

THE ADAPTIVE SIGNIFICANCE OF SEXUAL LABILITY IN PLANTS USING *ATRIPLEX CANESCENS* AS A PRINCIPAL EXAMPLE¹

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ABSTRACT

Experimental studies demonstrate that up to 20% of the individuals of *Atriplex canescens* and other species of the genus can alter their sexual state from one season to the next. Approximately 5% of the *A. canescens* individuals changed from an exclusively pistillate phenotype to an exclusively staminate phenotype or vice versa. Another 5% of the individuals changed their primary sexual emphasis, e.g., from an exclusively pistillate condition to a dominantly staminate, monoecious condition. In addition, 10% of the population changed from a unisexual state to a monoecious state in which staminate and pistillate flowers were approximately equal in number (or vice versa). In *Atriplex canescens*, sex change occurred in response to three stresses: an unusually cold winter, drought, and prior heavy seed set. When placed under stress, pistillate individuals are significantly more likely to change sex than staminate individuals. The ability to change sex appears to confer a survival advantage to the individual. Plants which change sex also appear to begin reproducing earlier than pistillate plants while producing as many seeds as pistillate plants do. Thus individuals that change sex appear to have some reproductive advantages in the population studied.

Recent ecological studies indicate that androecious (male) and gynoecious (female) individuals of several dioecious plant species exhibit partial niche separation; J. L. Harper has termed this pattern the Jack Sprat effect (Onyekwelu & Harper, 1979). The most commonly reported manifestation of the Jack Sprat effect is the segregation of androecious individuals and gynoecious individuals along strong environmental gradients. For example, Freeman et al. (1976) showed that the sexes of five dioecious plant species of the intermountain region of the western United States segregated along gradients of water availability or salinity. Androecious plants were proportionately more abundant at the stressful end of the gradient and gynoecious plants were proportionately more prevalent in favorable environments. In another study, Fox and Harrison (1981) demonstrated that slope exposure affected the sex ratio of *Hesperochloa kingii*. They typically found that androecious individuals of the species were more common in areas with low soil moisture whereas gynoecious in-

dividuals were usually more common in moister areas. Similar results have been observed by others (Davey & Gibson, 1917; Richards, 1975; Waser, pers. comm.). Cox (1981) showed that the sexes of *Trophis involucrata* and *Mercurialis perennis* segregate along gradients of phosphorus availability and pH, respectively, and Onyekwelu and Harper (1979) found differences in sex ratios of spinach in populations experiencing different intensities of intraspecific competition. In all of these cases, androecious plants were proportionately more abundant in the most stressful environments. Further evidence for partial niche separation between the sexes of dioecious plants comes from the studies of Putwain and Harper (1972), who showed that competition between members of the same sex was considerably more intense than competition between androecious and gynoecious plants of *Rumex acetosa* and *R. acetosella*.

A growing number of researchers have found physiological and morphological differences between the sexes of dioecious species (Heslop-Harrison, 1972; Adams & Powell, 1976; Lloyd

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& Webb, 1977; Valdeyron & Lloyd, 1979; Hancock & Bringham, 1979; Gross & Soule, 1981; Meagher & Antonovics, 1982). Such differences apparently arise as a result of natural selection operating differently on individuals of each sex. Selection appears to operate on differences in requirements for staminate and pistillate functions. For example, androecious and gynoeceous plants growing on common sites experience different levels of water stress. Gynoeceous plants of several species [*Atriplex hymenelytra* (Stark, 1970), *A. canescens*, *A. confertifolia*, *A. cuneata*, *A. corrugata* (Freeman & McArthur, 1982), *Hesperochloa kingii* (Fox & Harrison, 1981), *Simmondsia chinensis* (Hikmat et al., 1972), and *Spinacea oleracea* (Freeman, unpubl. data)] tend to be under greater water stress than androecious plants, particularly during midday in the fruiting season (Freeman & McArthur, 1982). Freeman and Vitale (unpubl. data) show that under severe water stress, the pistillate function in spinach was impaired to a greater degree than was the staminate function. In her studies of tropical orchids, Gregg (1973) has shown that shading more adversely influenced the pistillate than the staminate reproductive potential.

Whereas numerous studies indicate partial niche separation between the sexes of dioecious plants, little or no attention has been given to the evolutionary consequences of the Jack Sprat effect. Furthermore, few studies examine the selective forces that create staminate biased sex ratios in one environment and pistillate biased ratios in another.

If two species in physiological competition show partial niche separation, conventional theory would predict that the reproductive potential of those species would be unequal at some sites of coexistence, and that the physiological responses of the two species would differ significantly for at least some widespread and recurrent environmental stresses (Birch, 1953a, 1953b). In a similar fashion, if the sexes of dioecious plants do indeed display partial niche separation along a resource gradient, we would then expect androecious and gynoeceous plants to respond differently to at least some environmental variables. In such cases, if patch size is small relative to the distance androecious plants can disperse pollen, androecious and gynoeceous plants may not be equally fit in all environments.

Using sex allocation theory, Charnov and others (Charnov & Bull, 1977; Freeman et al., 1980; Charnov, 1982) have shown that if the sexes are

not equally fit in all environments and the environments are highly heterogeneous in time and/or space, and if an individual has little control over which environment it will experience, then genes allowing environmental control of sex will be favored over genes imparting strict genetic control of sexual expression. Given these assumptions, in some environments or at some times individuals of a dioecious plant species that can alter sexual expression in response to environmental cues can increase their genetic contribution to future generations. That over 50 dioecious plant species are known in which individuals have been observed to change sex or to produce hermaphrodite or monoecious offspring supports the hypothesis that labile sexual expression imparts some selective advantage to individuals in at least some situations (Freeman et al., 1980).

