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Sex Change in Plants: Old and New Observations and New Hypotheses

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Summary. Evidence is presented that individuals of a large number of dioecious and subdioecious plant species are able to alter their sexual state in response to changes in the ambient environment and/or changes in size or age. We suggest that lability of sexual expression probably has survival value where a significant portion of the females must otherwise bear the cost of fruit production in unfavorable environments. We demonstrate that in patchy environments of the proper scale and variability in quality, labile sexual expression will enhance an individual's genetic contribution to the next generation.

Introduction

The idea that the sex of an individual of a dioecious plant species is fixed throughout life and is determined solely by the genetic composition of the individual is prevalent in current literature despite the existence of a large literature to the contrary. An examination of introductory biology (Wilson et al. 1978) botany, (Haney 1978, Fuller et al. 1972; Fuller and Ritchie 1967) and mid level genetic texts (Garber 1972; Srb et al. 1965; Burns 1969; Strickberger 1976; Grant 1975 and Gardener 1975) demonstrates that the view most often presented is one in which sex is controlled completely by a chromosomal or genic system. Rarely does one find a discussion of the role of environment in the sex determination of individuals of dioecious plant species, although Haney (1978), Strickberger (1976) and Srb et al. (1965) do present some discussion of this phenomenon. Thus because other possibilities are not usually presented, readers may draw the conclusion that sexual expression of individuals of all dioecious species is genetically fixed and not responsive to environmental influences. However, workers seeking to establish the genetic basis of sex have recognized for over 60 years that hermaphrodites are common in the prevailingly dioecious plant species they have studied and that the sexual state of individuals sometimes changed (Yampolsky 1919; Heslop-Harrison 1924; Correns 1928). Indeed such a recognition lead Hartman (1956) to formulate his so-called "law of bisexual potentiality of both sexes" (also see Smith 1963).

The inconstancy of the sexual state of individuals of higher plants has been well documented for a number of taxa described as dioecious, subdioecious or sequential hermaphrodites by professional botanists. The labile nature of sex expression by individuals of many dioecious and sequentially hermaphroditic plant species is documented from the literature in Table 1. Our literature search shows that 25 families and over 50 species include unisexed individuals that have functioned as male at one time and females at another or have produced hermaphroditic offspring (the reason for including those which produce hermaphroditic offspring will be discussed later). Several of the species noted in Table 1 have been reported to have sex chromosomes. Of the 13 species Westergaard (1958) listed as having well differentiated sex chromosomes, individuals of 3 species (*Cannabis sativa*, *Humulus japonicus* and *Rumex hastatulus*) are known to exhibit sex change and/or to produce hermaphroditic offspring. In Table 1, we designate those species which are reported to have sex chromosomes to underscore the fact that sex change is a phenomenon of at least some dioecious plant species.

A large body of literature documents the fact that a variety of environmental factors are capable of altering the sexual expression of plant individuals that normally display but one sex at a time (Table 2). The ratio of male-to-female flowers on individuals of selected monoecious species and of male-to-female organs in flowers of perfect flowered taxa has likewise proven to be manipulatable through alteration of the plant's environment. As documented in Table 2, age, injury and disease have all been shown to alter the sexual expression of individuals of some species. Similarly, physical and chemical characteristics of the environment (e.g., light intensity, day length, temperature, soil fertility, relative availability of soil moisture and air chemistry) are reported to affect the sexual expression of a variety of species. Finally, plant physiologists have repeatedly demonstrated that the sexual expression of developing floral buds can be altered in predictable ways through the application of several plant hormones in different amounts and proportions (Table 2; for greater detail see Heslop-Harrison 1972 and Chailakhyan 1979).

It will be noted in Table 2 that some environmental variables predispose individual plants of labile sexual expression toward femaleness while other variables favor maleness. Some variables such as dry soils or high tissue levels of cytokinin seem to consistently favor one sex over the other, while other variables (e.g., gibberellins or trauma) sometimes favor maleness and at other times femaleness. Response in the latter case at least seems to be dependent upon the species and/or the physiological state of the individual.

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* Some workers reserve the term dioecious for plant species which consist of males and females only (no hermaphrodites). Such workers also exclude species in which sexual expression of individuals changes with time. Strict adherence to that definition would greatly reduce the number of species now recognized as dioecious in the world's floras. Regardless of definitions, lability of sexual expression of individuals and the occurrence of occasional hermaphrodites in prevailingly dioecious plant species are phenomena which deserve scientific investigation since they may have considerable evolutionary and ecological consequences

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Table 1. Species that are commonly described as dioecious but which include individuals known to display different sexual states (i.e., male or female) during their life or to produce hermaphroditic offspring. We have included species which taxonomists describe as monoecious to dioecious only when such species have been reported to have sex chromosomes (e.g., *Mercurialis annua*, *Ilex* sp., and *Empetrum nigrum*) or when the monoecious state appears to be related to the sex reversal phenomenon (as for *Arisaema triphyllum*, *A. dracontium*, *A. japonicus* and some Orchids). An asterisk designates species reported by Westergaard to have well-established heteromorphic sex chromosomes (Westergaard 1958). Nomenclature follows Bailey and Bailey (1976)

