower did not appear until 25 d after the emergence. Plants were examined everyday, and the flowers on each plant were counted until all flowering had ceased.

Data analyses—Adult morphological traits—Analyses of variance (ANOVA) were carried out (PROC GLM in SAS [SAS, 1999]) to analyze the maternal sex and population differences in the morphological and reproductive traits measured in the field. Gender, population, and their interactions were all treated as fixed variables in the analyses.

Progeny quantity—An ANOVA was carried out (PROC GLM in SAS) to evaluate the effects of gender, population, year, and their interactions on the total seed number produced. To further determine at what stage the difference in seed number might have arisen, individual ANOVA was carried out for each of the three components of total seed production: flower number, fruit set (number of fruits/number of flowers) and seed set (total number of seeds/number of fruits), using the same set of predicting variables as in the ANOVA described previously. Least square means were plotted for each of the four traits (total seed production and the three components) to illustrate the differences between the main effects.

Progeny quality—Seed mass—An ANOVA (PROC MIXED in SAS) was carried out to evaluate the effects of gender, population, year, and their interactions on individual seed mass. Because multiple seeds were collected from many maternal plants, maternal identity (ID) was also included as a random variable in this analysis to remove maternal effects unrelated to their gender. Maternal ID was nested under the interaction of year, population, and maternal gender. In addition to seed mass, progeny quality was also evaluated by their performance in the life history stages at or after seed germination. Logistic regressions (PROC CATMOD in SAS) were used to analyze the effect of gender on the probability of germination among seeds planted. Germination was treated as a categorical variable (0 for an ungerminated and 1 for a germinated seed). Because of the planting design (described earlier), populations were analyzed separately and, therefore, the predicting variables for each analysis only included the maternal gender and the initial seed mass. Maternal plant was not included in the analysis because of the small number of progeny in some maternal families.

Seedling performance—For the progeny traits measured in the first growing season, a preliminary MANOVA was first carried out to analyze the overall effect of maternal gender and maternal individual on the early seedling performance traits, including early and late seedling sizes in season one and the end-of-first-season belowground biomass. Maternal identity (ID) was included as a random variable. To further interpret any effects detected in the MANOVA, individual characters were subsequently analyzed using univariate ANOVAs (PROC MIXED in SAS) to identify the specific trait(s) that could account for the differences between the two maternal genders. Residuals for these traits were examined, and the variables were transformed when necessary to satisfy the assumption of normality. Significance tests were done using transformed data, but the means were reported using the original data.

The progeny quality in the second season was evaluated by four performance traits: reemergence, aboveground plant size, probability to flower, and flower production. The two continuous traits, plant size and the flower production, were analyzed using two separate ANOVAs. All the plants that reemerged after stratification were included in the plant size analysis, but only the ones that flowered were included in the flower production analysis. Reemergence and flowering probabilities were analyzed similar to germination described because of their categorical nature. PROC CATMOD in SAS was used for these logistic regression analyses with maternal gender as the predicting variable.

Female compensation—Female compensation (FC) was defined as the increase in female fitness when compared to hermaphrodites. With this definition, FC was calculated using the following equation: $FC_i = (W_{Fi}/W_{Hi}) - 1$, where W_{Fi} and W_{Hi} were the average fitness measurements of female and hermaphroditic plants focusing on a particular fitness component i , such as seed number or survival probability. Because female compensation was most often reported for seed number, one FC was calculated for seed number in each of the two populations studied. To summarize the fitness difference over all the life stages examined in this study, an accumulative female compensation was

calculated by multiplying the relative fitness (W_{Fi}/W_{Hi}) of four fitness components—seed number, germination probability, survival probability from first to second season, and reproductive probability in the second season—together and then subtract one from this value (i.e., accumulative FC = $\Pi(W_{Fi}/W_{Hi}) - 1$).

