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# Sex Determination in Monoecious and Dioecious Plants

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**REVIEW**

## INTRODUCTION

Angiosperm species that produce unisexual flowers present the opportunity for separate analysis of the male and female programs for floral differentiation and gametogenesis. A vast literature describes the genetic and physiological basis of sex determination in these species. (For reviews, see Westergaard, 1958; Grant, 1975; Frankel and Galun, 1977; Durand and Durand, 1984.) Recently, it has become feasible to pursue the molecular genetic basis of the male and female differentiation programs in certain plant species, as has already been profitably undertaken in several animal species (Hodgkin, 1987, 1989). This article reviews the unisexual flowering schemes found in angiosperms and summarizes available data on the control of floral polymorphism in the monoecious species maize (*Zea mays*) and in the dioecious species mercury (*Mercurialis annua*).

## MONOMORPHIC AND POLYMORPHIC FLOWERING SCHEMES

To best appreciate the systems available for the study of sex determination, it is worth first reviewing the different reproductive systems used by plants. The reproductive systems that pattern floral and sexual differentiation can be monomorphic, with a single bisexual flower type, or polymorphic, with two or more flower types. The majority of flowering plants are hermaphroditic, developing perfect flowers that contain both pistils and stamens. Hermaphroditic individuals produce both male and female gametes. Outcrossing is enhanced through genetic mechanisms such as self-incompatibility or heterostyly (style and stamen length variation that prevents selfing).

Polymorphic reproductive schemes, including dioecism, monoecism, and other variations, are estimated to appear in about 7% of dicot genera and 6% of monocot genera (Yampolsky and Yampolsky, 1922), although these classic estimates may be low (Bawa, 1980). Dioecious and monoecious plants develop unisexual flowers and thus possess at least two schemes for floral development within each species. In dioecious species, such as asparagus and mercury, individuals have either staminate or pistillate flowers and produce either male or female gametes, thus ensuring outcrossing (Durand, 1963; Lazarte and Palser, 1979). Gynodioecious and androdioecious species produce populations of hermaphrodites and females or males, respectively. The dioecious system, with separate male and female individuals, is of course the rule in animals, but is found in only 4% of angiosperm species. The ratio of males and females in a population of a dioecious species is generally based on genetic segregation of alleles at one or more loci. In some dioecious species, such as *Melandrium*, sex chromosomes have been identified cytogenetically, with the male generally the heterogametic (XY) sex and the female the homogametic (XX) sex (Blackburn, 1923; Winge, 1923). In either case, the sex of an individual is determined at fertilization.

In monoecious species, such as maize, individuals possess separate staminate and pistillate flowers and produce gametes of both sexes in physically separate parts of the plant. Monoecious plants can achieve outcrossing through self-incompatibility systems or through temporal dioecism, whereby pistillate and staminate flowers on a single individual mature at different times (Cruden, 1988). The ratio of male and female gametes in a monoecious population is not based on genetic segregation, but is more sensitive to epigenetic and environmental cues. Some monoecious plants are unisexual at any one time in their lives. For example, in jack-in-the-pulpit, sex of an individual is correlated with size; smaller individuals are male and larger individuals are female, although the plants are genetically identical (Policansky, 1981). Gynomonoecious and andromonoecious species produce bisexual and unisexual flowers on the same individual. The nature of monoecism and its variations suggests that these reproductive modes result from the differential regulation of sex determination genes throughout the development of an individual.

## SEX DETERMINATION IN PLANTS

What is meant by sex determination in plants? In most polymorphic species that have been carefully examined, a

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common set of floral organs (sepals, petals, stamens, pistils) is initiated in all flowers, but further development of stamens or pistils is selective, resulting in unisexual flowers. Sex determination is traditionally considered to be this selective abortion of the gynoecium or androecium of initially hermaphroditic floral primordia, but it should also be considered to include the differentiation of gametophyte (egg versus sperm) within the pistil or stamen, which occurs in all angiosperm flowers. Most work on sex determination has focused on the differentiation of pistillate and staminate flowers, with the underlying assumption that their meiotic products are determined as female and male gametes. The selective abortion aspect of sex determination has been best marked in mutations affecting dioecious and monoecious species (such as *tassel seed-2* in maize), while pistil-versus-stamen differentiation may be easiest to study with mutants of bisexual flowers [such as *pistillata* in *Arabidopsis thaliana* and *stamenless-2* in tomato (Haughn and Somerville, 1988; Rastogi and Sawhney, 1988)].

