SEX RATIO, SEED PRODUCTION, BIOMASS ALLOCATION, AND THE COST OF MALE FUNCTION IN *CUCURBITA FOETIDISSIMA* HBK (CUCURBITACEAE)

Joshua R. Kohn[1]
Biology Department, University of Pennsylvania, Philadelphia, PA 19104

Abstract.—In the gynodioecious plant *Cucurbita foetidissima* (Cucurbitaceae), females were common in all eight populations examined and made up 32% of adult plants. Females produced 1.5 (SE = 0.2) times as many seeds as did hermaphrodites. The observed difference in seed production alone is not great enough to explain the maintenance of females, especially at their current frequency. Females and hermaphrodites did not differ in number of nodes per stem, stems per plant, internode length, or size of leaves. Females produced more female biomass (fresh or dry weight) than hermaphrodites, but total investment in sexual biomass did not differ. Thus, the biomass of male flowers produced by hermaphrodites was about equal to the extra female biomass produced by females. The results support the existence of a trade-off between male and female reproduction.

Most species of plants are hermaphroditic, but a few are gynodioecious, containing both hermaphrodite and female (male-sterile) individuals. Theoretical models of the sex ratio under gynodioecy predict that females must gain more than twice as much fitness through female function as do hermaphrodites for a nuclear gene for "femaleness" to persist (Lewis, 1941; Lloyd, 1974; Charnov et al., 1976; Charlesworth and Charlesworth, 1978). For any advantage greater than twofold, these models predict the sex ratio.

One way females might achieve increased female fitness is by producing more seeds than are produced by hermaphrodites. Increased seed production might result if resources not spent on male function could be used to increase female function, a trade-off central to sex-allocation theory (Charnov, 1982). While several studies have compared seed production by females and hermaphrodites in gyodioecious species (reviewed by Gouyon and Couvet [1987]), there has been no attempt to relate differences found to allocation by hermaphrodites to male function. Such a comparison is difficult for species in which hermaphrodites produce cosexual flowers, since some floral parts (e.g., petals) cannot be unambiguously assigned to one sexual function or the other.

Since hermaphrodites of *C. foetidissima* produce separate staminate (male) and pistillate (female) flowers, measuring allocation to male and female function is relatively simple, and the resources allocated by hermaphrodites to male function can be compared to the extra allocation to female function by females, if any. Here, I compare seed production, biomass allocation to sexual function, and vegetative characteristics of females and hermaphrodites of *Cucurbita foetidissima,* in order to evaluate the trade-off between male and female function in terms of both fitness and allocation.

Females might also increase their fitness by producing seeds that survive more often than seeds of hermaphrodites. In species in which hermaphrodites are self-compatible, seeds of females might survive better because all of their seeds are outcrossed, while hermaphrodites might frequently self-fertilize and their seeds survive poorly as a consequence (Lewis, 1941; Lloyd, 1974; Charlesworth and Charlesworth, 1978). This occurs in *Cucurbita foetidissima.* Females produce seeds that survive their first year in nature three times more often than seeds from hermaphrodites, apparently due to the benefits of outcrossing (Kohn, 1988*a*).

Previous studies of gynodioecy have been hampered by the complex mode of inheritance of male-sterility often found in wild gynodioecious species. In nearly all cases studied, gynodioecy involves some form of interaction between cytoplasmic factors

―――――――
[1] Present address: Department of Botany, University of Toronto, Toronto, ON M5S 3B2, Canada.

causing male sterility and nuclear genes that restore it (Kesseli and Jain, 1984; van Damme and van Delden, 1982; van Damme, 1983; Horovitz and Dulberger, 1983; Ganders, 1978; Kheyr-Pour, 1980; Sun, 1987; but see Conner [1973]). Theoretical treatments of gynodioecy under nucleo-cytoplasmic control show that the requirement for increased female fitness of females is less stringent than the twofold difference needed with nuclear inheritance (Charlesworth, 1981; Delannay et al., 1981; Ross and Gregorius, 1985). However, predictions vary depending on the exact genetics of the model system, and in some models, no stable equilibrium exists (Gouyon and Couvet, 1987). In nature, these systems can be complex, involving more than one male-sterility cytotype and multiple nuclear restorer genes (van Damme and van Delden, 1982; Kheyr-Pour, 1980; Sun, 1987). In *C. foetidissima,* male-sterility appears to be caused by a single dominant gene or supergene (see below), and thus it is an appropriate species in which to test sex-ratio models.

MATERIALS AND METHODS

Cucurbita foetidissima (Cucurbitaceae), buffalo gourd, is native to grasslands and desert washes of the southwestern U.S. and northern Mexico (Bailey, 1943). Like most members of its genus, *C. foetidissima* is found on disturbed sites, primarily roadsides (Bailey, 1943; Bemis and Whitaker, 1969). Populations generally consist of a series of discrete patches, each separated from the next by tens to thousands of meters. The plant has a perennial root that can weigh up to 70 kg (Dittmer and Talley, 1964). From this root 1–30 stems, each up to 12 m long, are produced yearly. Buffalo gourd can reproduce vegetatively by producing adventitious roots at the nodes which can become autonomous after the vines die back each fall.