Family	Species	Reference
Araceae	*Arisaema dracontium* (L.) Schott.	Schaffner 1922, 1925a
	A. japonica Bl.	Maekawa 1929
	A. triphyllum (L.) Schott.	Schaffner 1922, 1925a, 1926
Aquifoliaceae	*Ilex* sp.[1]	Menniger 1967
	Ilex opaca Ait.	Clark and Orton 1967
Cannabinaceae	*Cannabis sativa* L.*	Schaffner 1921, 1923a, 1925c, 1931; Hirata 1924; Huhnke et al. 1950; Sengbush 1952; Heslop-Harrison 1964
	Humulus japonicus Siebold & Zucc.	Schaffner 1923b; Tournois 1911, 1912, 1914
Caricaceae	*Carica papaya* L.	Hofmeyr 1938, 1939; Storey 1953
Caryophyllaceae	*Silene alba* L. (*Lychnis alba*)	Schull 1910, 1911; Allen 1940
	S. dioica (L.) Clairv.*	Schull 1911
	S. otites L.*	Correns 1928; Newton 1931; Sansome 1938
	S. re omeri Frim.	Correns 1928
Chenopodiaceae	*Atriplex canescens* Pursh.	McArthur 1977
	A. confertifolia Torr. & Frem.	McArthur (unpublished data); Freeman and Harper 1980
	A. corrugata S. Wats	Freeman and McArthur (unpublished data)
	A. cuneata A. Nels.	Freeman and McArthur (unpublished data)
	A. lentiformis (Torr.) S. Wats	Freeman and McArthur (unpublished data)
	A. tridentata Kuntze	Freeman and McArthur (unpublished data)
	Spinacia oleracea L.*	Bemis and Wilson 1953; Thompson 1955 Freeman and Kalled (unpublished data)
Compositae	*Antennaria dioica* (L.) Gaertn.	Ubisch 1936
	Cirsium arvense (L.) Scop.	Correns 1928
	Petasites japonicus Siebold & Zucc.	Ikeno 1937
Cycadaceae	*Cycas circinalis* L.	Menninger 1967
Empetraceae	*Empetrum nigrum* L.*	Blackburn 1938
Ephedraceae	*Ephedra viridis* Coville	Freeman and McArthur (unpublished data)
Equisetaceae	*Equisetum* (gametophyte)	Dzhaparidze 1963
Eucommiaceae	*Eucommia ulmoides* D. Oliver	Dzhaparidze 1963
Euphorbiaceae	*Mercurialis annua* L.	Yampolsky 1919; Gabe 1939; Kuhn 1939
Liliaceae	*Asparagus officinalis* L.	Rick and Hanna 1943
Moraceae	*Castilloa elastica* Sesse	Bosse 1935
	Morus alba	Schaffner 1925a; Zhukovskii 1940; Dzhaparidze 1963
Myricaceae	*Myrica gale* L.	Davey and Gibson 1917
Orchidaceae	*Catasetum expansum* Rchb. f.	Gregg 1973
	C. macrocarpum L.C. Rich. ex Kunth	Gregg 1973
	C. macroglossum Rchb. f.	Gregg 1973; Dodson 1962
	C. platyglossum Schltr.	Dodson 1962
	C. ventricosum Batem.	Gregg 1973
	Cycnoches densiflorum Rolfe	Gregg 1973
	C. dianae Rchb. f.	Gregg 1973
	C. lehmannii Rchb. f.	Dodson 1962
	C. stenodactylon Schltr.	Gregg 1973
	Mormodes buccinator Lindl.	Dodson 1962
Poaceae	*Buchloe dactyloides* Nutt.	Worsdell 1916
	Leucopoa kingii S. Wats.	Harper, Freeman and McArthur (personal observation)
Polygonaceae	*Ruprechtia* sp.	Menninger 1967
	Rumex hastatulus Baldw.	Smith 1963
Ranunculaceae	*Thalictrum dasycarpum* Fisch. & Ave-Lall	Schaffner 1925a
	T. dioicum L.	Schaffner 1923c, 1925a
	T. fendleri Engelm.	Kuhn 1939
Salicaceae	*Populus tremuloides* Michx.*	Erlansson and Herman 1927
	Salix sp.	Nilsson 1918; Raino 1927

Table 1 (continued)

Family	Species	Reference
	Salix alba L.	Heslop-Harrison 1924
	S. andersonii Sm.*	Heslop-Harrison 1924
	S. aurita L.*	Worsdell 1916
	S. caprea L.*	Heslop-Harrison 1924
	S. cinerea L.*	Heslop-Harrison 1924
	S. grandifolia Seringe	Heslop-Harrison 1924
	S. silesiaca Willd.	Heslop-Harrison 1924
Taxaceae	*Taxus baccata* L.	Keen and Chadwick 1954
	T. cuspida Siebold & Zucc.	Keen and Chadwick 1954
	T. media Rehd.	Keen and Chadwick 1954
Urticaceae	*Urtica cannabina* L.	Negodi 1931
	U. caudata Vahl.	Negodi 1929
	U. dioica L.	Strasburgen 1910; Zuk 1970
Valerianaceae	*Valeriana dioica* L.	Correns 1928
Vitaceae	*Vitis* (wild population of several species are dioecious. The cultivated hermophrodites have been selected from wild stock (Allen 1940)	Negru 1936; Allen 1940; Hedrick and Anthony 1915; Negi and Olmo 1966

[1] *Ilex serrata* has been reported to have sex chromosomes (Nakajima 1942)