Mathematical models developed by Charnov and Bull (1977) predict that if monoecious individuals were placed in a common environment where staminate and pistillate functions had unequal fitness, floral sex ratios would be locally altered to favor the more successful sex. That kind of a response appears to have occurred in *Acer grandidentatum* (Barker et al., 1982), *Juniperus osteosperma*, *Quercus gambelii*, and *Sarcobatus vermiculatus* (Freeman et al., 1981).

VARIABLE FITNESS OF ANDROECIOUS AND GYNOECIOUS INDIVIDUALS IN COMMON ENVIRONMENTS

Sex allocation theory predicts that labile sex expression may evolve where patch quality differentially affects staminate and pistillate fitness. To test that theory, the first question requiring attention is, "Are androecious and gynoeceous plants equally fit in all environments?" Due to the difficulty of quantifying reproductive success of androecious plants, few studies have examined the influence of environment on relative fitness of androecious and gynoeceous individuals of dioecious plant species. We are aware of only four studies that document differences in the environment and associated fitness of androecious and gynoeceous plants (Gregg, 1973; Fox & Harrison, 1981; Freeman & Vitale, unpubl. data; Freeman et al., unpubl. data). If androecious and gynoeceous individuals are not equally fit in all environments, a plant may enhance its fitness by changing sex; thus, sex change may be viewed as an adaptation to patchy en-

TABLE 1. The effect of environment on the fitness of androecious and gynoeious plants of four orchid species. Plants were grown in full or 50% of full sunlight. The fitness values were computed by dividing number of inflorescences in partial shade by the number produced in full sun (data from Gregg, 1973).

Species	Growing Condition	Relative Fitness	
		Androecious	Gynoeious
<i>Cycnoches warscewiczii</i>	Full sun	1.00	1.00
	Bright shade	17.50	1.00
<i>Catasetum expansum</i>	Full sun	1.00	1.00
	Bright shade	4.71	0.18
<i>Cycnoches densiflorum</i>	Full sun	1.00	1.00
	Bright shade	0.63	0.11
<i>Cycnoches stenodactylon</i>	Full sun	1.00	1.00
	Bright shade	0.42	0.06

vironments. If androecious and gynoeious individuals have equal fitness in all environments, nothing would be gained by changing sex. We will now examine the four studies that have noted differences in the environment and that report measures of staminate and pistillate fitness. We will consider whether fitness differences exist between the two sexes and whether those differences are correlated with environmental differences.

Gregg (1973) conducted manipulative experiments with four species of polygamous orchids. She grew plants in full sun and then in "bright shade" (50% full sun) and noted the sex expressed and the number of inflorescences per plant. In order to determine the relative performance of androecious and gynoeious plants, we have divided the number of inflorescences produced in the shade by the number produced in full sun for both sexes (Table 1). The data demonstrate that gynoeious plants produce relatively fewer inflorescences in shade compared with androecious plants. For two species, androecious performance was enhanced by shading. The results of her studies coupled with those of Dodson (1962), which demonstrated that androecious plants of some orchid species are proportionally more abundant in shady areas and gynoeious plants more common in light gaps, suggest a differential response of androecious and gynoeious plants to shading (partial niche separation).

Fox and Harrison (1981) compared the sex ratios of populations of *Hesperochloa kingii*, a dioecious grass, growing in mesic versus xeric environments. They found six to seven bar differences in soil water potential between xeric and

mesic sites. As previously noted, they observed proportionately more androecious plants in the xeric environment. Fox and Harrison (1981) also used the number of inflorescences per individual as a measure of fitness. Because both sexes usually produced the greatest number of inflorescences in mesic environments, we report fitness of both sexes as 1.0 on those sites. To allow easy comparison, the inflorescences/plant ratios on xeric sites are given as a fraction of the number produced on the more moist paired site (Table 2). In three of the four cases considered, androecious plants were appreciably more fit than were gynoeious plants on xeric sites. The fourth case was puzzling to Fox and Harrison and is to

TABLE 2. The effect of environment on the fitness of androecious and gynoeious plants of *Hesperochloa kingii* (Fox & Harrison, 1981). See text for an explanation of fitness values.

Site	Description	An- Gynoe-	
		droe- noe-	cious cious
		Fit- Fit-	ness ness
A	Moist alluvial bench	1.00	1.00
	Dry sandy slope	1.00	0.57
B	Moist north-facing slope	1.00	1.00
	Dry south-facing slope	0.50	0.24
C	Moist grassy bottom land	1.00	1.00
	Dry south-facing slope	0.61	0.11
D	Moist sagebrush bench	1.00	1.00
	Dry west-facing slope	0.89	1.42
Overall } Moist		1.00	1.00
Average } Dry		0.75	0.59

us as well, because the fourth site shows the greatest difference in sex ratio between moist and dry microhabitats in the study, i.e., a slight pistillate biased sex ratio was observed in the wet environment ($S/P = 0.69$) whereas a significantly staminate biased sex ratio occurred in the dry environment ($S/P = 3.76$ and $\chi^2 = 24.39$, $P < 0.01$). Thus, data for sex ratios are in agreement with our predictions, but the relative fitness values obviously do not agree with our thesis. When we include the data from this aberrant site (D), the overall averages show that dry environments depressed pistillate fitness more than staminate fitness (Table 2) although the difference is not significant ($t = 0.69$, $P < 0.53$). When site D is excluded the difference is highly significant ($t = 5.6$, $P < 0.05$).