Cucurbita foetidissima has been investigated as a potential arid land crop because of the high protein and oil content of its seeds and the starch in its root (DeVeaux and Shultz, 1985; Scheerens and Berry, 1986). Previous studies have revealed the existence of two sexual morphs in nature (Dossey et al., 1981). Monoecious plants (hereafter called hermaphrodites) produce separate staminate and pistillate flowers; gynoecious plants (females) produce pistillate flowers only. Buffalo gourd plants do not change sex. Gender appears to be controlled in a simple Mendelian fashion. Half of the seeds of females become females, and half become hermaphrodites, while all seeds of hermaphrodites become hermaphrodites (Yousef, 1976; Dossey et al., 1981; Kohn, unpub.). Thus, females appear to be the heterogametic sex. The large, yellow, bell-shaped flowers, similar to those of cultivated squashes, last a single morning and are visited chiefly by solitary bees of the Anthophorid genera *Peponapis* and *Xenoglossa* ("*squash bees*"; Hurd and Linsley, 1964; Hurd et al., 1971; Ordway et al., 1987).

Population Sex Ratio.—To estimate the adult sex ratio, I censused eight buffalo gourd populations in southeastern Arizona and western New Mexico within roughly a 300 km radius of Tucson, AZ (see Table 1 for locations). A population was defined as a series of patches along a roadside separated from the next series by more than 50 km or by a mountain pass. At each patch, the number of root crowns of each sex was recorded. In dense patches, where vine growth was too thick and tangled to count individual root crowns, the entire patch was classified as either all-hermaphrodite, all-female, or mixed. Adult population sex ratios were calculated both on the basis of the number of individual root crowns of each sex and by the number of patches of each sex class. Since *C. foetidissima* can reproduce vegetatively, the number of genets within a patch is unknown.

Vegetative Characteristics.—In all, 234 hermaphrodites and 162 females were tagged as part of a long-term demographic study. At the time of tagging, the number of main stems was recorded. Plants were tagged during the middle of the growing season, after all main stems were initiated. The average number of nodes per stem was determined for the plants censused for fruit production (see below) and the sexes were compared by analysis of variance. Lengths and widths of the first five fully expanded, triangular-shaped leaves and the length of the internode leading to each leaf were measured on 20 plants of each sex, chosen at random

TABLE 1. Frequencies of hermaphrodites (H) and females (F) in eight populations of *C. foetidissima* by individual plant (root crown) and by entire patches. Mixed patches averaged 50% female. Vines in dense patches were too intertwined to sex individual plants. Population locations denote highways (e.g., US80 lies along U.S. Highway 80). Total number of patches (countable + dense) = 143; 33.2% female, calculated as ([H&F]/2 + F)/143.

Population	Location	Plants			Countable patches			Dense patches		
		H	F	%F	H	H&F	F	H	H&F	F
AZ82-83	15 km N of Sonoita to Patagonia, AZ	149	43	22.4	8	3	3	5	3	0
US666	5 km N of Sunsites to Elfrida, AZ	75	29	38.7	7	2	1	0	1	1
AZ186	Chiracahua National Monument to junction with Arizona Highway 181 and S 15 km along AZ 181	69	33	32.4	11	3	3	1	1	0
US80	18 km N of Rodeo, NM to Apache, AZ	43	39	47.5	6	3	6	0	0	0
US89	10 km N and S of Chino Valley, AZ	188	68	26.5	9	6	2	6	4	2
US89a	Cottonwood to Jerome, AZ	26	7	21.2	5	1	2	0	0	0
AZ260	Springerville to junction of Arizona Highway 373	158	53	25.1	11	7	1	1	0	1
AZ277	Snowflake, AZ W 20 km	42	77	64.7	6	3	6	1	0	1
Total:		750	349	31.8	63	28	24	14	9	5

from the US80 population (for location, see Table 1). Only one plant of a given sex from any patch was measured, so each plant represents a unique combination of genotype and site.

Reproductive Allocation. — Four patches, each containing both sexes, were selected for detailed study of relative fruit production (locations are given in Fig. 2). In each patch, five adults of each sex were chosen at random, and the sexual expression (e.g., no flower, male flower, female flower, fruit) of every node on five primary stems and their side branches was recorded for three years, 1984–1986. This was facilitated by the fact that each flower type leaves a distinctive dried skeleton that persists for several weeks. The average numbers of male flowers, female flowers, fruits, and nodes per stem on each plant were calculated, and the variation due to sex, site, year, and the interaction of these factors was determined for each trait using analysis of variance.

In late August 1986, 1–8 ($\bar{x} = 2.5$) mature (yellowing) fruits were collected from every plant that produced fruit (82 females and 90 hermaphrodites) along a 30 km section of U.S. Highway 80 north of Rodeo NM, a population studied intensively for measurement of gene flow by pollen (Kohn, 1988*b*). These fruits came from a total of 43 patches, of which 29 contained only hermaphrodites, eight contained only females, and sev-

en contained both. The length and width of each fruit was measured, and each fruit was weighed fresh. Seeds were removed, dried at 35°C for two days, and then allowed to reach constant weight at room temperature. Seeds were counted from a subsample of all fruits collected (177 fruits from 65 hermaphrodites and 46 females from 34 patches: 19 all-hermaphrodite, eight all-female, and seven containing both). Pericarp material was dried to constant weight at 60°C. Since the number of genets within a patch is not known, the means for each sex from each site were used in the analysis. Means were compared by the Mann-Whitney *U* test, because standard transformations failed to remove heterogeneity of variances.