What are the genetic systems governing the differentiation of male and female floral parts? Are there pivotal male/female regulatory genes? What are their products and targets of action? When do they act? How do they promote or suppress growth of pistils and stamens? How do endogenous factors (e.g., growth regulators) and exogenous factors (e.g., day length) act on the sex-determining systems? Genetic and physiological studies of maize and mercury, both of which normally produce unisexual flowers, suggest that these plant systems might be useful for answering the above questions at a molecular level. In the following discussion, we summarize the features of the sex determination systems in these two plants that make them attractive for mechanistic studies.

## MAIZE—PISTIL ABORTION IN TASSELS, STAMEN ABORTION IN EARS

Sex determination in a monoecious plant is best understood in maize. The terminal inflorescence or tassel of the maize plant develops from the shoot apical meristem into a thin panicle, normally branched at the base. (For descriptions of maize floral morphogenesis, see Weatherwax, 1916; Bonnett, 1948, 1953; Cheng, Greyson, and Walden, 1983). At maturity, the tassel bears only male flowers. The lateral inflorescences, or ears, terminate short branches that develop from axillary buds. The ears are thickened spikes that normally bear only female flowers. Despite their many differences at maturity, early in development, tassels and ears are morphologically indistinguishable except for the presence of branch primordia on the tassel (Cheng, Greyson, and Walden, 1983). Hermaphroditic flowers, consisting of identical complements of (in order) glumes, lemmas, paleas (all small, leaflike bracts), stamens, and a pistil, are initiated on both inflorescences, as shown in Figure 1. Later in development, pistils in florets on the tassel and stamens in florets on the ear are arrested in development and degenerate. Secondary sex characteristics such as the branching pattern of the inflorescence and morphology of the glumes are apparent before the differential growth of the stamens and pistils takes place, while thickness of the supporting rachis of the tassel or ear may be determined later in the development of the inflorescence.

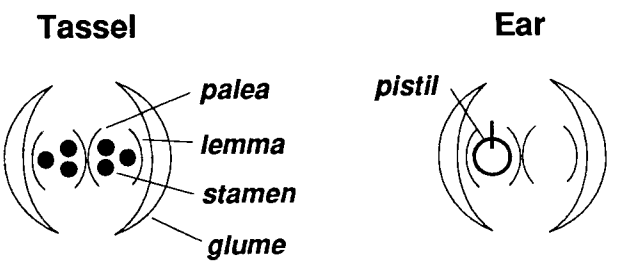


**Figure 1.** Schematic Diagram of Florets in Normal Tassel and Ear of Maize.

What genetic systems control these alternate modes of differentiation? The characteristics of several kinds of mutants, including *dwarfs* and *tassel seeds*, suggest that monoecy results from active suppression of organs of the inappropriate sex at ears and tassels and that gibberellins (GAs) play a role in the suppression.

## MAIZE DWARF MUTANTS—LIMITED FEMALENESS?

The andromonoecious *dwarf* mutants have reduced stature, ears bearing florets in which the stamens have continued to develop and the pistils may have been arrested, and tassels that are normal (except that the anthers may fail to exsert). The *dwarfs* have been mapped to six unlinked loci, and include recessive and dominant mutations (Coe, Neuffer, and Hoisington, 1989). Biochemical and physiological analyses of the *dwarf* mutations suggest that GAs are important for female development in maize and may be a primary signal in sex determination. Phinney (1956) first showed that the size and flowering characteristics of the recessive *dwarfs* could be cured by the application of exogenous GA, and that they produced lower-than-normal endogenous levels of GA1 (Phinney, 1961).

Are GAs pivotal in maize sex determination or are they the agents of a decision made higher up in a regulatory cascade? Recent work has correlated high and low levels of GAs with female and male differentiation, respectively. First, exogenously added GAs can feminize normal tassels (Nickerson, 1957; Hansen, Bellman, and Sacher, 1976; Krishnamoorthy and Talukdar, 1976). Second, the endog-

enous levels of GA1 are 100-fold greater in ear shoots than at the shoot apex (Rood, Pharis, and Major, 1980). Third, wild-type tassels can be feminized by environmental conditions such as short day length and low light (Richey and Sprague, 1932; Heslop-Harrison, 1960). Reduced light intensity results in higher endogenous levels of GAs (Rood, Pharis, and Major, 1980). Finally, each of the recessive *dwarf* mutations [*d1*, *d2*, *d3*, *d5*, and *anther ear* (*an*)] has proved to affect a different step in the biosynthesis of GA1 (Phinney, 1984). The dominant mutation *D8* has normal levels of GA1 and does not respond to exogenous GA (Fujioka et al., 1988). Clonal analysis of this mutation and of *Miniplant* (*Mpl*), possibly an allele of *D8*, has shown that these mutations are cell-autonomous; i.e., sectors of wild-type tissue that had lost *D8* or *Mpl* had no effect on the neighboring mutant tissue, at least in some regions of the plant (Harberd and Freeling, 1989). These studies suggest that *D8* is involved in the reception of GA. Analogous experiments with the recessive *dwarf* mutants have not been performed, but would be expected to show non-cell-autonomous phenotypes due to diffusion of GAs from wild-type to mutant sectors.