Freeman and Vitale (unpubl. data) germinated spinach seeds in a common environment and then randomly assigned seedlings to well watered, 'wet' treatment and a water stressed, 'dry' treatment. Plants in the 'wet' treatment received five times more water than stressed plants. The average number of viable pollen grains per anther multiplied by the average number of anthers per plant was used as the measure of staminate fitness. Pistillate fitness was taken as the average number of germinable seeds produced/gynoeceous plant. Using Freeman and Vitale's data, we express staminate and pistillate fitness in stressed conditions as a fraction of that in the 'wet' treatment. Androecious plants in the 'dry' environment had a relative fitness of 0.77 while the relative fitness of gynoeceous plants in the 'dry' environment was only 0.16.

Freeman et al. (unpubl. data) have compared the reproductive biomass of androecious and gynoeceous individuals of *Atriplex canescens* growing on steep slopes versus alluvium at slope bases. Androecious reproductive biomass was taken as the weight of staminate catkins prior to dehiscence of exerted stamens. Gynoeceous reproductive biomass was taken as the weight of fruits just before fruit abscission. Because gynoeceous plants on alluvial soils produced more fruits than gynoeceous plants on slopes, we calculated relative fitness of the latter by dividing their reproductive biomass by the comparable variable for gynoeceous plants on alluvium. Relative fitness of slope and alluvium androecious plants was similarly computed. Relative fitness of 'slope' androecious plants was 0.82, but relative fitness of 'slope' gynoeceous plants was only 0.33 ($t = 4.82$, $P < 0.001$).

In each of the foregoing cases, the relative performance of gynoeceous plants on stressed sites was less than the relative fitness of androecious plants. Such a response would be predicted if the sexes actually showed partial niche separation as suggested by Freeman et al. (1976) and Onyekwelu and Harper (1979). However, we note that it is not necessary for gynoeceous individuals to respond less well than androecious individuals under stress to validate the assumption of sex allocation theory. It is only necessary that fitness of androecious and gynoeceous plants be unequal under some conditions. Some physiological, morphological, and anatomical studies of dioecious plants have shown differences between androecious and gynoeceous plants, but in most cases there is little indication that the differences have ecological or evolutionary significance (Lloyd & Webb, 1977; Freeman et al., 1980). In contrast, the foregoing case studies suggest that the staminate and pistillate functions are unequal in common environments. Such results have obvious practical consequences, but they also suggest possible avenues for the evolution of at least some dioecious plant taxa and/or taxa capable of reversing sexual expression. Linking unequal fitness of male and female gametes at common sites to evolution of a dioecious species will require evidence that androecious plants in stressful environments sire more descendants by exporting pollen to more mesic sites than could be produced by nearby stressed gynoeceous plants. If such a condition existed, plants with pistillate flowers in dry environments could increase their genetic contribution to future generations by producing staminate flowers instead. In the only experimental study known that attempts to evaluate the fitness of stressed and unstressed androecious and gynoeceous plants, Freeman and Vitale (unpubl. data) show that androecious plants from a dry environment that sired three gynoeceous plants there and one in a wetter environment would leave more offspring in the second generation, on average, in the moist than in the dry environment (54 in the moist versus 21 in the dry), because gynoeceous plants were sixfold more fit in the moist than dry environments.

SEX CHANGES AND TERMINOLOGY

The foregoing evidence indicates that androecious and gynoeceous individuals of at least some dioecious plant species are not equally fit in all environments. Because we know of no mechanism by which seeds can choose the environment

in which they fall, some plant species satisfy the assumptions of sex allocation theory and would be predicted to be capable of switching sex by that theory. The question we now address is, "Do individuals of dioecious plant species change sex (or, in the case of annuals, show environmental sex determination)?" Also, do individuals of monoecious plant species alter their floral sex ratios in response to changes in environmental quality?

Dioecious species, by definition, contain only unisexual individuals. Obviously a plant that changes sex must be genetically bisexual and is not strictly speaking dioecious. The ecological and evolutionary significance of altered sex expression is equivalent to dioecy, however. We will refer to species that display environmental sex determination or change sex as subdioecious.

Typically, *Atriplex canescens* individuals are either unisexual (Gynoeceous = G, or Androeceous = A) or monoecious (Mo = having both staminate and pistillate flowers on the same individual). A plant that is exclusively gynoeceous one year and exclusively androeceous another has changed sexual expression. But what of a plant that changes from a unisexual phenotype to a monoecious phenotype? Has it changed sex? Clearly the change is one of degree and not of kind. We would agree that an exclusively gynoeceous individual one year that displayed a single staminate flower among a myriad of pistillate flowers the next has not changed its primary sexual expression. Nevertheless, the plant has demonstrated a genetic capacity to produce staminate flowers. We will consider any gynoeceous plant that later obtains an appreciable fraction of its fitness (say 20%) through pollen has changed its sexual state. For convenience, changes of less than 20% will be described as sexual inconstancy rather than change of the primary sexual state. We will call changes exceeding 20% sex change. When 20–80% of the flowers are of the sex not previously displayed, we will describe the plant as monoecious. If changes exceed 80%, we will refer to the situation as a change in primary sexual expression.