Table 2. Some factors known to modify the sexual expression of vascular plants under controlled conditions. Where more than one worker has shown altered sexual expression for a given species under a given kind of treatment, we have cited pertinent review articles in order to minimize the table's length. Morphological changes in which organs of one sex or the other were induced or caused to abort were observed by all authors, but most of the references do not provide proof that the organs produced viable gametes. No distinction is made between ultimate and proximal factors since in several cases the distinction is often described as either obscure or artificial. An asterisk indicates dioecious species. Species not asterisked are monoecious or perfect flowered taxa on which the ratio of male/female flowers is significantly altered by the environmental factor considered. Nomenclature follows Bailey and Bailey (1976)

Factor	Direction	Species	Reference
Abscisic acid	♂ → ♀	*Cannabis sativa* L.*	Vince-Prue 1975
	♂ → ♀	*Cucumis sativa* L.	Vince-Prue 1975
	♂ → ♀	*Cucurbita pepo* L.	Vince-Prue 1975
Age (size)	♂ → ♀	*Arisaema japonica* Bl.	Heslop-Harrison 1957
	♂ → ♀	*A. triphyllum* (L.) Torr.	Heslop-Harrison 1957
	♂ → ♀	*Castilloa elastica* Sesse*	Dzhaparidze 1963
	♂ → ♀	*Catasetum macrocarpum* L.C.	
	♂ → ♀	Rich. ex. Knuth	Gregg 1973
	♂ → ♀	*Cynoches densiflorum* Rolfe	Gregg 1973
	♂ → ♀	*Eucommia ulmoides* D. Oliver*	Dzhaparidze 1963
	♂ → ♀	*Ilex opaca* Ait.	Clark and Orton 1967
	♂ → ♀	*Metasequoia glyptostrobodies*	H.G. Baker (personal communication)
Auxin	♂ → ♀	*Cannabis sativa* L.*	Heslop-Harrison 1956
	♂ → ♀	*Cleome iberidella* Welw. ex Oliv.	DeJong and Bruinsma 1974
	♂ → ♀	*Cucumis sativa* L.	Heslop-Harrison 1957, Minina 1938
	♂ → ♀	*Cucurbita pepo* L.	Heslop-Harrison 1957
High boron	♂ ← ♀	*Cannabis sativa* L.*	Herich 1956
Carbon monoxide	♂ → ♀	*Cannabis sativa* L.*	Heslop-Harrison 1972
	♂ → ♀	*Cucumis sativa* L.	Minina & Tylkina 1947
	♂ → ♀	*Mercurialis ambigua* L.	Heslop-Harrison 1972
Cold weather	♂ ← ♀	*Atriplex canescens* Pursh.*	McArthur 1977
	♂ ← ♀	*Cycas circinalis* L.*	Menninger 1967
Dry Soil	♂ ← ♀	*Acer grandidentatum* Nutt.	Barker et al. (in review)
	♂ ← ♀	*Arisaema triphyllum* L. Schott.	Pickett 1915
	♂ ← ♀	*Cucumis sativa* L.	Minina 1952
	♂ ← ♀	*Juniperus osteosperma* (Torrey) Little	Freeman et al. 1981
	♂ ← ♀	*Quercus gambelii* Nutt.	Freeman et al. 1981
	♂ ← ♀	*Sarcobatus vermiculatus* (Hook.) Torr.	Freeman et al. 1981
	♂ ← ♀	*Triticum aestivum* L.	Minina 1952

Table 2 (continued)