I collected 3–5 female flowers from each of nine females and nine hermaphrodites and five male flowers from each hermaphrodite on the morning they opened. Each plant was from a different patch, chosen at random from the US80 population, and so represents a unique genet. Each flower had been tied shut the evening before opening so that no pollinators could visit. For female flowers, the length and width of the ovary and the length of the corolla were measured, and each flower was weighed fresh, dried to constant weight at 60°C, and then weighed again. Using the average fresh and dry weights of fruits and flowers from females
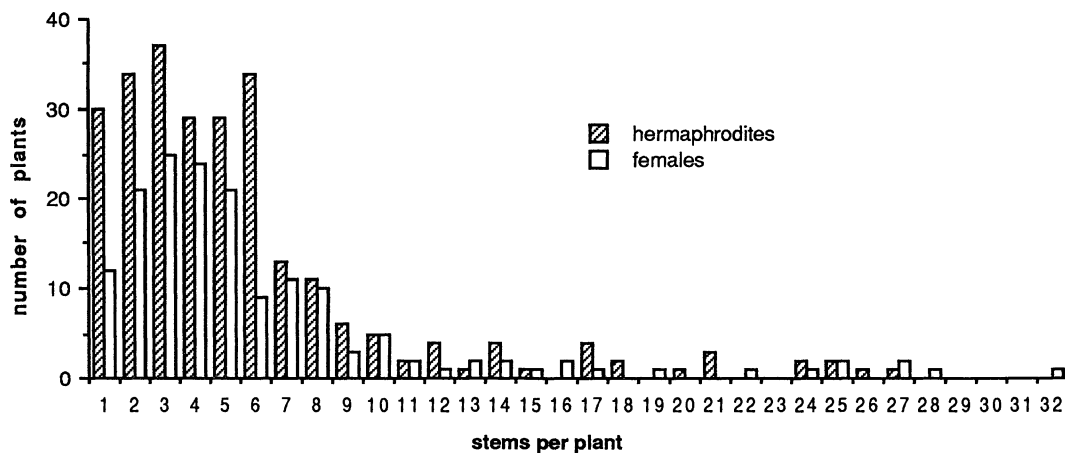
FIG. 1.   The numbers of primary stems for 234 hermaphrodites and 162 females of *Cucurbita foetidissima*. Sexes do not differ significantly (Kolmogorov-Smirnov test, $D = 0.055$, ns) in terms of this trait.

and hermaphrodites, I estimated the biomass allocated to sexual function by plants from the four patches where flowering and fruiting had been censused over three years.

RESULTS

Population Sex Ratio.—Females were common in every population and made up about 32% of all plants, whether calculated on the basis of individual root crowns or based on the sex of patches (Table 1). Population sex ratios based on root crowns varied from 21.2% to 64.7% female; 74% of all patches were unisexual.

Vegetative Characteristics.—There was no difference between the sexes in the number of stems per plant (Fig. 1; Kolmogorov-Smirnov test, $D = 0.055$, $P > 0.7$). There also was no significant difference between the sexes in terms of leaf length, leaf width, total leaf area, or internode length (Table 2) or in terms of nodes per stem (Table 3).

Thus, the sexes did not differ in their gross aboveground vegetative morphology.

Reproductive Allocation.—Females produced 1.8 (SE = 0.2) times as many fruits per stem as did hermaphrodites (Table 3; $P < 0.05$). The difference in fruit production between the sexes was relatively consistent across sites and years (Fig. 2). Increased fruit production by females was due, at least in part, to increased production of female flowers. Females produced 2.0 (SE = 0.4) times as many pistillate flowers per stem as did hermaphrodites (Table 3; $P < 0.001$). Fruit : pistillate-flower ratios of females and hermaphrodites did not differ ($F_{[1, 4]} = 1.3$, ns). Hermaphrodites produced 18.4 (SE = 1.1) staminate flowers per stem.

The pattern of flowering for hermaphrodite (monoecious) plants was similar to that reported for monoecious cucurbit crop species (Whitaker, 1931; Rodrigues Pereira, 1968). Plants rarely produced more than one flower per node. The earliest (closest to the

TABLE 2.   Analyses of variance for leaf length, leaf width, and internode length for 20 plants of each sex. Five fully expanded leaves were measured for each plant. Only one plant of a given sex was used from any one site in order to insure that each plant represents a unique genet.

		Internode length		Leaf length		Leaf width	
Source	d.f.	MS	F	MS	F	MS	F
Sex	1	968	0.3	6,962	1.4	4,940	1.5
Plant(sex)	38	2,994	8.9**	4,717	20.3**	3,276	19.0**
Error	160	334		231		172	

** $P < 0.01$.

TABLE 3.   A) Analyses of variance for the production of fruits, pistillate flowers, and nodes by females (F) and hermaphrodites (H). Analyses were performed on means per stem for each plant in each year and follow Winer (1971 pp. 371–378) for mixed-model ANOVA with one fixed main effect (sex) and two random main effects (site and year). Fruit and flower data were squareroot-transformed, which removed heterogeneity of variances. B) Mean numbers of fruits, pistillate flowers and nodes produced by females and hermaphrodites. Confidence limits for relative fruit and pistillate flower production were jackknifed using Tukey's method (Sokal and Rohlf, 1981 pp. 796–797) by calculating relative fruit production 12 times with one of the 12 combinations of site and year removed. Means with the same superscript letter are not significantly different.