RESULTS

Adult morphological traits—Overall, within each population, female and hermaphroditic plants did not differ significantly in any of the vegetative traits measured (Table 1). However, populations differed significantly for all of these traits. Specifically, plants in MP tended to have more but smaller leaves, consistent with a typical response to higher light intensity experienced in MP than in OT. In contrast to the vegetative traits, petal lengths differed significantly between the two sexes. Petals of hermaphrodites were on average 37.5 and 37.24% longer (Table 1) than petals of females in MP and OT, respectively. Plants in MP tended to have larger flowers than OT, but the difference was not significant. The pattern of significant gender effect on reproductive but not vegetative traits was consistent with the study by Ågren and Wilson (1991).

Progeny quantity—Maternal gender had a significant effect on the total number of seeds produced: female plants produced more seeds than hermaphrodites ($F_{1,548} = 4.48, P < 0.05$). In 2003, females produced 50.4 and 40.6% more seeds than hermaphrodites in MP and OT, respectively (Fig. 1a). The differences decreased in 2004 to 13.9 and 25.1% for MP and OT but were still statistically significant (Fig. 1a). In addition, plants in MP tended to produce significantly more seeds than OT ($F_{1,548} = 30.34, P < 0.0001$; Fig. 1a). The gender effect did not vary between populations or between years; indicated by the lack of any significant interactions among the genders and other variables.

Univariate ANOVAs of the three reproductive components separately showed that seeds per fruit was the main variable that differed between females and hermaphrodites (Fig. 1b–d). Gender effect was not significant in the other two components: flower number and fruit set. In contrast, a significant population effect was detected in all three components (MP > OT for all traits, $P < 0.05$). Additionally, the gender difference in seeds per fruit varied between years, as indicated by the significant interaction between year and gender in the ANOVAs ($F_{1,548} = 4.08, P < 0.05$). Overall, the difference in seeds per fruit between the two genders is higher in year 2003 than in year 2004 (Fig. 1d). Although the difference between

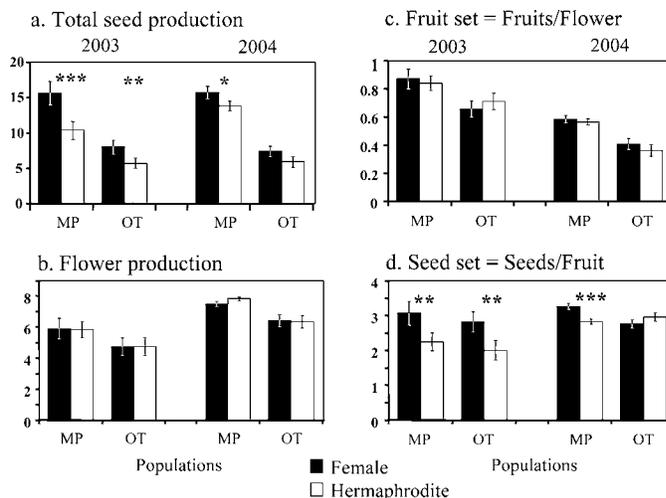


Fig. 1. Female plants of *Geranium maculatum*, on average, produced more seeds (a) than their hermaphroditic counterparts in the same population due to higher seed set (d). Female and hermaphrodites produced similar number of flowers (b) and fruit set (c). The asterisks indicate that the difference between gender groups was significant at $P < 0.05$ (*), $P < 0.01$ (**) or $P < 0.005$ (***) levels.

genders appeared higher in MP than in OT, the population effect was not statistically significant (Fig. 1).