Factor	Direction	Species	References
Ethylene	♂→♀	*Cucumis sativa* L.	Rudich et al. 1969, Fraenkel and Galun 1977
		C. melo L.	Rudich et al. 1969
		Cucurbita pepo L.	Rudich et al. 1969
Gibberellins	♂←♀	*Cannabis sativa* L.*	Chailakhyan 1979
	♂→♀	*Cleome iberidella* Welw. ex Oliv.	DeJong and Bruinsma 1974
	♂→♀	*Cleome spinosa* Jacq.	DeJong and Bruinsma 1974
	♂→♀	*Cucumis sativa* L.	Heslop-Harrison 1972
	♂→♀	*C. melo* L.	Brantely and Warren 1960
	♂→♀	*Ricinus communis* L.	Shifriss 1961
	♂←♀	*Spinacea oleracea* L.*	Chailakhyan 1979
Growth retardant	♂→♀	*Cucumis melo* L.	Halvey & Rudich 1967
Eriophid mites	♂→♀	*Salix andersoniana* Sm.*	Heslop-Harrison 1924
	♂→♀	*S. aurita* L.*	Heslop-Harrison 1924
	♂→♀	*S. caprea* L.*	Heslop-Harrison 1924
	♂→♀	*S. cinerea* L.*	Heslop-Harrison 1924
	♂→♀	*S. grandifolia* Seringe*	Heslop-Harrison 1924
	♂→♀	*S. silesiaca* Willd.*	Heslop-Harrison 1924
Cytokinins	♂→♀	*Cannabis sativa* L.*	Chailakhyan 1979
	♂→♀	*Kalanchoe integra* Medic. (*K. crenata*)	Heslop-Harrison 1972
	♂→♀	*Cleome spinosa* Jacq.	DeJong and Bruinsma 1974
	♂→♀	*Spinacea oleracea* L.*	Chailakhyan 1979
High light intensity	♂→♀	*Catasetum expansum* Rchbif.*	Gregg 1973
	♂→♀	*C. macrocarpum* (L.) Rich. ex Kuth*	Gregg 1973
	♂→♀	*C. macroglossum* Rchbif.	Gregg 1973, Dodson 1962
	♂→♀	*C. platyglossum* Schltr.	Dodson 1962
	♂→♀	*C. ventricosum* Batem.	Gregg 1973
	♂→♀	*C. densiflorum* Rolfe	Gregg 1973
	♂→♀	*Cynoches dianae* Rchbif.	Gregg 1973
	♂→♀	*C. lehmannii* Rehb. f.	Dodson 1962
	♂→♀	*C. stenodactylon* Schltr.	Gregg 1973
	♂→♀	*Cucumis sativa* L.	Gregg 1973
	♂→♀	*Elaeis guinanemsis* Jacq.	Gregg 1973
	♂←♀	*Kulanchoe* (*Bryophyllum*) *daigremontiam* Hamet & Perr., A. Berger	Heslop-Harrison 1972
	♂→♀	*Mormodes buccinator* Lindl.	Dodson 1962
Manure	♂→♀	*Arisaema triphyllum* (L.) Schott.	Schaffner 1922
	♂→♀	*Humulus japonicus* Siebold & Zucc.*	Heslop-Harrison 1957
Methylene blue	♂→♀	*Cucurbita sativa* L.	Dzhaparidze 1963
High nitrogen	♂→♀	*Begonia semperflorens* Link & Otto	Matzke 1938
	♂→♀	*Ceratopteris thalictroides* (L.) Brongn. (gametophyte)	Dzhaparidze 1963
	♂→♀	*Cleome spinosa* Jacq.	Murneek 1927
	♂→♀	*Cucumis anguira* L.	Heslop-Harrison 1957
	♂→♀	*C. melo* L.	Heslop-Harrison 1957, 1972
	♂→♀	*C. sativa* L.	Heslop-Harrison 1957, 1972
	♂→	*Lycopersicum esculentum* Mills	Heslop-Harrison 1972
	♂→♀	*Osmunda regalis* L. (gametophyte)	Dzhaparidze 1963
	♂→♀	*Zea mays* L.	Heslop-Harrison 1957
	♂→♀	*Spinacia oleracea* L.*	Quagliotti 1972
Photoperiod long day	♂←♀	*Cannabis sativa* L.*	Heslop-Harrison 1957, 1972
	♂←♀	*Cucumis anguira* L.	Hall 1949
	♂←♀	*C. sativa* L.	Heslop-Harrison 1957
	♂←♀	*Heteropogon contortus* (L.) Beauv. ex R. & S.	Tothill and Knox 1968
	♂←♀	*Humulus japonicus* Siebold & Zucc.*	Heslop-Harrison 1957
	♂←♀	*Xanthium strumerium*	Heslop-Harrison 1957
	♂←♀	*Zea mays* L.	
Photoperiod short day	♂→♀	*Ambrosia artemisifolia* L. (*A. elatior* L.)	Heslop-Harrison 1957
	♂→♀	*A. trifida* L.	Heslop-Harrison 1957
	♂→♀	*Cannabis sativa* L.*	Heslop-Harrison 1957

Table 2 (continued)

Factor	Direction	Species	Reference
	♂ → ♀	*Cucurbita pepo* L.	Heslop-Harrison 1957
	♂ → ♀	*Cucumis sativa* L.	Heslop-Harrison 1957
	♂ → ♀	*Heteropogon contortus* L. Beauv. ex R. & S.	Heslop-Harrison 1957, 1972
	♂ → ♀	*Humulus japonicus* Siebold & Zucc.*	Heslop-Harrison 1957, 1972
	♂ → ♀	*Silene pedula* L.	Heslop-Harrison 1957, 1972
	♂ → ♀	*Spinacia oleracea* L.*	Heslop-Harrison 1957, 1972
	♂ → ♀	*Xanthium pennsylvanicum* Wallv.	Heslop-Harrison 1957, 1972
	♂ → ♀	*X. strumarium* L.	Heslop-Harrison 1957, 1972
	♂ → ♀	*Zea mays* L.	Heslop-Harrison 1957, 1972
Potassium	♂ → ♀	*Ricinus communis* L.	Dzhaparidze 1963
"Rich soil"	♂ → ♀	*Arisaema triphyllum* (L.) Torr.	Heslop-Harrison 1957
	♂ → ♀	*A. dracontium* (L.) Schott.	Heslop-Harrison 1957
	♂ → °	*Begonia semperflorens* Link & Otto	Matzke 1938
	♂ → ♀	*Cucumis sativa* L.	Dzhaparidze 1963
	♂ → ♀	*Equisetum* (gametophyte)*	Dzhaparidze 1963
High temperature	♂ ← ♀	*Ambrosia trifida* L.	Heslop-Harrison 1957
	♂ ← ♀	*Carica papaya* L.	Lange 1961
	♂ ← ♀	*Citrullus lanatus* (Thunb.) Matsum & Nakai	Heslop-Harrison 1957
	♂ ← ♀	*Cucurbita pepo* L.	Heslop-Harrison 1957
	♂ ← ♀	*Cucumis sativa* L.	Frankel and Galun 1977
	♂ ← ♀	*Spinacia oleracea* L.*	Thompson 1955
Trauma	♂ → ♀	*Acer negundo* L.*	Worsdell 1916
	♂ → ♀	*Cannabis sativa* L.*	Dzhaparidze 1963
removal of leaves or flowers or crown pruning	♂ → ♀	*Carica papaya* L.	Dzhaparidze 1963, Heslop-Harrison 1957
	♂ → ♀	*Cleome spinosa* Jacq.	Heslop-Harrison 1957
	♂ → ♀	*Cucumis sativa* L.	Heslop-Harrison 1957
	♂ → ♀	*Mercurialis annua* L.*	Heslop-Harrison 1957
	♂ → ♀	*Morus alba* L.*	Dzhaparidze 1963
	♂ → ♀	*Musa paradisiaca* L.	Heslop-Harrison 1957
removal of storage tissue	♂ ← ♀	*Arisaema japonica* Bl.	Heslop-Harrison 1957
	♂ ← ♀	*A. triphyllum* (L.) Torr.	Heslop-Harrison 1957