A.				Fruits		Pistillate flowers		Nodes	
	Source	d.f.	F ratio	MS	F	MS	F	MS	F
a)	Year	2	a/e	4.7	3.1	6.5	3.3	7,260	9.3*
b)	Sex	1	(b + g)/(d + f)	3.8	8.8*	10.7	17.6*	86	2.6
c)	Site	3	c/e	2.9	1.9	4.4	2.3	11,303	14.5**
d)	Year × sex	2	d/g	0.3	2.1	0.1	0.4	12	0.1
e)	Year × site	6	e/h	1.5	6.1***	2.0	3.8**	782	1.7
f)	Sex × site	3	f/g	0.2	1.1	0.5	1.3	117	0.5
g)	Year × sex × site	6	g/h	0.1	0.6	0.4	0.7	244	0.5
h)	Error	94		0.2		0.5		449	

B.		Mean		
	Sex	Fruits	Pistillate flowers	Nodes
	Female	2.92[a]	3.84[a]	53.2[a]
	Hermaphrodite	1.62[b]	1.89[b]	50.9[a]
	Female : hermaphrodite ratio	1.8 (SE = 0.2)	2.0 (SE = 0.4)	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

root) flowering nodes produced staminate flowers only. On later nodes, monoecious plants produced a more or less regular repeating sequence of a pistillate flower, a few staminate flowers, a pistillate flower, and so on (Fig. 3). Females had fewer nodes to the first pistillate flower (female mean = 10.6, hermaphrodites mean = 14.7; $F = 140$, $P < 0.001$) and had fewer nodes between successive pistillate flowers, although this latter effect was not significant ($F = 4.8$, $0.1 > P > 0.05$). Scheerens et al. (1987) reported similar phenological differences between agriculturally grown hermaphrodite and female plants of buffalo gourd.

Fruits of hermaphrodites were larger, heavier, and contained more seeds than did fruits from females, while seed mass did not differ (Table 4). Differences in fruit size, mass, and seed number do not appear to be due solely to pollen-limited seed set in females. Fruit traits of females from patches containing both sexes did not differ from those in all-female patches (all Mann Whitney U tests, $P > 0.2$). Differences between females and hermaphrodites in fruit size and seed number may be due to physiological

differences associated with gender, as the data on pistillate flower size suggest (see below).

Pistillate flowers from female plants tended to be smaller and lighter than those from hermaphrodites on the day of opening (Table 5). Staminate flowers weighed 7.4 g fresh (SE = 0.3) and 0.61 g dry (SE = 0.02). Females allocated more biomass to female function than did hermaphrodites, but there was no difference in total allocation to sexual biomass (Table 6). The biomass of male flowers produced by hermaphrodites nearly balanced the additional biomass allocated to female function by females. Hermaphrodites allocated 31% fresh weight and 25% dry weight of their sexual biomass to male function.

DISCUSSION

Females produced 1.5 (±0.2 [SE]) times as many seeds as hermaphrodites (1.8 ± 0.2 times more fruits per stem but only 0.86 ± 0.05 times as many seeds per fruit). The existence of females in *C. foetidissima* cannot be explained by their greater seed production, at least not under models that as-
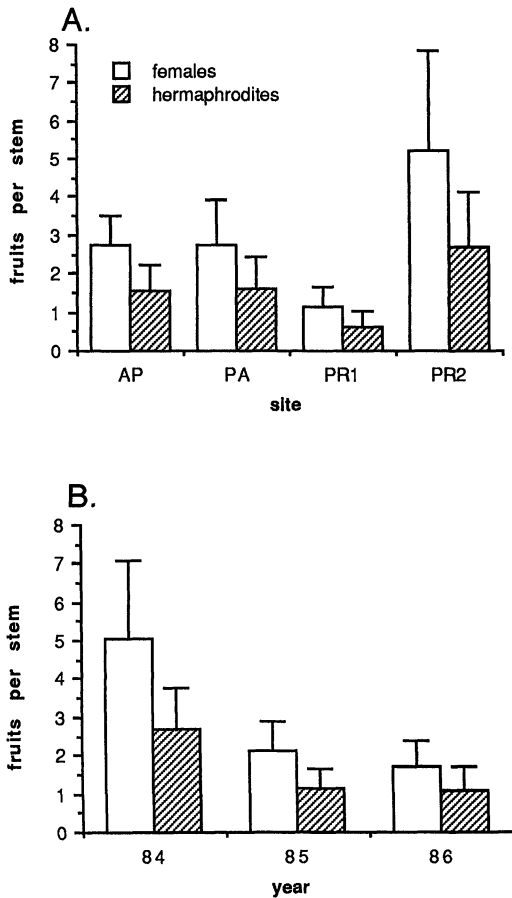
A.

B.