A number of researchers, most notably Lloyd and Bawa (in press), are willing to concede that sexual inconstancies occur but do not believe that individuals change their primary sexual expression. Furthermore, they argue that if plants do change primary sexual expression, the fraction of the population so affected is trivially small. We will present evidence suggesting that in the

case of *Atriplex canescens*, the Lloyd and Bawa position is inconsistent with the data. If plants do track the environment as hypothesized in sex allocation theory, then small changes in ratios of staminate to pistillate flowers from year to year on monoecious plants would also be predicted and should be more frequent than large changes. Thus, plants that respond to modest environmental changes may appear to be only sexually inconstant. Absence of large changes in floral sex ratios of individuals would constitute strong evidence against sex allocation theory. If large changes can be documented, sex allocation theory would be strengthened.

SEXUAL STATES IN *ATRIPLEX CANESCENS*

In 1977, McArthur reported that some individuals of a half sib family of *Atriplex canescens* changed sexual expression. Work has continued with this population to the present. Several kinds of data on the sexual state of individuals now exist. Annually, all individuals have been classified as androeceous (A), gynoeceous (G) or monoecious (Mo). In Table 3, the kinds of changes observed are listed. As expected, the bulk of the changes were between gynoeceous and monoecious or androeceous and monoecious states; only 33 of 665 individuals changed from androeceous to gynoeceous or vice versa. An additional six plants were monoecious at one time in their life, exclusively androeceous another year, and exclusively gynoeceous in yet another year. Changes between androeceous and gynoeceous sexual states support sex allocation theory. However, gynoeceous ↔ monoecious and androeceous ↔ monoecious changes could represent either sexual inconstancies or major changes of sexual expression, depending on ratios of staminate and pistillate flowers of individual plants. These data by themselves are not sufficient to allow discrimination between sexual inconstancy and sex change without the addition of floral sex ratio data.

Fruits were collected from 14 of 35 plants that had been androeceous and monoecious but never gynoeceous. Fruit production of these monoecious plants was compared with average fruit set of gynoeceous plants in the same year. Most of the androeceous ↔ monoecious plants had a single episode of sexual change. In cases in which plants had multiple episodes, the year of largest fruit set was used. Plants producing less than 20% as much fruit by weight as the average gynoeceous plant were classified as sexually inconstant. Plants

TABLE 3. Summary of floral phenotypes in the U103p family of *Atriplex canescens* over the period 1972–1978. The population is maintained at the Snow Field Station, Ephraim, Utah (McArthur & Freeman, 1982).

Floral Phenotype ^a	1972	Number of Plants					Probability of Constant Phenotypes
		Died Without Changing Phenotype	Constant Phenotype Through 1978 ^b	Changed Phenotypes (at least one year) to:			
				G	A	Mo ^c	
G	372	40	149	—	22	161	0.51
A	228	39	155	11	—	23	0.85
Mo	34	2	1	12	13	6	0.09
0	<u>31</u>	<u>8</u>	<u>1</u>	<u>3</u>	<u>6</u>	<u>13</u>	0.29
Totals	665	89 ^d	306	26	41	203	

^a G = Gynoeceous; A = Androeceous; Mo = Monoecious; 0 = No flowers.

^b G, A, and Mo, phenotypes considered constant if only departure was to 0 phenotype.

^c Includes plants that were G or A some years in addition to being Mo for at least one year.

^d Actually 101 plants died and seven were sacrificed for pathological study by 1978. The other 19, however, are accounted for under "changed phenotypes."

producing 20–80% as much fruit as an average gynoeceous plant were considered to have changed from unisexual to a monoecious state, and those producing greater than 80% of the average fruit crop were considered to have changed their primary sexual expression. These data show that 36% of the 14 test plants were sexually inconstant, 43% were monoecious and 21% changed their primary sexual expression. Thus by our criteria, over 64% of the androeceous $\leftrightarrow$ monoecious plants made significant changes in sexual expression during the period of record. Had we counted multiple episodes of sex changes rather than only the year of largest fruit set, percentages for the sexual states would be: sexually inconstant, 42; functionally monoecious, 46; and changes in primary sexual expression, 12.

The foregoing results suggest that seven (21% $\times$ 35) of the androeceous $\rightarrow$ monoecious plants changed their major sexual expression, whereas an additional 15 plants were monoecious for at least one year. Thus the total number of plants changing sexual emphasis should be increased by the seven plants that were staminate and became pistillate biased monoecious individuals.

In order to provide a complete inventory of individuals capable of sex change in the population, we must add plants that changed from pistillate to predominantly staminate biased monoecious individuals (80% or more staminate flowers) to the 46 plants noted above. We also collected fruit from plants displaying gynoeceous and monoecious states but not the exclusively

androeceous phenotype. If such plants were simply sexually inconstant, only a slight reduction in fruit set would be expected when the plant was monoecious. We now compare fruit crop of gynoeceous $\leftrightarrow$ monoecious plants against average fruit crop of the same plants while they were functioning as exclusive gynoeceous plants. If reduction in fruit crop was less than 20%, plants were classified as sexually inconstant. When fruit set reduction exceeded 80%, plants were considered to have had a change in primary sexual expression. Changes between 20 and 80% in fruit production were considered as possible changes to the monoecious condition. Again, we considered all changes and the largest change exhibited. Data exist for only 48 of the 173 plants. When all changes are considered, 46% were less than 20%, and 38% exceeded 80% reduction in fruit set. The remaining 17% of changes fell between 20 and 80% reduction in fruit set. When we consider only the largest changes, 33% of the changes were less than 20%, 52% exceeded 80%, and 15% exceeded 20% but were less than 80%. These data document a drastic reduction in fruit set as plants changed from strictly gynoeceous to a monoecious condition. Two possible explanations for the results exist: (1) plants changed to a primarily staminate biased monoecious state, or (2) plants were only sexually inconstant but had low fruit production.