The data in Table 2 reveal a strong tendency for environmental stresses to induce maleness. For example, low soil fertility, dry soils, extreme temperatures, and low light intensity all tend to incline the sex ratio toward males. For species in which the cost (in either increased mortality or decreased competitive ability) of reproducing as a female significantly exceeds that of reproducing as a male, a system of labile sexual expression that favors maleness in times of stress should have survival value.[1] Such a system would be particularly advantageous in environments that are highly variable from year-to-year (as in deserts) or that have favorable and unfavorable patches intermixed at such a scale that each seed has a roughly equal chance of falling into good or poor habitat (as along streams in arid regions). Individuals capable of responding to such environmental patchiness with endogenous hormonal levels capable of inducing the sex that could most successfully pass on genes to the next generation from a given patch should be favored.[2] As we will show in succeeding paragraphs,

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[1] Several studies have demonstrated that the female sexual functions do indeed place females of several species under greater stress than males. For example, Lysova and Khizhnyak (1975) have shown that males and females of *Acer negundo* and *Fraxinus lanceolata* on similar sites grow at equal rates until the females matured the first seed crop after which females grew slower than males. The differential growth rate of males and females seemed to increasingly diverge with the number of seed crops produced. Stark (1970) has shown that females of *Atriplex hymenelytra* (Torr.) S. Wats. are often under greater water stress than males on common sites. Hikmat et al. (1972) have shown similar results for male and female plants of the desert shrub, *Simmondsia chinensis* (Link) C.K. Schneid. Freeman and McArthur (in manuscript) have likewise shown that fruiting females of three dioecious species (*Atriplex canescens*, *A. confertifolia* and *A. tridentata*) are under greater water stress than associated males

[2] Several research groups working in widely separated geographical zones and dealing with diverse taxa have independently shown that the dioecious species they investigated) exhibit partial niche differentiation, that is the sexes were found to segregate along environment gradients. Spatial segregation of males and females of dioecious species has been reported for the following families: Myricaceae (Davey and Gibson, 1917), Orchidaceae (Dodson 1962; Gregg 1973), Aceraceae and Oleaceae (Lysova and Khizhnyak 1975), Rosaceae (Richards 1975), Chenopodiaceae, Ephedraceae, (Freeman et al. 1976 and Waser 1980, in manuscript), Poaceae, and Ranunculaceae (Freeman et al. 1976), Buxaceae (Cole 1979; Waser 1980, in manuscript). All of the foregoing workers have reported a similar distribution of males and females in space (i.e., males are more commonly encountered in harsh environments, while females are most often found in favorable sites), although Bawa and Opler (1977) could not detect a segregation of male and female trees along a moisture gradient in Costa Rica. It thus appears that some species in all the foregoing taxa do perceive their environment as patchy with respect to the success of males and females on favorable and marginal sites

some evidence already exists to support the hypothesis that natural selection has equipped at least some plants with environmental monitoring systems that permit the individual to adjust sexual expression and thus increase the likelihood that genetic material will be transmitted to another generation.

Catarino (1964, cited in Heslop-Harrison, 1972) showed that applications of cytokinins to *Kalanchoe crenulata* resulted in the regression of stamens and the enlargement of the ovary. Negi and Olmo (1966, 1972) were able to feminize male *Vitis vinifera* with exogeneous cytokinins. Moreover, when Skene (1972) grew the same clone of *Vitis vinifera* on three different root stocks, he found that the differences in fruit yield were correlated with differences in the cytokinin concentration of the sap. More recently, Louis and Durand (1978) have demonstrated that the male sterile gene of *Mercurialis annua* is the gene(s) controlling production of cytokinins. Chailakhyan (1979) has recently shown that the ratio of cytokinin to gibberillin controls the sex of *Spinacia oleracea* L. and *Cannabis sativa* individuals. When gibberillins exceed cytokinins, the individual is most likely to mature as a male: if the reverse is true, most individuals develop as females. In addition to cytokinins and gibberillins, auxin, ethylene and abscisic acid have each been implicated in control of sexual expression (see Table 2 and Heslop-Harrison, 1972, Friedlander et al. 1977 and Vince-Prue 1975 for further discussion and references).

There is good evidence that environment has a pronounced effect on hormonal levels. For example, under water stress there is reduced transport of cytokinins from the root (the site of biosynthesis) to the shoot (Itai and Vaadia 1965, 1970). Increases in salinity also reduce the transport of cytokinins (Itai et al. 1968, 1973). In addition, drought brings about an increase in the levels of abscisic acid in the shoot (Kaldeway et al. 1974). The reduction in cytokinin would be expected to bring about a shift towards maleness (Table 2, and Chailakhyan 1979). Shifts towards maleness on sites with dry soils have been reported by Pickett (1915), Freeman et al. (1976) Freeman and McArthur (in manuscript) and McArthur and Freeman (in manuscript). Drought is not the only environmental condition which influences the levels of various hormones: flooding (Burrows and Carr 1969), heat (Itai and Ben-Zioni 1974; Itai et al. (1973) and salinity (Itai et al. 1968, 1973) all influence phytohormone levels. Thus, it appears possible that external environment can modify the sexual expression of individual plants through alteration of endogenous hormone levels. This possibility has broad implications and merits careful evaluation by plant physiologists and developmental morphologists.