FIG. 2. Fruit production of females and hermaphrodites A) by site and B) by year. Site locations are: AP = west side of U.S. Highway 80, 200 m south of Apache, AZ; PA = west side of Arizona Highway 82, 15.2 km north of Patagonia, AZ; PR1 = east side of U.S. Highway 89, 500 m north of Chino Valley, AZ; PR2 = west side of U.S. Highway 89, 7 km south of Chino Valley, AZ. Error bars represent two standard errors.

sume Mendelian inheritance of gender. If seed production alone were responsible for the present frequency of females, they would have to produce approximately three times as many seeds as do hermaphrodites (Lewis, 1941; Lloyd, 1974; Charnov et al., 1976; Charlesworth and Charlesworth, 1978). This is clearly not happening. In fact, the relative seed fecundity of females may be overestimated in this study, because relative fruit production was estimated using data from patches containing both sexes. While plants in all-female patches isolated from the next

pollen source by up to one kilometer still set some fruit, some reduction in fruit set may occur. The relative fecundity of females in buffalo gourd is below that found in many other gynodioecious species (median = 2.3, N = 23 species, range = 1.1–1,916; data from Gouyon and Couvet [1987]).

Increased survival of seeds from females, partial cytoplasmic control of male sterility, or a nonlinear relationship between seed or fruit production and fitness could explain the existence of females in buffalo gourd. Differential survival of seeds from the two sexes can explain the existence of females at their current frequency. Naturally pollinated seeds of females survive their first year in nature three times more often than naturally pollinated seeds from hermaphrodites. Hand cross- and self-pollinated seeds of hermaphrodites survive as well as naturally pollinated seeds of females and hermaphrodites, respectively (Kohn, 1988a). In addition, electrophoretic analysis of seeds indicates that hermaphrodites self-fertilize about 90% of the time (Kohn, 1988b). Further studies of the genetic basis of gynoecy are ongoing.

While females represented 32% of plants overall, the proportion of females varied from 21% to 65% across populations. This variation could result from sampling error (since relatively few patches were sampled per population), founder effects, or geographical variation in the relative fitness of females. The biology of C. foetidissima is likely to result in a large amount of stochastic sex-ratio variation. If a patch is founded by an hermaphrodite, all future offspring produced within that patch, whether sexual or vegetative, will be hermaphroditic, because seeds of hermaphrodites become hermaphrodites (Dossey et al., 1981; Yousef, 1978; Kohn, unpub.). Further, if seeds from an all-hermaphrodite patch pioneer a series of new patches, all of these will be entirely hermaphroditic. If a seed of either sex founds a patch on a site conducive to vegetative reproduction, the frequency of that sex will increase, at least for the population sex ratio based on root crowns. While the frequencies of males and females of some dioecious species vary with moisture, soil type, or light gradients (Freeman et al.,
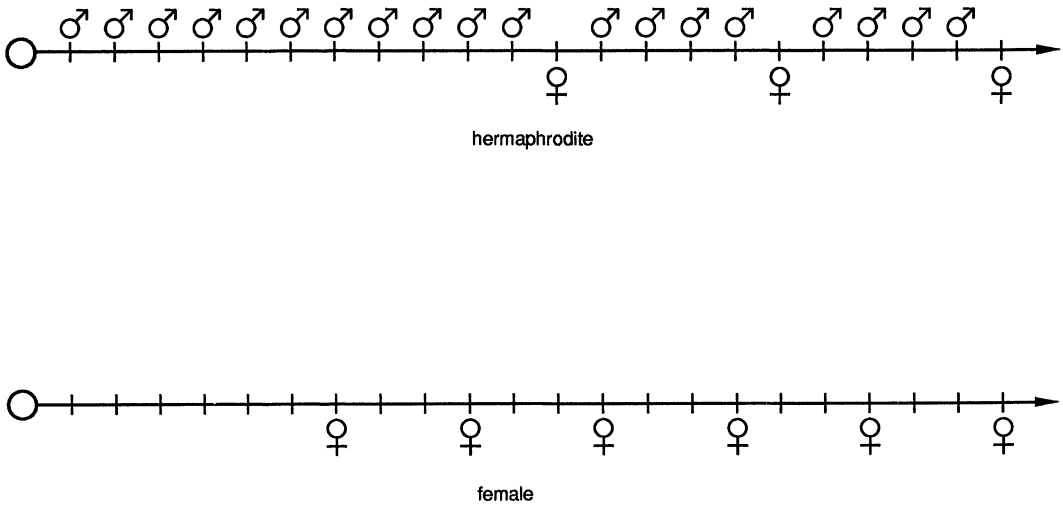
FIG. 3. Schematic representation of flowering in hermaphrodites and females of *Cucurbita foetidissima.* Circles represent root crowns; arrows are growing stems. Male and female symbols refer to the sex of flowers at the indicated nodes.

1976), no segregation along any environmental gradient within populations was apparent, nor were there any obvious environmental correlates of population sex ratio variation in this study.

Nearly three quarters of all patches of buffalo gourd were unisexual (Table 1). This is likely to have important ramifications for the reproductive biology of this species. For instance, just under half of the patches that contain females contain only females, and this may sometimes lead to pollen-limited fruit set. Some all-female patches contain more than 50 ramets, and in patches that contain both sexes, ramets of a given sex are often distinctly clumped. This implies that clonal reproduction may be common within patches, and electrophoretic data support this conclusion. Within patches,

plants of a given sex usually share a common genotype at electrophoretic loci (Kohn, 1988*b*). This may increase the likelihood of both self-fertilization (within genets) among hermaphrodites and inbreeding among females due to kin-mating.