The association of GAs and sex differentiation in maize is thus far a correlation. Once it becomes possible to induce endogenous GA synthesis at precise times and locations by transgenic manipulations (e.g., Medford et al., 1989), it may be possible to establish a causal relationship between differential GA concentrations and male or female differentiation. The collection of *dwarf* mutants could be valuable in providing a low background of endogenous GAs for such experiments.

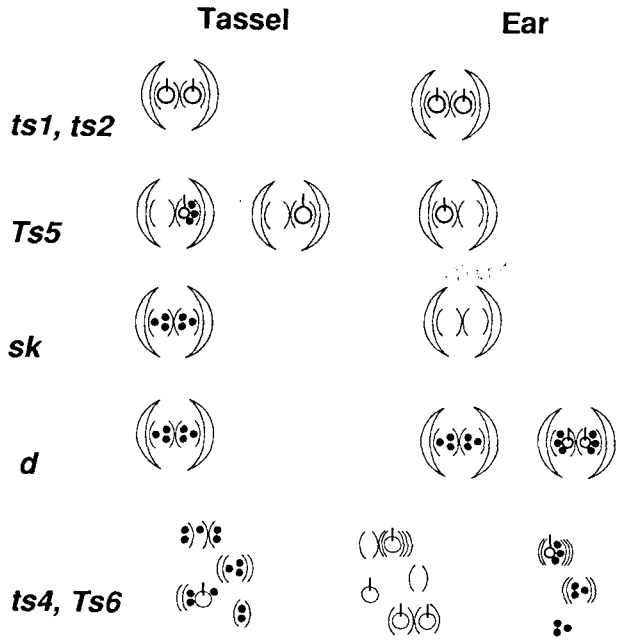


**Figure 2.** Schematic Diagrams of Florets of Various Sex Determination Mutants of Maize.

*ts*, *tassel seed*; *sk*, *silkless*; *d*, *dwarf*. Symbols for floral parts are as identified in Figure 1. For *ts4* and *Ts6*, several examples of the disorganized proliferation of floral organs found on both tassel and ear are shown. *ts4* tends to cause more proliferation than *Ts6*.

## MAIZE TASSEL SEED MUTATIONS—UNLIMITED FEMALENESS?

Whereas the *dwarf* mutations cause extreme maleness through failure to suppress male/promote female development on ears, the *tassel seed* mutations do the reverse. In *tassel seed* mutants, pistils develop in florets on the normally staminate tassel (Nickerson and Dale, 1955). *tassel seed* mutants may also exhibit crowding of kernels on the ears as a result of the development of the lower flower of each spikelet pair, which normally is aborted. There are at least five *tassel seed* mutations, dominant (*Ts*) and recessive (*ts*), that have been mapped to unlinked loci (Coe, Neuffer, and Hoisington, 1989). Figure 2 diagrams the combinations of male and female floral organs found in florets of several of the *tassel seed* mutants. *tassel seed-1* and *tassel seed-2* have the simplest phenotype: a complete transformation of the male florets of the tassel to female (see Figure 3) and development of the lower florets on the ear. Transformations in other mutants are less complete. *ts4* and *Ts6* cause a proliferation of floral organs on the tassel and ear, forming irregular male, female, perfect, and sterile florets. *Tassel seed-5* mutants have normal ears and nearly normal tassels that exhibit some perfect and some female florets.