Recent works by Freeman and Kalled (unpublished data) demonstrates the role of water stress on sex ratio of spinach populations. They transplanted spinach seedlings (from a common seed source and grown in a common environment) into wet and dry soil environments. The wet environment received 5 × the water applied to the dry environment. They obtained ratios of 82 females to 42 males in wet environment and 46 females to 79 males in dry environment. Since only 3 plants died in each treatment and all plants flowered, the results are best explained by the hypothesis of labile sexual expression.

Despite numerous reports discussing the effect of environment on the sexual state of unisexual individuals and production of hermaphroditic offspring by unisexual parents, such phenomena are rarely city by either geneticists or evolutionists. However, Vasek (1968) and Freeman and McArthur (in manuscript) have noted the frequency of sex change in nature. In his studies on Juniper, Vasek found that 7.3% of the individuals of *J. australis* and 24.5% of *J. osteosperma* individuals changed sex over a 2 to 5 year period. In their study Freeman and McArthur marked over 1,400 individuals representing seven species growing in natural populations in Utah. They found that 9% of the *Atriplex canescens*, 13% of the *A. confertifolia*, 22% of the *A. corrugata*, 11.5% of the *A. cuneata*, 30% of the *A. lentiformis*, 20% of the *A. tridentata* and 2.5% of the *Ephedra viridis* individuals changed sex between 1978 and 1979. Hermaphrodites were observed in all species, and hermaphrodites displayed a larger percentage change in sexual expression between the two years than was recorded for either males or females.

In other recent work, McArthur (1977), and McArthur and Freeman (in manuscript) have demonstrated that environmental factors are strongly correlated with the sexual expression of individuals of the subdioecious species *Atriplex canescens* (Pursh) Nutt., to alter their sexual state. They document sex switching following three environmental stresses: 1) an unusually cold winter, 2) drought and 3) heavy seed set by females. During the flowering period following each of the stressing events, there was a pronounced shift towards maleness in the population of over 600 individuals. When each stressing condition was lifted, the proportion of females in the population increased. Over 40% of the plants involved in the study changed their sexual state during the seven years of observation. Over 200 plants displayed the monoecious state during some period of the study, but only one individual remained monoecious in all seven years (McArthur and Freeman, in manuscript). Zuk (1970) has also observed that monoecious individuals of *Urtica dioica* L. may become dioecious and dioecious individuals may become monoecious. He was able to demonstrate that there was no apparent genetic distinction between monoecious and dioecious individuals. Since few researchers have examined the same individual plant year-after-year, it is impossible to determine whether the hermaphrodites reported by most observers maintained that condition throughout their life. The results of Zuk (1970), McArthur (1977) and McArthur and Freeman (in manuscript) have prompted us to include species in Table 1 that are normally regarded as dioecious but which occasionally produce hermaphroditic offspring.

In the remainder of this paper, we will present a hypothesis concerning conditions under which individuals should be expected to alter their sexual expression. We also review ecological conditions under which individuals are known to have displayed different sexual states. Finally, we will suggest new avenues of research.

A Simple Model

A body of theory has been developed recently concerning the conditions under which natural selection will favor the ability of an individual to allocate or reallocate resources to the male or female sex function (Charnov and Bull 1977). The theory applies to plants in the following way.

Suppose a dioecious species with labile sex inhabits an environment consisting of two kinds of patches (call them wet and dry). Assume a wet-patch individual reproducting as a female will produce w_2 as many seeds as a dry-patch individual reproducing as a female. Thus, w_2 is the relative fitness of the female function in the wet versus the dry patch. Likewise, let w_1 be the average number of ovules a wet-patch male will fertilize relative to a dry-patch individual reproducing as a male. Finally, let P be the proportion of the environment made up of dry patches. P could also be considered the proportion of seeds which fall in dry patches (or if mortality differs among patches, P would be the proportion of the reproductives which are in dry patches). Let r_1 equal the probability that an individual in the dry patch becomes a male

(r_2 is the same for wet patches). Our question now becomes: What r_2 and r_2 probabilities form an Evolutionarily Stable Strategy (ESS) (Maynard-Smith 1976)? We seek an r_1 and r_2 such that any mutant individuals, which alter their values to $\hat{r}_1$ and $\hat{r}_2$, are selected against. Using a population genetic argument based on the assumption of random mating and random dispersal, Charnov 1979a; also see Charnov, et al. 1978 has shown that mutants are selected against providing the following inequality is satisfied:

$$(2 \geqq) \frac{P\hat{r}_1+(1-P)\hat{r}_2 w_1}{Pr_1+(1-P)r_2 w_1} + \frac{P(1-\hat{r}_1)+(1-P)(1-\hat{r}_2)w_2}{P(1-r_1)+(1-P)(1-r_2)w_2}.$$

The game is now to find r_1 and r_2 such that the inequality is satisfied for all possible $\hat{r}_1$ and $\hat{r}_2$.