There were no differences between the sexes in terms of stems per plant, nodes per stem, or leaf size. Because the sexes are similar vegetatively, it is worthwhile to investigate their comparative sexual allocations, since, for instance, they appear to have the same photosynthetic surface area. However, it is not known whether the sexes differ in terms of root mass, root morphology, or the photosynthetic capacity of their leaves.

Fruit production in this species is largely concurrent with the production of staminate flowers. In many species, there is a sep-

TABLE 4. Size, fresh weight, dry weight, seed number, and seed weight for naturally pollinated fruits of females and hermaphrodites. Data were analyzed using means for each combination of patch and sex to avoid replication of values from the same genet. Values are means with sample sizes (number of patches) in parentheses.

Trait	Females		Hermaphrodites		U
Fruit length (mm)	67.3	(14)	70.1	(29)	286*
Fruit width (mm)	66.8	(14)	70.8	(29)	318**
Fresh weight (g)	151.8	(14)	185.1	(29)	321**
Dry weight of pericarp (g)	12.2	(15)	15.4	(29)	335**
Number of seeds per fruit	225.4	(15)	263.5	(26)	268[a]
Mean seed weight (g)	0.049	(15)	0.046	(26)	252

[a] $P = 0.05$.
* $P < 0.05$; ** $P < 0.01$.

TABLE 5. Size and weight of pistillate flowers from nine females and nine hermaphrodites. For each plant 3–5 were measured. Each plant came from a different site.

Trait	Mean for females	Mean for hermaphrodites	F	P
Fresh weight (g)	11.87	13.79	3.03	0.1
Dry weight (g)	0.94	1.07	3.40	<0.1
Corolla length (mm)	89.3	91.8	0.21	>0.01
Ovary length (mm)	24.5	27.0	5.10	<0.05
Ovary width (mm)	18.7	20.4	4.37	0.054

aration in time between flowering and fruit provisioning. This can mean that the pool of resources available for each sexual function differs (Goldman and Willson, 1986), which could affect the predictions of allocation theory (Geber and Charnov, 1987). In buffalo gourd, hermaphrodites provision both staminate flowers and fruits concurrent with fruit provisioning by females. Pistillate flowers of hermaphrodites develop precociously in comparison with staminate flowers; a pistillate flower will be open on the same day as a staminate flower approximately seven nodes closer to the root (Scheerens et al., 1987; pers. observ.). Fruits reach full volume ten days after pollination, although seed maturation may take a month or more (Ba-Amer and Bemis, 1968; Alves Costa and Bemis, 1972). During most or all of this period, male flowers continue to be produced.

Females plants produce more female biomass than do hermaphrodites, but total sexual biomass production is similar for both sexes (Table 6). Thus, there appears to be a trade-off between biomass allocation to male and female function. In contrast, gynoecious varieties of cucumber do not yield more fruit than monoecious morphs (Denna, 1973; Wehner and Miller, 1985). Also, in monoecious cucumbers, removal of pistillate flower buds results in increased vegetative growth, whereas removal of staminate buds has no measurable effect, suggesting that there is little cost of male function (Silvertown, 1987).

There are several reasons why the results of this study might differ from the findings for cultivated cucumbers. First, allocation to male function by hermaphrodite C. foetidissima may be particularly high. Since the plant is monoecious and has very large flowers, each male flower represents a relatively large biomass investment. In addition, the presence of females may have selected for increased allocation to male function by hermaphrodites. There is no evidence of this, however. Flowers are large in all other (purely monoecious) Cucurbita species, and the ratio of male flowers to fruits reported here is similar to those reported for cultivated, monoecious Cucurbita species and for monoecious species in general (Sutherland, 1986). The proportion of biomass allocated to male function by hermaphrodites is also similar to that reported for wild monoecious species (data in Goldman and Willson [1986]). On the other hand, data from cultivated cucumbers may be misleading, since there has been strong artificial selection on fruit size. This may have increased allocation to female function so much that allocation to male function is now negligible, especially when plants are given optimal levels of water and fertilizer. Finally, the nature of the trade-off in allocation between female and hermaphrodite morphs may depend on the specific male-sterility gene(s) involved. Van Damme (1984) showed that fecundity of females and hermaphrodites in Plantago lanceolata depended on both plasmon type and genotype at restorer loci. By comparing the allocation of the two morphs, one learns what happens under these genetic conditions, but perhaps little about what is physiologically possible given a different male-sterility mutation.

While the data suggest a direct trade-off between biomass allocated to male versus female function, alternative explanations exist. First, the trade-off is evaluated at only one point; an approximately 30% investment in male function by hermaphrodites resulted in an approximately 30% reduction in allocation to female biomass by hermaphrodites relative to females. This single

TABLE 6.   A) Analyses of variance and B) means for allocation of sexual biomass by females and hermaphrodites. Biomass allocation was estimated using the fresh and dry weights of fruits and flowers produced by plants of each sex (Tables 3, 4) and multiplying by the number of fruits, nonfruiting female flowers, and male flowers produced by each plant of each sex in the four patches in which phenology was censused during 1984–1986 (Table 2). F ratios were calculated as in Table 2.