In addition to recording fruit production by plant, we have also subjectively rated overall reproductive potential (staminate plus pistillate

functions) of monoecious plants. The rating scale ranged from 0 to 9 and was based upon the numbers of flowers of each sex. Although the subjective rating data are crude, they do give some indication of the importance of the male sexual functions on plants that have never displayed the exclusively androecious phenotype. Such data exist for 84 plants that displayed the gynoeceous and monoecious phenotypes, but were never exclusively androecious. If these gynoeceous monoecious plants were only slightly sexually inconstant while in the monoecious state, one would predict that their overall reproductive potential as androecious individuals would be slight. However, if primary sexual expression changed, one would expect high subjective ratings and a low fruit production. It is important to note that pollen was not limiting in this population (McArthur et al., 1978).

Plants were assigned to one of the ten categories of 'reproductive potential,' and the mean number of grams of fruit produced (and standard deviations) were computed for each category. For example, plants that displayed the gynoeceous phenotype in 1975 and were given the rating of 1, produced, on the average, 1 g of fruit; plants given a rating of 9 in 1975 produced an average of 325 g of fruit. In 1974, gynoeceous plants with a subjective rating of 9 produced an average of 499 g of fruit. Given the standards for plants with exclusively pistillate flowers, we can examine fruit set of monoecious individuals and assign each individual to a reproductive potential class solely on the basis of fruit set. For example, a plant that was phenotypically monoecious in 1975 and produced 60 g of fruit would be assigned to gynoeceous reproductive class 4 on the basis of fruit production. If the plant had been rated as 4, we would conclude that the bulk of its reproduction was through the gynoeceous function. If, on the other hand, a monoecious plant produced 60 g of fruit and received a rating of 9, one would conclude that a substantial fraction of the rating arose from production of staminate flowers. Thus, the important parameter was the difference in a plant's rating as a monoecious individual and its expected rating based solely upon fruit production. Individuals showing differences less than or equal to two classes were classified as sexually inconstant. If the difference was three or four classes, we considered the plant to have changed to a functionally monoecious state, and if the difference was greater

than five, the plant was considered to have changed its primary sexual expression. The data show that 48 of the 84 plants (57%) were sexually inconstant, 25 plants (30%) changed from the gynoeceous to functionally hermaphroditic state, and 11 plants (13%) changed sexual expression.

These data are consistent with conclusions drawn from Table 3, and suggest that both explanations for the reductions in fruit sets may be valid (i.e., some plants become predominantly staminate, whereas others become monoecious but produce little fruit). They also provide a conservative estimate of the number of plants that were gynoeceous and changed to prevalently staminate biased monoecious individuals. Multiplying 13% by the number of plants that were gynoeceous or monoecious but never androecious (173), we obtain an estimate of 23 gynoeceous plants that became prevalently staminate biased bisexual plants. Adding this to the number of plants observed to change from androecious to gynoeceous (33) plus the number of androecious plants that changed to pistillate biased monoecious individuals (7) plus the six plants that displayed all three phenotypes, gives a total of 69 plants that changed sex completely or changed their primary sexual expression (roughly 10% of the total of 665 individuals studied). This is still only part of the story, for we have not considered plants that changed from the unisexual to the monoecious state, for which 20 but less than 80% of their flowers were of the sex opposite to that previously produced. For the androecious to monoecious class, 26 plants are tallied ($35 \text{ plants} \times 0.4615$). For gynoeceous to monoecious, the number would be 52 plants (173×0.2979). Thus, by our criteria $69 + 78$ or 147 plants of 665 (21%) changed their sexual state. We consider this a conservative estimate for two reasons: (1) many sex changes were recorded during the drought of 1976–1978, but those data were not usable, because corresponding fruit set data were not taken, and (2) at least some plants considered sexually inconstant on the basis of available data have the potential to change sex under other conditions. The latter consideration is dramatized by plant #7–40, which, by the criteria employed here, was a sexually inconstant gynoeceous individual. That plant was cloned into 24 ramets, seven of which have flowered. Five of the seven ramets produced only staminate flowers and produced as many flowers as the average ramet from pure

TABLE 4. The number of individuals changing sex in natural populations of five species of *Atriplex*. All populations consist of a sample of 200 individuals chosen at random, except for *A. lentiformis*. The *A. lentiformis* population included all 70 individuals. The observations cover the five years from 1978 to 1983.