By considering (1) to be a function of $\hat{r}_1$ and $\hat{r}_2$ (for fixed r_1 and r_2) and taking derivatives with respect to $\hat{r}_1$ and $\hat{r}_2$, it is easy to show that the r_1 and r_2 we seek are those which maximize the *product of the male fitness times the female fitness* or:

$$(Pr_1+(1-P)r_2W_1)\times(P(1-r_1)+(1-P)(1-r_2)W_2). \tag{2}$$

If $w_2 > w_1$ then *an individual gains more in terms of female reproductive success when in a wet patch.* The solution to this maximization is as follows:

$$1-r_1=\begin{cases}\frac{1}{2}\left(1-w_2\frac{1-P}{P}\right) & w_2>\frac{1-P}{P}\\ 0 & w_2<\frac{1-P}{P}\end{cases} \tag{3}$$

$$r_2=\begin{cases}\frac{1}{2}\left(1-1/w_1\times\frac{P}{1-P}\right) & \frac{P}{1-P}<w_1\\ 0 & \frac{P}{1-P}>w_1\end{cases} \tag{3}$$

These results are shown in Fig. 1. This solution makes at least two important predictions: 1) the sex ratio in the wet patch is always biased towards females, while that in the dry goes toward males and 2), the bias strongly depends upon the fraction of the environment that is made up of each kind of patch and so may change from time-to-time or place-to-place. Thus, the expression of sex is a relative character. It is not possible to answer whether an individual in the wet patch should be a male or female, or the probability of one or the other, without knowing what the entire breeding environment is like (i.e., what is P?).

The model proposed above is simple, but we believe that it captures a basic point – that selection can favor "choice of sex" providing the environment is patchy relative to the individual reproductive-success value of being a male or a female (Charnov and Bull 1977).

There are at least two other ways in which an environment can be "patchy" relative to the value of being a male or a female. 1) Reproductive success could be dependent upon age or, more likely, some measure of size that is loosely correlated with age. This may give rise to sequential hermaphroditism or sex change, a condition in which an individual reproduces early in life as one sex and then changes to the other for the remainder of its life. 2) The reproductive success of an individual could be dependent upon the sexual state of neighboring individuals. Such social effects have been suggested for higher plants (Lloyd 1974a, Charnov and Bull 1977) and are extremely well documented for lower forms (Van der Ende 1976, Charnov et al. 1978).

Ghiselin (1969) suggested that natural selection should favor sequential hermaphroditism over fixed sex when an individual's reproductive success as a male or a female is closely related to age or size, and where the relationship is different for each sex. For example, if large size increases the egg output of a female, but does not aid males in competition to fertilize eggs, selection would favor genes which cause an individual to operate as a male while small, but as a female at a later age or larger size. The reverse order of sex change would, of course, be favored if large size or older age were relatively more important for male reproductive success. The genetic theory of sex change which specifies the ESS, sex order and time of change, has been developed by several people (Warner et al. 1975; Leigh et al. 1976; Charnov 1979a, b) and applied to reef fish (Warner et al. 1975) and Pandalid shrimp (Charnov 1979b).

Warner et al. (1975) noted in their studies of the blue headed wrasse that individuals changed from female to male when they became large enough to defend a breeding territory. The equations used by Warner et al. (1975) and Leigh et al. (1976) dealt with the age of individuals. The age criterion was used for convenience, but the salient parameter was size. The individual changed sex when it could defend a given resource or territory. Sequential hermaphroditism in plants is probably superimposed upon environmental sex determination (our patchy environment model) since plant size is rarely a simple function of age.

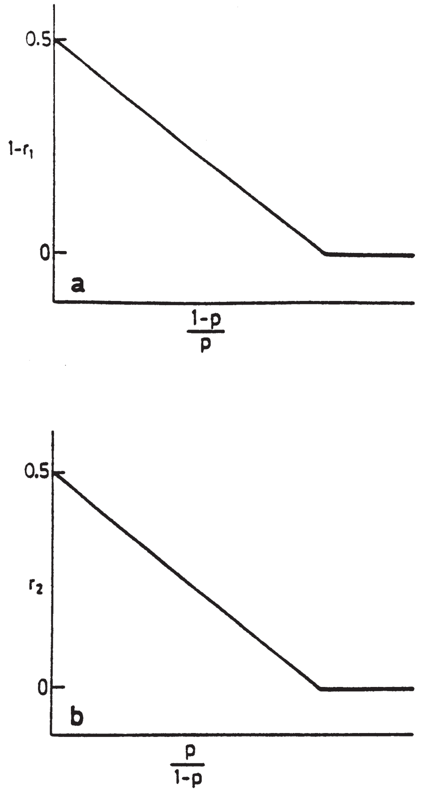

Fig. 1. Patchy environment sex ratios. **a** As the ratio of wet to dry patches increases, the proportion of individuals in the dry patch reproducing as females declines from 0.5 to 0. **b** As the ratio of dry to wet patches increases, the proportion of individuals in the wet patch reproducing as males declines from 0.5 to 0. P is the proportion of the environment made up of dry patches; r_1 is the probability that an individual in a dry patch becomes male. r_2 is the same for wet patches. W_1 is the relative fitness of wet patch male to a dry patch male, and w_2 is the relative fitness of a wet patch female compared to a dry patch female