Are the *tassel seed* mutants affecting the same pathway as the *dwarf* mutants? The biochemical basis for the *tassel seed* phenotype is unknown. One series of experiments suggested that application of exogenous GA could "cure" the phenotypes of several *tassel seed* mutants (Nickerson, 1960), but it was not possible at that time to assess the quantity of GA actually internalized by plants. Furthermore, the external applications had pleiotropic effects on overall growth and development and may have obscured rather than cured the phenotype. At least one of the *tassel seed* genes has a nondiffusible product. Johri and Coe (1983) recovered a wild-type sector with sharp boundaries on an irradiated *Ts6*/+ plant, suggesting that the product of the *Ts6* allele cannot diffuse over distances and may be cell-autonomous. Analogous experiments have not been completed with recessive *tassel seed* mutants, but they might be expected to have non-cell-autonomous phenotypes if they correspond to synthetic genes for the diffusible agents to which the dominant (receptor?) genes respond. The few *dwarf-tassel seed* double mutants that have been constructed thus far suggest that the *dwarf* and *tassel*


**Figure 3.** Tassels of Normal and *ts2* Maize.

**(A)** Normal maize.
**(B)** *ts2* maize.
In the mutant, male florets are converted to female florets; the branching pattern is unchanged.

*seed* pathways are independent (E. Irish, unpublished results).

Several other maize mutants have phenotypes related to the *tassel seeds* (Coe, Neuffer, and Hoisington, 1989). *silkless* (*sk*) prevents the development of silks (styles) on the ears; male development is normal on the tassel. In *silky* (*si*) mutants, silk development is extreme on ears and male development is incomplete on tassels. *teosinte branched* (*tb*) causes the branches that normally develop into ear shoots to elongate and terminate with a tassel-like inflorescence. Some of the lowest tassel branches are converted into miniature ears by the mutation *terminal ear* (*te*) (Mathews, Grogan, and Manchester, 1974). Various alleles of *ramosa-3* (*ra3*) cause basal branching of the ear and pistil development in the tassel. Do the *tassel seeds* and these related genes make up a genetic pathway that regulates sexual differentiation or do they act independently? Genetic studies suggest that the products of some of these genes interact.

## INTERACTION OF MAIZE SEX DETERMINATION GENES

Several of the *tassel seed* and other sex determination genes have been placed in combination with one another. In some cases, the resulting epistasis suggests that they act on a common pathway that either suppresses pistil development in the tassel but not the ear or, alternatively, suppresses stamen development on the ear but not the tassel. For example, epistatic interactions occur between *ts2* and *sk*; the double mutant has a *tassel seed* phenotype (Jones, 1934). Similarly, the *ts2-tb* double mutant has completely feminized inflorescences, while *ts1*, which has a phenotype identical to that of *ts2*, in combination with *tb* has inflorescences with both staminate and pistillate florets (Miku, 1973; Mustyatsa and Miku, 1975). The set of double mutants that has been constructed is insufficient to permit the proposal of an unambiguous pathway of genetic inter-

actions. However, from the interactions already observed, it seems likely that one or a few morphogenetic pathways will emerge from further studies.

Once the male/female decision is made, the differentiation paths that follow appear to be relatively stable. Excised immature tassels and ears will continue sexual differentiation in culture. Cultured tassels develop male florets that continue through meiosis and normal pollen formation, in the absence of GAs. (Cytokinins are required for continued growth; Polowick and Greyson, 1982, 1985.) Cultured immature ears do not develop as extensively. At early stages, the sex of ear florets is influenced by cytokinin levels, while later stages are stably female (Bommineni and Greyson, 1987).

In summary, studies with maize mutants suggest that the restriction of male differentiation to tassels and female differentiation to ears relies in part on the different local concentrations of GA at the two sites. Local GA concentration (and other endogenous and exogenous signals) may be monitored by pivotal sex determination genes that in turn activate male or female differentiation pathways. One might predict that such pivotal genes would have alternate states at some critical time in male and female tissue. For example, pistil-suppression genes (*tassel seed* genes?) would be "on" in the tassel primordium and "off" in the ear primordium. As described above, genetic evidence for such a hierarchy is still sketchy, but as individual *tassel seed*, *dwarf*, and other sex-related genes are cloned and analyzed, it should become possible to propose and test more mechanistic models.

## MERCURY—PISTIL ABORTION IN MALES, STAMEN ABORTION IN FEMALES

It is possible that dioecious species use an analogous system of selective suppression to fix individuals as male or female. Studies with the dioecious mercury plant (a poisonous herb) suggest that genes establishing individuals as male or female may control sex expression by setting extreme endogenous levels of auxin and cytokinin growth regulators. Three genes (*A*, *B1*, and *B2*) that control sexuality have been identified in this species, based on degree of feminization of segregating males by exogenous cytokinins (Louis and Durand, 1978; Louis, 1989). The dominant alleles promote maleness and vary in strength: $A > B1 > B2$. Two fertility restorer genes (*R1*, *R2*) have been identified for a cytoplasmic factor controlling male sterility. More than 64 genotypes have been constructed from combinations of alleles of these genes, including strong males, weak males, strong females, weak females, as well as sterile plants (Durand and Durand, 1983).