Species	Type of Change in Sexual Morph	
<i>A. canescens</i>	G ↔ A or G ↔ Mo ↔ A	9
	G ↔ Mo	8
	A ↔ Mo	17
<i>A. confertifolia</i> (Desert Experimental Range Population)	G ↔ A or G ↔ Mo ↔ A	17
	G ↔ Mo	8
	A ↔ Mo	8
<i>A. confertifolia</i> (Purgatory Basin Population)	G ↔ A or G ↔ Mo ↔ A	6
	G ↔ Mo	0
	A ↔ Mo	2
<i>A. corrugata</i>	G ↔ A or G ↔ Mo ↔ A	12
	G ↔ Mo	9
	A ↔ Mo	54
<i>A. cuneata</i>	G ↔ A or G ↔ Mo ↔ A	6
	G ↔ Mo	26
	A ↔ Mo	11
<i>A. lentiformis</i>	G ↔ A or G ↔ Mo ↔ A	9
	G ↔ Mo	9
	A ↔ Mo	5
<i>A. tridentata</i>	G ↔ A or G ↔ Mo ↔ A	11
	G ↔ Mo	39
	A ↔ Mo	9

androecious plants. Clearly, this “sexually inconstant gynoeceious plant” retained the genetic capacity to produce staminate flowers in abundance given the “right” circumstances.

The above data suggest that individuals of *Atriplex canescens* change sex. Some dismiss these results because they are derived from a population of half sibs descended from a single gynoeceious plant. Data from Freeman and McArthur (unpubl. data), however, demonstrate sex change in natural populations of *A. canescens*, *A. confertifolia*, *A. corrugata*, *A. cuneata*, *A. lentiformis*, and *A. tridentata* (Table 4). In the majority of cases, individuals changed from a unisexual to a monoecious state, but complete changes were also observed in all species. Furthermore, extensive studies on natural populations and clones of *A. canescens* derived from natural populations are in agreement with these results. The half sib family of *A. canescens*, then, is not atypical for

the genus; sex change seems deeply entrenched in species of *Atriplex* of the intermountain west of North America.

RELATED STUDIES IN SEX CHANGE

In addition to our own studies, well documented records of individuals that change sex under natural conditions have been reported for: *Juniperus australis* and *J. osteosperma* (Vasek, 1966), *Acer pensylvanicum* (Hibbs & Fischer, 1979), *Acer saccharinum* (Sakai, unpubl. data), and *Elaeis guineensis* (Williams & Thomas, 1970). In addition, there are voluminous data on *Arisaema triphyllum* and *A. dracontium*, sequential hermaphrodites (typically individuals begin by producing staminate flowers and change to production of pistillate flowers) that are widely acknowledged to change sex (see Gow, 1915; Pickett, 1915; Schaffner, 1922; Maekawa, 1924; Camp, 1932; Sokamoto, 1961; Policansky, 1981; Bierzychudek, 1982; Lovett-Doust & Cavers, 1982). In all of these species, some individuals are reported to change from the unisexual to a monoecious state. Unfortunately, however, there is a paucity of information concerning the percentage of staminate and pistillate flowers produced by monoecious plants of these species.

MECHANISMS AND CONSEQUENCES OF SEX CHANGE IN *ATRIPLEX CANESCENS*

The foregoing data suggest that the assumptions of sex allocation theory are valid for many plant species in a variety of distantly related families. The magnitude of change in several different populations demonstrates that sex change is not numerically trivial. At this point we are left with a number of unanswered questions: (1) What conditions induce plants to change sex? (2) Does changing sex enhance an individual's fitness? (3) By what mechanisms do plants change sex? (4) Is sex change compatible with the current understanding of the genetics of sex determination in plants?

In regard to the question of the conditions that induce plants to change sex, we have recorded the sexual expression of each individual in the half sib family of *Atriplex canescens* through the period 1968–1978. This includes a severe cold period (1972–1973) and a major drought (1976–1978). In both stressful periods, significantly more plants shifted away from femaleness (i.e., G → Mo or A, and Mo → A) than towards femaleness

TABLE 5. Direction of change in sexual state following severe external stress. The winters of 1973–1974 and 1974–1975, were normal for temperatures and precipitation. The winter of 1972–1973 was unusually cold, and the winter of 1975–1976 was much drier than normal. Magnitudes of difference in population changes in sexual expression in normal and stressful years are tested for significance by Chi-square analyses. G = Gynoeceious; A = Androeceious; Mo = Monoecious. The expected values are shown in parentheses.

Year	Type of Sex Change			
	G to Mo		A to Mo	
	or A	Mo to A	Mo to G	or G
1972–1973	85 (48.8)	10 (10.6)	7 (28.5)	12 (26.1)
1973–1974	16 (52.2)	12 (11.4)	52 (30.5)	42 (27.9)
$\chi^2 = 98.2$				$P < 0.01$
Year	G to Mo		A to Mo	
	or A	Mo to A	Mo to G	or G
1974–1975	13 (25.5)	6 (1.5)	10 (4.8)	8 (5.2)
1975–1976	104 (91.5)	1 (5.5)	12 (17.2)	16 (18.8)
$\chi^2 = 34.1$				$P < 0.01$

(A → G or Mo and Mo → G) (Table 5). In addition to such obvious external stresses, we have examined the influence of prior year fruit production on sexual expression in the next year (Table 6). Plants that produced heavy fruit crops ($X > 125\%$ of the plant's annual longterm average crop) changed sex more readily than plants that had light ($X < 75\%$ of the plant's average crop) or normal fruit crops ($0.75\bar{x} < X < 1.25\bar{x}$). We also observed that mortality was significantly greater among plants on the edge (43%) of the half sib family plantation than among individuals growing in the center (11%) of the population. We consider that edge plants are more stressed for water because of their greater exposure to light and wind. When the incidence of complete sexual changes ($G \leftrightarrow A$) are compared for plants occupying the edges versus those in the interior of the patch, significantly more changes occur in plants growing around the edges (Table 7). We have emphasized temperature and water relations in the foregoing analyses, but the work of Gregg (1973), Cox (1981), Schaffner (1922,