Some Observations on Sex Change

Individuals of *Arisaema triphyllum* (Shaffner 1925a, b)*, *A. japonicus* (Maekawa 1929), *Eucommia ulmoides*, *Castilloa elastica* (Dzhaparidze 1963), *Ilex opaca* Ait. (Clark and Orton, 1967) and *Metasequoia glyptostrobodies* (H.G. Baker personal communication) normally produce male flowers first and female flowers only after a delay of several seasons. The percentage of female flowers apparently increases with age. Moreover, sex and size of the pseudocorm (a storage structure) are related in several species of orchid (Gregg 1973). Individuals with large pseudocorms are generally female, while the male's pseudocorms are smaller. Gregg's results are suggestive of sequential hermaphroditism, since the orchid species considered exhibit sex change (Gregg 1973). We have observed a similar correlation between size and sex in *Atriplex confertifolia* and (Torr. & Frem.) S. Wats *A. canescens* (Pursh) Nutt. (i.e., the smaller individuals are usually male). Again this is particularly suggestive of sequential hermaphroditism inasmuch as individuals of both species are known to change sex (McArthur 1977; Freeman and McArthur, in manuscript).

There are, of course, substantial differences between the sequential hermaphroditism exhibited by the blue headed wrasse (Warner et al. 1975) and that suspected for plants. The fish becomes male for life when it reaches a given size and defends a breeding territory that is a relatively stable resource. In contrast, the resources important to plants may fluctuate strongly and frequently, particularly with respect to water in arid and semiarid environments. If sexual expression in plants is indeed correlated with the resource state, it would be advantageous for the sexual expression to fluctuate in synchrony with variable environments as has been observed in *Atriplex canescens* (McArthur 1977 and McArthur and Freeman, in manuscript, and Freeman and McArthur in manuscript see also Barker et al. in manuscript).

Schaffner (1922, 1925a, 1926) and others listed below have shown that the sexual expression of individuals of some dioecious and sequential hermaphroditic species is related to their physiological state. Schaffner found that removal of a portion of the corm of a female of *Arisaema triphyllum* caused the plant to exhibit one of three sexual states when it flowered again depending on the amount of corm removed. The plant assumed the monoecious habit if a relatively small portion of the corm was removed; removal of a greater portion resulted in the production of male flowers only, and removal of a still greater part of the corm resulted in nonflowering. As the plant recovered, it passed though the stages in reverse order (i.e., if a sufficient amount of corm was removed to cause a female to become male, the plant produced male flowers first, then both male and female, and finally only female flowers).

Other cases are known in which stressed plants revert to the male state. McArthur (1977) found that, in the flowering season following an unusually severe winter, 86 females of a population of about 600 *Atriplex canescens* individuals became either male or monoecious, 10 monoecious individuals became male, and only 11 male and monoecious individuals became female. Obviously, stress triggered a shift toward maleness. In the more normal year which followed, there was a shift back towards femaleness. Frost damage has been reported to trigger a similar shift from femaleness to maleness in cycads (Menniger 1967). As previously noted, McArthur and Freeman (in manuscript) have shown significant retreat from the female habit by saltbush plants stressed by drought and heavy seed set. Barker et al. (in manuscript) have made similar observations for the polygamous tree, *Acer grandidentatum*. Minina (1952) has shown that, under conditions of low soil moisture or low relative humidity, cucumbers have only male flowers. She also reports that the female sex organs of wheat are more susceptible to water stress than are the male organs. Schaffner (1922) has shown that well-fertilized plants of *Arisaema triphyllum* tend to be female. This fact led him to conclude that the burden of seed production is commonly borne by the most vigorous individuals. Other authors (Giard 1898; Davey and Gibson 1917; Mukerji 1936; Dzhaparidize 1963; Brubaker 1969; Gregg 1973) have come to a similar conclusion.

Data also exist which suggest that environmental variables other than available moisture, nutrients, and storage reserves can induce sex change. Dodson (1962) and Gregg (1973) have shown that sex change is related to light intensity in several orchid species that are sequentially hermaphroditic or dioecious. Shaded plants which are male often become monoecious or female when placed in the sun. Likewise, females often become monoecious or male when placed in the shade. Males in nature are normally most abundant in the shade and females in the sun. Thus, the orchids show a differential sex ratio along a gradient of light intensity. Dodson's (1962) and Gregg's (1973) work suggests that other dioecious species of tropical forests should be investigated for differential sex ratios along strong light gradients.

Most botanical references that we have consulted treat sex change as an unusual event of intellectual interest only. However, the data of McArthur (1977), McArthur and Freeman (in manuscript), Freeman and McArthur (in manuscript), Gregg (1973), Vasek (1968), Schaffner (1922, 1925a, 1926), and Pickett (1915) suggest that the phenomenon must be considered to have great ecological importance. Unfortunately, only the data of McArthur (1977), McArthur and Freeman (in manuscript) and Freeman and McArthur (in manuscript) are based upon large populations in field situations. Clearly similar studies with other species are needed before the broad ecological and evolutionary significance of sex change among individuals of dioecious and sequentially hermaphroditic plants can be fully understood.

Conclusion

Many researchers have shown that sexual expression can be changed in numerous dioecious and sequentially hermaphroditic species. Even some dioecous species reported to have sex chromosomes have the potential of producing monoecious offspring and/or of changing sex. We have shown that dioecious individuals with the capability of sex change will have a selective advantage over individuals lacking this ability in patchy or changing environments. We suggest that variable sexual expression may be common among species that produce unisexual flowers and that such species should possess a reproductive advantage in environments that are heterogeneous in time and/or space.

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