Progeny quality—Seed mass—Among the seeds collected, there was a significant gender effect ($F_{1,524} = 17.18, P < 0.001$) on seed mass although the magnitude of the difference was rather small. More specifically, females produced seeds that were on average 6.0 and 10% heavier than seeds produced by hermaphrodites in MP (contrast for the difference between means of the two genders: $t = 1.24, P = 0.21$) and OT (contrast $t = 2.01, P = 0.045$) in 2003, respectively (Fig. 2). In 2004, the difference increased to 17.6% in MP (contrast $t = 4.37, P < 0.001$) but dropped to -0.5% in OT (contrast $t = 0.26, P = 0.54$) (Fig. 2). With regard to population difference, MP plants produced seeds that weighed slightly less than those of the OT plants ($F_{1,524} = 10.27, P < 0.005$) (Fig. 2) probably due to the significantly more seeds they produced than the OT plants. The effect of year was not significant ($F_{1,524} = 0.09, P = 0.77$).

Maternal gender and initial seed mass influenced the probability for seed germination in OT but not in MP. In OT, heavier seeds tended to have higher germination rates than lighter seeds ($\chi^2 = 6.04, P < 0.01$) and seeds from female

TABLE 1. Morphological traits measured on female and hermaphroditic plants of *Geranium maculatum* in two populations in their natural habitat. Values listed are least square means estimated from the ANOVA analysis with the standard errors inside the parentheses.

Trait	Pop. MP ^a		Pop. OT ^a	
	F	H	F	H
Basal leaf number	3.71 (0.08)	3.62 (0.08)	3.04 (0.13)	2.80 (0.12)
Largest basal leaf width (mm)	46.80 (0.60)	47.42 (0.54)	49.44 (0.93)	51.42 (0.83)
Cauline leaf size (mm)	49.70 (0.38)	49.80 (0.42)	50.63 (0.72)	51.92 (0.62)
Petal length (mm)	11.01 (0.39)	15.11 (0.29)* ^b	11.98 (0.53)	16.52 (0.35)**
Inflorescence height (cm)	45.01 (0.52)	45.32 (0.51)	46.13 (0.89)	47.81 (0.77)

Note: F = female, H = hermaphrodite

^a Populations differed significantly in all the traits listed in the table at the $P < 0.05$ level.

^b Maternal gender groups differed significantly for the indicated trait at $P < 0.05$ level (*) and at $P < 0.01$ level (**).

mothers germinated better than seeds from hermaphroditic mothers ($\chi^2 = 3.85$, $P < 0.05$) (Table 2). Because both seed mass and gender were included simultaneously in the model, the significant gender effect suggested that the higher germination in female families was not only due to seed provisioning mediated through seed mass but also could be due to other factors.

Seedling performance—Among the germinated plants, MANOVA showed that the seedlings differed significantly between genders only in OT but not in MP. Seedlings from female families in OT tended to have larger early sizes, late sizes, and rhizome mass than their hermaphroditic counterparts in the first growing season (Table 2). Most plants (>97%) survived the dormant period in the cold room and began growing again in the second season. Rhizome mass but not maternal gender explained significant variation in the probability for reemergence (Table 2).

The only second-season traits that differed between maternal genders were plant size and flowering probability, but only in OT. This was most likely due to the more significant gender difference in the plant size at the end of the first season (Table 2) in OT than in MP, including both the above- and belowground portions of the plants. The probabilities for reemergence in the second season did not differ between the maternal genders in either MP or OT. Among the plants that produced flowers in the second growing season, the number of flowers they produced also did not differ between the maternal gender groups.

Female compensation—The female compensation for seed number was calculated to be 0.41 for the OT population and 0.50 for the MP population in 2003 and 0.25 and 0.14 in 2004, respectively (Fig. 1a). The FC for the seed mass was 0.06 and 0.1 for MP and OT in 2003, and 0.18 and -0.005 (not different from 0) in 2004, respectively (Fig. 2). The FC for the seedling performance from germination to reproduction was 0 for MP and 0.5 for OT (Table 2). The accumulated FC was 0.50 for MP and 0.88 for OT.