TABLE 6. In this table we examine the hypothesis that a heavy seed set in year X may influence the sex of individuals in year X + 1. Because not all individuals appear to be capable of changing sex, we selected those which could change sex and then classified them into two groups, i.e., those that changed in year X + 1 and those that did not. We then ranked the seed set of the individuals in year X into three categories, i.e., $x < 0.75 \bar{x}$; $0.75 \bar{x} < x < 1.25 \bar{x}$; $1.25 \bar{x} < x$.

	75% <		
	$x < 75\%$	$x < 125\%$	$125\% < x$
Did Not Switch	8 (7.47)	13 (8.19)	6 (11.34)
Switched	23 (23.53)	21 (23.51)	41 (35.66)
$\Sigma \chi^2 = 6.67; P < 0.05.$			

1925, 1927) and others suggests that factors such as light intensity and mineral nutrient availability may also affect sexual expression of plants. Gregg (1973) showed that when gynoeceious or large monoecious individuals of the tropical orchids she studied were placed in the shade, they produced staminate flowers. Androeceious plants placed in full sunlight often produced pistillate flowers. Such effects of light on sexual expression suggest that studies of sexual expression of cohorts of dioecious tropical forest trees are needed during the period when individuals move from shaded forest floor and subdominant positions into the canopy. Are the mortality rates of androeceious and gynoeceious plants equal? Are androeceious and gynoeceious plants equally fit at all ages and in all positions within and below the canopy? Do individuals change sex? Studies on *Castilloa elastica* (summarized in Dzhaparidze, 1967) show that sequential hermaphroditism occurs in at least one tropical tree species. Unfortunately, we currently have only indirect measures to predict whether sex change will enhance fitness. Cole (1954) was the first to emphasize the contribution of early reproduction to fitness. In this connection, we find that *Atriplex canescens* plants of variable sexual expression reproduce significantly earlier in life than constant gynoeceious individuals but later than constant androeceious individuals (Table 8). Results are based on 70 ramets from sexually labile individuals, 70 ramets of constant androeceious plants and 61 ramets from constant gynoeceious plants. Of the 70 androeceious ramets, 69 flowered in the second year after cloning; 34 sexually

TABLE 7. Comparison of the distribution (edge versus the interior of the patch) of plants that have completely changed sex (A $\leftrightarrow$ G) versus those that have never changed sex. Expected values are shown in parentheses.

	A	G	Constant
Edge	28 (18.0)		108 (118.0)
Interior	31 (41.0)		278 (268.0)
$\chi^2 = 9.22$ $P < 0.01$			
	A	G	Other Classes of Sex Change
Edge	28 (19.7)		68 (76.3)
Interior	31 (39.3)		160 (151.7)
$\chi^2 = 6.6$ $P < 0.01$			

labile ramets also flowered, but only six gynoe-cious plants had flowered by the end of the second growing season (Table 8). Of the ramets from sexually labile individuals that flowered, 11 were staminate, 21 were monoecious but prevailingly staminate, and two were exclusively pistillate.

In addition to the time of onset of reproduction, parental longevity and the number of offspring per reproductive event have an effect on the fitness of an individual (Cole, 1954). We have obtained two measures of longevity: the first is based on the average age at death of individuals in the half sib family; the second considers mortality through time in ramets of common age from constant staminate, constant pistillate, or sexually labile individuals. In the half sib population, the average gynoe-cious plant died at an earlier age than either androecious or sexually labile plants. Plants that changed sex lived significantly longer than either androecious or gynoe-cious plants (Table 9). In our second set of data, no mortality was observed among ramets from sexually labile individuals after seven years. Androecious plants exhibited 99% survivorship, but gynoe-cious survivorship was only 87% after seven years. The ability to change sex thus appears adaptive, at least as far as age at first reproduction and survivorship are concerned.

Finally, we examine fruit production of constant gynoe-cious plants and plants that vacillate

TABLE 8. Incidence of flowering among two-year old ramets of *Atriplex canescens*. The analysis is of the number of plants in each category. Expected values in parentheses.

Plantation 1 (irrigated)	Androe- cious	Gynoe- cious	Sexually Labile
Flowering	69 (36.86)	6 (35.28)	34 (36.86)
Nonflowering	1 (33.14)	61 (31.72)	36 (33.14)
$\chi^2 = 110.99$ $P < 0.001$			
Plantation 2 (non-irrigated)	Gynoe- cious	Sexually Labile	
Flowering	6 (19.56)	34 (20.44)	
Nonflowering	61 (47.44)	36 (49.56)	
$\chi^2 = 25.99$ $P < 0.01$			

between the gynoe-cious and monoecious states. We have no valid way of comparing reproductive output of androecious plants and sexually labile individuals, but we can compare fruit production of sexually labile plants and gynoe-cious plants. For the four years for which fruit production data are available, plants that changed sexual expression at some time in their life averaged 327 g of fruit per year, whereas constant gynoe-cious plants averaged 330 g per year. We point out, however, that the very highest fruit producers are constant gynoe-cious plants (McArthur et al., 1978). In addition, of course, the sexually labile individuals also reproduced via pollen in at least one year. For the period of record, it would appear that plants that change sex are not disadvantaged, but indeed may enjoy a fitness advantage in terms of offspring produced per year. A more complete demographic analysis is needed and is under way.