| | | Fresh weight | | | | Dry weight | | | |
| | | Sexual biomass | | Female biomass | | Sexual biomass | | Female biomass | |
A. Source	d.f.	MS	F	MS	F	MS	F	MS	F
Year	2	1,105	3.7	1,156	3.7	122.3	3.6	125.1	3.5
Sex	1	11	0.5	519	11.7*	1.5	0.6	58.1	11.0*
Site	3	532	1.8	643	2.1	62.3	1.8	72.1	2.0
Year × sex	2	43	1.6	33	1.0	4.5	1.5	3.9	1.1
Year × site	6	301	5.1***	313	4.6***	34.4	5.2***	35.3	4.8***
Sex × site	3	39	1.4	14	0.4	3.8	1.2	1.7	0.5
Year × sex × site	6	27	0.5	32	0.5	3.1	0.5	3.5	0.5
Error	94	59		68		6.6		7.3	

| B. | | Biomass (g) | |
Character		Females	Hermaphrodites
Fresh weight, sexual		459.7	433.9
Fresh weight, female		459.7	297.5
Dry weight, sexual		53.1	45.4
Dry weight, female		53.1	34.1

* $P < 0.05$; *** $P < 0.001$.

point gives little information as to the overall shape of the allocation trade-off function. Second, biomass may not be the appropriate currency of the trade-off (Goldman and Willson, 1986; Silvertown, 1987). Photosynthate may not be limiting, since leaves subtending developing fruits can sometimes increase their photosynthetic rate (Barrett and Amling, 1978). Nutrients such as nitrogen could be the real currency of the trade-off. However, fruits of wild *C. foetidissima* from Colorado contain 4.3% nitrogen (Lancaster et al., 1983), while staminate flowers collected in this study contained 4.2% nitrogen (SE = 0.1%; N = 5 plants, 3 flowers/plant), so nitrogen allocation to sexual function by the two sexes may also be equal. In *Cucurbita,* the currency of the trade-off could be meristems, rather than biomass. *C. foetidissima,* like all members of its genus, very seldom produces more than a single flower per node. By not making staminate flowers, female plants free more meristems to become pistillate.

Regardless of the physiological currency, male function in buffalo gourd is very costly in terms of female fitness. By not producing male flowers, females are able to produce 50% more seeds than hermaphrodites. In addition, hermaphrodites pay an even greater cost for male function in terms of seed quality. Seeds of females are all outcrossed, and apparently because of this, their seeds survive three times more frequently than seeds of hermaphrodites (Kohn, 1988a, 1988b).

LITERATURE CITED

ALVES COSTA, J. T., AND W. P. BEMIS. 1972. After-ripening effect on seed germination and viability of *Cucurbita foetidissima* seed. Turrialba 22:207–209.
BA-AMER, M. A., AND W. P. BEMIS. 1968. Fruit and

seed development in *Cucurbita foetidissima*. Econ. Bot. 22:297–299.

BAILEY, L. H. 1943. Species of *Cucurbita*. Gentes Herbarum 6:267–322.

BARRETT, J. E., AND H. J. AMLING. 1978. Effects of developing fruits on production and translocation of C^{14}-labeled assimilates in cucumber. Hort-Science 13:545–547.

BEMIS, W. P., AND T. W. WHITAKER. 1969. The xerophytic *Cucurbita* of northwestern Mexico and southwestern United States. Madroño 20:33–41.

CHARLESWORTH, B., AND D. CHARLESWORTH. 1978. A model for the evolution of dioecy and gynodioecy. Amer. Natur. 112:975–997.

CHARLESWORTH, D. 1981. A further study of the problem of the maintenance of females in gynodioecious species. Heredity 41:27–39.

CHARNOV, E. L. 1982. The Theory of Sex Allocation. Princeton Univ. Press, Princeton, NJ.

CHARNOV, E. L., J. MAYNARD SMITH, AND J. BULL. 1976. Why be an hermaphrodite? Nature 263:125–126.

CONNER, H. E. 1973. Breeding systems in *Cortaderia* (Gramineae). Evolution 27:663–678.

DELANNAY, X., P.-H. GOUYON, AND G. VALDEYRON. 1981. Mathematical study of the evolution of gynodioecy with cytoplasmic inheritance under the effect of a nuclear restorer gene. Genetics 99:169–181.

DENNA, D. W. 1973. Effects of genetic parthenocarpy and gynoecious flowering habit on fruit production and growth of cucumber *Cucumis sativus* L. J. Amer. Soc. Hort. Sci. 98:602–604.

DEVEAUX, J. S., AND E. B. SHULTZ. 1985. Development of buffalo gourd (*Cucurbita foetidissima*) as a semiaridland starch and oil crop. Econ. Bot. 39:454–472.

DITTMER, H. J., AND B. P. TALLEY. 1964. Gross morphology of tap roots of desert cucurbits. Bot. Gaz. 125:121–126.

DOSSEY, B. F., W. P. BEMIS, AND J. C. SCHEERENS. 1981. Genetic control of gynoecy in the buffalo gourd. J. Hered. 72:355–356.

FREEMAN, D. C., L. G. KLIKOFF, AND K. T. HARPER. 1976. Differential resource use by the sexes of dioecious plants. Science 193:597–599.

GANDERS, F. R. 1978. The genetics and evolution of gynoecy in *Nemophila menziesii* (Hydrophyllaceae). Can. J. Bot. 56:1400–1408.