DISCUSSION

I show here the evidence to support the female compensation hypothesis in *G. maculatum*. Female compensation was observed in both seed number and progeny quality. However, the magnitude of FC varied between populations and years. A

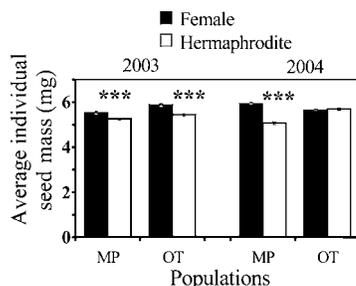


Fig. 2. Female plants of *Geranium maculatum* produced heavier seeds than hermaphroditic plants except in population OT in 2004. The asterisks indicate that the difference between gender groups was significant at $P < 0.005$ (***) levels.

moderate level of accumulative FC was found in both study populations. I discuss each of these points in greater details.

Female compensation in seed number—Theoretical studies have shown that female compensation is a necessary condition for male sterile mutants to invade and persist in an originally hermaphroditic population (Lewis, 1941; Lloyd, 1974, 1975; Charlesworth and Charlesworth, 1978; Charlesworth, 1981). Results from this study showed that female plants of *G. maculatum* achieved such compensation by producing more and larger seeds and better-performing seedlings than coexisting hermaphroditic plants. On average, females produced from 13 to 50% more seeds than hermaphrodites in the same population. This higher seed production in females was not due to differences in the original reproductive potential (i.e., the flower number; see Fig. 2 and Ågren and Willson, 1991) or differences in the fruit number but, rather, female plants appeared to be able to convert more of the ovules into seeds within a fruit (Fig. 2).

There are at least three possible factors that might be responsible for the higher seeds per fruit in females than in hermaphrodites in the same population. First, higher seed production could be due to resource reallocation from floral organs to seed production. As shown in this study, the main morphological traits that distinguish females from hermaphrodites in *G. maculatum* are the flowers that they produce. Hermaphroditic flowers are 1.45 times longer in petal, 3 times longer in anthers, and twice as long in the filaments as female flowers. These measurements were similar to an earlier report by Ågren and Willson (1991) on two Illinois populations (H : F petal lengths of 19.2 : 13.5 mm; H/F = 1.42). The reduced size of floral organs in females should allow these plants to conserve carbon, nitrogen, phosphorus, and other nutrients that would otherwise have been needed for production of petals (Schemske, 1978), pollen (Rabie et al., 1983; Ashman, 1994; Bacha et al., 1997), and nectar (Southwick, 1984; Ashman and Stanton, 1991; Pyke, 1991; Harder and Barrett, 1992; Ashman and Schoen, 1997). Furthermore, several species that maintain smaller petals require less water (Nobel, 1977; Galen et al., 1999). Combined, these saved resources could be reallocated to either make more seeds or better-provisioned seeds by the female plants.

The second possibility is that inbreeding depression reduces the number of mature seeds produced by hermaphrodites. *Geranium maculatum* is self-compatible and Ågren and Willson (1991) found evidence for a high selfing rate (>60%) and a high level of inbreeding depression (ranging between 0.5 and 0.75). Though the high selfing rates were estimated using an IL population, a similar pattern is suspected in the GA populations because of low pollinator activity (e.g., as low as 0.05 visits/flower in 5 h in OT). If a proportion of hermaphrodite seeds were the product of selfing but all female seeds were from outcrossing, inbreeding depression could lead to the reduced seed number and seed mass observed in this study. The gender difference might be smaller if females tended to receive pollen from genetically related individuals. This is a phenomenon likely to occur in species with limited seed dispersal such as *G. maculatum*. Further studies that examine selfing, biparental inbreeding rates, and their impacts on inbreeding depression would allow a better evaluation on the contribution of inbreeding depression to the maintenance of females in *G. maculatum*.

Finally, females might have received more pollen grains per

TABLE 2. Fitness measurements for seedlings produced by female and hermaphroditic maternal plants of *Geranium maculatum* in two populations in Georgia, USA. Values listed, except for germination (%), reemerging (%) and flowering (%), are least square means estimated from the ANOVA analysis with the standard errors inside the parentheses. See Materials and Methods, Data analyses section for details of the analyses.