The third question posed earlier concerns the mechanism(s) by which plants change sex. Although we lack experimental data on how plants change sex, it is important at this stage that plausible models be formulated. Two fairly well studied models could account for our observations on *Atriplex canescens*. The first is derived from the work of Chailakhyan and Khryanin (1978). They have shown that in spinach (which, like *Atriplex*, is a member of the Chenopodiaceae) and hemp, the ratio of cytokinin to gibberillic

TABLE 9a. Age at death of *Atriplex canescens* individuals of different sexual morphs. All individuals are from the half sib population of McArthur (1977). All plants originated from seed germinated in 1968. The population is cultivated at the Snow Field Station, Ephraim, Utah.

Sexual Morph	Initial Number of Individuals	% Mortality 1972–78	Average Age at Death (years) ^a
A	190	21.6	4.85 ± 1.56
G	203	20.2	5.78 ± 1.82
Mo	261	8.0	7.71 ± 1.31

^a All means differ significantly from each other.

acid controls sexual expression. With cytokinin in excess, plants generally produce pistillate flowers. Itai and Vaadia (1970) have shown that under conditions of water stress, cytokinin is not transported to above ground parts from sites of synthesis in the root. Chailakhyan and Khryanin (1978) have shown that gibberillic acid continues to be synthesized in leaves when plants are stressed for water. Thus, should a plant experience severe water stress, cytokinin flow to stem tips appears to diminish, whereas gibberillic acid continues to be produced. Under such conditions, even a plant genetically predisposed to produce cytokinin in abundance, and thus produce pistillate flowers, might instead produce staminate flowers.

Pharis (1975) has shown that the ratio of polar to nonpolar gibberillic acids determines sex expression in some conifers. Polar gibberillic acids tend to yield microsporangiate forms while nonpolar forms tend to yield megasporangiate forms. Under water stress, polar gibberillic acids are not converted to nonpolar forms, and again, plants produce predominantly microsporangiate reproductive structures.

Lastly, we return to the question of genetic controls of sexual expression, a theme that two of us have previously discussed (McArthur, 1977; Freeman et al., 1980; McArthur & Freeman, 1982). It seems likely that not all dioecious or subdioecious plants are capable of changing sexual expression. In some species, sex appears to be rigidly controlled by genetics. Perhaps the most absolute case of such control occurs among the mistletoes (*Viscum*) in which gynoeocious plants inherit a large translocation ring, a feature that androecious plants lack (Wiens & Barlow, 1979).

TABLE 9b. Mortality among *Atriplex canescens* individuals of different sexual morphs. Ramets were taken from plants taken from a population native to the Book Cliff area of east central Utah.

Morph	% Survival After 7 Years
Mo	100
A	99
G	87

Other rigid genetic systems are also known to occur (Westergaard, 1958; Lloyd & Bawa, in press). It is not clear how common such systems are. The problem is complicated because even in species such as *Atriplex canescens*, which are known to contain individuals with labile sexual expression, an appreciable fraction of the population does not seem capable of sex change and shows no form of sexual inconstancy. Sexual expression in such individuals is constant and indifferent to environmental fluctuations. We have observed thousands of plants over nearly a decade. Many have maintained a constant unisexual state throughout the entire period. When such constant androecious and gynoeocious plants are cloned and placed in a variety of environments, sexual expression of ramets is always that of the parent plant. There is thus little doubt of a strong genetic component to sexual expression in *Atriplex*, particularly in *A. canescens*. Nevertheless, we also find many individuals of *A. canescens* and many other species with subdioecious individuals that express more than one sexual state in their life. The work already presented in this paper indicates that at least three sexual morphs occur: androecious, gynoeocious, and labile. We recognize that the third sexual morph may require further subdivision when detailed genetic studies are made. We believe that all of the observed facts can be accommodated by known genetic mechanisms since sexual expression depends on both the quantities of and ratios among hormones, and hormone production is affected by both genetic and environmental factors. Given differential effects of environmental stress on hormones controlling sexual expression, tissue differentiation and flower morphs could be dramatically altered in kind or degree from year to year on the same individual. We thus fail to see any compelling reasons to interpret *A. canescens* as a two morph or diphasic model as do Lloyd and Bawa (in press). A variety

of data for *A. canescens* argues for at least three sexual morphs with the labile morph capable of producing staminate flowers only, pistillate flowers only, or monoecious individuals having a variety of staminate to pistillate flower ratios. Our clonal studies, which will be summarized elsewhere, show that all of these phenotypes can be derived from a single sexual labile individual in a single year under common garden conditions.

CONCLUSIONS

The picture now emerging of sex expression in *A. canescens* is far more dynamic than most have previously believed. Some individuals appear capable of widely divergent floral sex expression in response to variable local environmental conditions and the individual's own physiological state. Modifications range from modest adjustments to complete changes of sexual expression. Such modifications appear to be adaptive. How such modifications are achieved, through interactions of environment, physiology, and genetics are subjects requiring further investigation. Likewise, mechanisms by which androecious, gynoeceous, and sexually labile individuals persist in common populations remain to be identified.

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