GEBER, M. A., AND E. L. CHARNOV. 1986. Sex allocation in hermaphrodites with partial overlap in male/female resource inputs. J. Theoret. Biol. 118:33–43.

GOLDMAN, D. A., AND M. F. WILLSON. 1986. Sex allocation in functionally hermpahroditic plants: A review and critique. Bot. Rev. 52:157–194.

GOUYON, P.-H., AND D. COUVET. 1987. A conflict between two sexes, females and hermaphrodites, pp. 245–261. *In* S. C. Stearns (ed.), The Evolution of Sex and its Consequences. Birkhauser-Verlag, Basel, Switzerland.

HOROVITZ, A., AND R. DULBERGER. 1983. The genetic basis of gender in *Silene vulgaris*. Heredity 51:371–376.

HURD, P. D., AND E. G. LINSLEY. 1964. The squash

and gourd bees—genera *Peponapis* Robertson and *Xenoglossa* Smith—inhabiting America north of Mexico (Hymenoptera:Apoidea). Hilgardia 35:375–477.

HURD, P. D., E. G. LINSLEY, AND T. W. WHITAKER. 1971. Squash and gourd bees (*Peponapis, Xenoglossa*) and the origin of cultivated *Cucurbita*. Evolution 25:218–234.

KESSELI, R., AND S. K. JAIN. 1984. An ecological genetic study of gynodioecy in *Limnanthes douglasii* (Limnanthaceae). Amer. J. Bot. 71:775–786.

KHEYR-POUR, A. 1980. Nucleo-cytoplasmic polymorphism for male sterility in *Origanum vulgare* L. J. Hered. 71:253–260.

KOHN, J. R. 1988a. Why be female? Nature. 335:431–433.

———. 1988b. Costs and benefits of gender in *Cucurbita foetidissima* (Cucurbitaceae) HBK. Ph.D. Diss. Univ. Pennsylvania, Philadelphia.

LANCASTER, M., R. STOREY, AND N. W. BOWER. 1983. Nutritional evolution of buffalo gourd: Elemental analysis of seed. Econ. Bot. 37:306–309.

LEWIS, D. 1941. Male sterility in natural populations of hermaphrodite plants: The equilibrium between females and hermaphrodites to be expected with different types of inheritance. New Phytol. 40:56–63.

LLOYD, D. G. 1974. Theoretical sex ratios of dioecious and gynodioecious angiosperms. Heredity 32:11–34.

ORDWAY, E., S. L. BUCHMANN, R. O. KEUHL, AND C. W. SHIPMAN. 1987. Pollen dispersal in *Cucurbita foetidissima* (Cucurbitaceae) by bees of the genera *Apis, Peponapis,* and *Xenoglossa* (Hymenoptera: Apidae, Anthophoridae). J. Kans. Entomol. Soc. 60:489–503.

RODRIGUES PEREIRA, A. S. 1968. Sex expression in floral buds of acorn squash. Planta 80:349–358.

ROSS, M. D., AND H.-R. GREGORIUS. 1985. Selection with gene-cytoplasm interactions. II. Maintenance of gynodioecy. Genetics 109:427–439.

SCHEERENS, J. C., AND J. W. BERRY. 1986. Buffalo gourd: Composition and functionality of potential food ingredients. Cereal Foods World 31:183–191.

SCHEERENS, J. C., Y. M. R. YOUSEF, A. E. RALOWICZ, A. C. GATHMAN, AND H. M. SCHEERENS. 1987. Floral development, flowering patterns, and growth rate of monoecious and gynoecious buffalo gourd. J. Amer. Soc. Hort. Sci. 112:574–578.

SILVERTOWN, J. 1987. The evolution of hermaphroditism: An experimental test of the resource model. Oecologia 72:157–159.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd Ed. Freeman, San Francisco, CA.

SUN, M. 1987. Genetics of gynodioecy in Hawaiian *Bidens* (Asteraceae). Heredity 59:327–336.

SUTHERLAND, S. 1986. Patterns of fruit-set: What controls fruit-flower ratios in plants? Evolution 40:117–128.

VAN DAMME, J. M. M. 1983. Gynodioecy in *Plantago lanceolata* L. II. Inheritance of three male sterility types. Heredity 50:253–273.

———. 1984. Gynodioecy in *Plantago lanceolata* L. III. Sexual reproduction and the maintenance of male steriles. Heredity 52:77–93.

VAN DAMME, J. M. M., AND W. VAN DELDEN. 1982. Gynodioecy in *Plantago lanceolata* L. I. Polymorphism for plasmon type. Heredity 49:303–318.

WEHNER, T. C., AND C. H. MILLER. 1985. Effect of gynoecious expression on yield and earliness of a fresh-market cucumber hybrid. J. Amer. Soc. Hort. Sci. 110:464–466.

WHITAKER, T. W. 1931. Sex ratio and sex expression in the cultivated cucurbits. Amer. J. Bot. 18:359–366.

WINER, B. J. 1971. Statistical Principles in Experimental Design. McGraw-Hill, N.Y.

YOUSEF, Y. 1976. Sex expression in the buffalo gourd *Cucurbita foetidissima* HBK. Ph.D. Diss. Univ. Arizona, Tucson.

Corresponding Editor: A. G. Stephenson