Trait	Pop. MP		Pop. OT	
	F	H	F	H
Germination (%)	68	71	45	50*
Seed mass ^a (mg)	5.76 (0.1)	5.43 (0.07)* ^b	6.11 (0.13)	5.56 (0.1)***
1st season				
Early size (mm ²)	421.7 (45.88)	474.36 (30.93)	364.94 (22.15)	273.14 (16.31)**
Late size (mm ²)	4965.55 (332.51)	5198.68 (233.66)	4886.93 (273.26)	4309.38 (201.17)
Rhizome mass (g)	4.97 (0.29)	4.69 (0.21)	3.74 (0.23)	2.94 (0.17)*
2nd season				
Reemerging (%)	98.67	96.97	98.39	97.27
Plant size (mm ²)	3782.17 (253.76)	3756.12 (180.01)	2511.06 (183.16)	1859.37 (143.29)**
Flowering (%)	71.62	70.62	49.18	32.71*
Flower no.	6.69 (1.10)	7.17 (1.07)	3.82 (1.02)	3.90 (1.02)

Note: F = female, H = hermaphrodite

^a Values are average mass for seeds that germinated. See Fig. 1 for the average mass for all seeds collected.

^b Maternal groups differed on the indicated trait at $P < 0.05$ level (*), at $P < 0.01$ (**), $P < 0.0001$ (***).

flower than the hermaphrodites, resulting in higher seed production for the former. This possibility seems unlikely considering the smaller petal size and the lack of pollen source nearby (within the same flower). Indeed, Williams et al. (2000) found that female plants in *G. richardsonii* generally received lower pollinator visitation and fewer pollen grains than hermaphrodites. Other studies had shown that such a deficit in pollen receipt could intensify when the female frequency increased in the population (Aizen, 2001; Ashman and Diefenderfer, 2001).

Progeny quality—Progeny quality was examined in two ways, the more commonly used measure of seed mass and a more direct measurement of seedling performance at multiple life stages. Seed mass was 6 and 10% higher in females than in hermaphrodites of MP and OT populations. Though progenies from female mothers performed similarly to hermaphrodites in MP, they outperformed progenies from hermaphrodites by 50% in OT in terms of the cumulative probability to flowering in the second season (49 vs. 32%). It is difficult to reconcile the small difference in female compensation in seed mass between the two populations (10% in OT vs. 6% in MP) and the large difference in seedling performance (50% in OT vs. 0% in MP) if seed mass were the only factor accountable for the seedling performance. Other factors, such as nutrient provisioning (Avila-Sakar and Dominguez, 2000) or inbreeding coefficients (e.g., Kohn and Biardi, 1995; Sakai et al., 1997), that cannot be measured by biomass, are also likely to have contributed to the difference in seedling performance between genders.

One caveat for the results of seedling performance is that it was evaluated in the greenhouse, a rather benign environment compared to the plants' natural habitat. The degree of difference between genders may, therefore, be an underestimate in this study. Future studies that evaluate seedling performance derived from hand pollination and in the field conditions would be most valuable.

Variation in female compensation—Though both genders had little yearly variation on the seed production and individual seed mass (notice the similarity between 2003 and 2004 for a given gender in Figs. 1a and 2), female compensation ($F/H - 1$)

1) fluctuated both between years and between populations. Female compensation for seed number was about twice as high in 2003 than in 2004 and higher in MP for 2003 but higher in OT for 2004. This temporal and spatial variation in female compensation is not unusual in gynodioecious species, including one example in the same genus *Geranium*. Asikainen and Mutikainen (2003) found that FC ranged from 0.2 to 0.7 in *G. sylvaticum* across populations.

In addition to the three factors described previously, pollen limitation has also been suggested to explain at least a portion of the spatial variation seen in female compensation. Female compensation through seed production observed in the current study (averaged 0.3 for both MP and OT) is about half of what Ågren and Willson found (0.6). In another mixed population in GA with only 2% of female plants (Bear Hollow, not included in the results reported previously), females produced 75% more seed relative to the hermaphrodites ($FC = 0.75$). When these populations are examined together, FC appeared to correlate negatively with female frequencies in these populations (Fig. 3). This pattern is consistent with the prediction that females might have reduced seed compensation when they are present in higher frequencies within a population as a result of greater pollen limitation. The small number of populations used in the current analysis prohibits any conclusions from being drawn regarding the effect of sex ratios on female compensation.

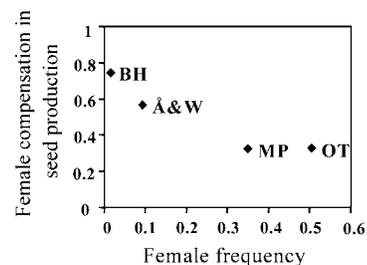


Fig. 3. Negative relationship between female compensation ($F/H - 1$) in seed production and the female frequency in the population. MP and OT are the two populations reported in this study. BH is a population located in Athens, Georgia, USA. Å&W is the Illinois population studied by Ågren and Willson (1991).

However, the preliminary pattern found here, along with similar results from other gynodioecious plants (McCaughey and Brock, 1998; Graff, 1999; Asikainen and Mutikainen, 2003), suggests that pollen limitation is a potentially important factor for the reproductive success of *G. maculatum* and deserves further study. Additional populations with a wider range of sex ratios are needed to directly test the effect of pollen limitation on female compensation.

Evolution of gynodioecy in *Geranium maculatum*—Given the accumulative female compensation estimates reported in this study, is it of a sufficient level to warrant the persistence of females in this species? Answers to this question depend, in part, on the genetic mechanism responsible for male sterility in *G. maculatum* (Lewis, 1941; Lloyd, 1975; Charlesworth and Charlesworth, 1978; Charlesworth, 1981). Male sterility can be caused by either nuclear or cyto-nuclear mutations, and the requirement for female compensation is different for these two systems. Nuclear control of gender would result if the gene(s) causing male sterility were located in the nucleus and would be transmitted through both pollen and seeds. Because females can only produce seeds, transmission of the male sterile allele would be at a 50% disadvantage relative to the allele allowing male fertility. To remain in the population, females would have to produce at least twice as many seeds as hermaphrodites in order to make up the fitness loss from the inability to produce pollen grains, which account for half of nuclear transmission to next generation. Cyto-nuclear control of gender would result if the gene(s) causing male sterility were located in one of the organelles located in cytoplasm (most likely the mitochondria). Because these organelles are only transmitted through seeds in most angiosperms, in the absence of a nuclear restorer gene, virtually all seeds produced by female plants would be expected to be female. As a result, any level of seed production in females that is above the level shown by hermaphrodites would be sufficient for females to remain in a population with hermaphrodites.

Based on these theoretical criteria, the amount of female compensation in *G. maculatum*, by itself, would be sufficient for a cyto-nuclear system but not for a nuclear control system. Because female compensation in this and another species in the same genus, *G. sylvaticum* (FC = 0.2–0.7 for seed number), are both below 100%, we can reasonably predict that the genetic system for male sterility is more likely to be of the cyto-nuclear nature. A direct test for this hypothesis using crosses between hermaphrodites from different populations would be most informative and is currently underway.

In summary, female plants in *G. maculatum* did produce more seeds and, at least in one population, also produced seedlings with better performance than their hermaphroditic counterparts within the same population. The amount of compensation through increased seed fitness did contribute to the maintenance of female plants in natural populations; however, the magnitude of compensation seemed to vary both spatially and temporally. Other factors such as pollen limitation, inbreeding depression, and resource limitation could also influence the evolution of this sexual system in *G. maculatum* and warrant further studies.

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