Are growth regulators the agents for male and female suppression? Cytokinins and auxins are correlated with female and male differentiation, respectively, in mercury plants. Genetic males are easily feminized by cytokinins. This was demonstrated in physiological studies involving either grafting of genotypes with different endogenous hormone levels (Durand, 1967) or the exogenous application of hormones (Louis and Durand, 1978). However, genetic females can be masculinized only by in vitro culture of nodal explants in the presence of auxins (Champault, 1973). Male and female floral apices exhibit diagnostic patterns of auxins and cytokinins (Dauphin, Teller, and Durand, 1979; Dauphin-Guérin, Teller, and Durand, 1980; Champault, Guérin, and Teller, 1985). Female apices were found to have only *trans*-zeatin and low levels of auxin. Male apices had no detectable *trans*-zeatin but instead zeatin nucleotide and higher levels of auxin. The level of auxin in males was strongly correlated with the genotype (Durand and Durand, 1984; Hamdi, Teller, and Louis, 1987).

How do the male and female genotypes differ? Each genotype appears to maintain characteristic endogenous levels of growth regulators, even when subjected to tissue culture. Morphological sex differences are not apparent in juvenile plants or in vegetative tissues in mercury. Nevertheless, callus derived from male or female shoot apices retained distinct levels of these growth substances. Tissue derived from males maintained higher levels of auxin and tissue from females maintained higher levels of cytokinins, in the absence of any morphological differentiation (Champault, Guérin, and Teller, 1985). These correlations suggest that the genes characterized thus far in mercury plants are involved in maintaining endogenous growth regulator levels, but need not be switches for male/female floral differentiation.

What initiates male or female differentiation? Recent studies have identified molecular markers that are specific for early stages in the differentiation of male, female, or sterile flowers. The markers include several isozymes (Kahlem, 1975, 1976; Bazin, Chabin, and Durand, 1975), specific tRNAs (Louis, 1983), and translatable mRNAs (Delaigue, Poulain, and Durand, 1984; Delaigue et al., 1986). These differentiation-specific probes may be useful in identifying the system that induces them and possibly responds to the levels of auxin/cytokinin established in a given genotype.

## OTHER SYSTEMS

Studies of sex determination in many other species suggest that a variety of distinct stategies may be employed to produce unisexual flowers. Each system appears to be influenced by a distinct combination of recognized growth regulators. In general, most studies support the model of alternate, suppressible pathways for male and female differentiation (Durand and Durand, 1984). For example, as-

paragus is dioecious with distinguishable sex chromosomes (Loptien, 1979); XY and YY individuals produce staminate flowers, XX individuals produce pistillate flowers (Franken, 1970; Lazarte and Palser, 1979). Under some conditions, XY individuals are andromonoecious, producing staminate and bisexual flowers. A limited series of genetic studies has suggested that genes controlling the sexual characters of individuals segregate as a dominant female-suppressor and a dominant male-activator on the Y chromosome. The ability to utilize the *Agrobacterium*-mediated transformation system (Hernalsteens et al., 1984) and the small genome size of asparagus (Galli et al., 1988) may eventually facilitate a molecular analysis of these activities.

In the diploid dioecious species *Melandrium* (campion), experimental variation of X, Y, and autosome dosage showed that the presence or absence of Y chromosomes is the primary determinant of maleness or femaleness, while the number of X chromosomes or autosomes present modifies the expressed maleness (reviewed in Westergaard, 1958; Frankel and Galun, 1977). In related experiments, variation of the X-to-autosome ratio between 0.5 and 1.5 had no effect on sex expression. The large Y chromosome of *Melandrium* could be fragmented by segregation from triploids. Experiments with such fragmented Y chromosomes suggested that separate male-promoting and female-suppressing loci reside on the Y, although conclusive genetic studies are lacking.

In the monoecious plant cucumber, the normal pattern of sex expression is the development of male flowers at basal nodes, followed by nodes bearing male and female flowers, terminating with nodes bearing only female flowers (Durand and Durand, 1984). Exogenous application of hormones can alter this pattern, auxin feminizing plants by shortening the male and mixed phases, GAs masculinizing by delaying the appearance of female flowers. The allele *st* has the same effect as auxin application, while *m/m* plants have perfect flowers (Frankel and Galun, 1977).

## PROSPECTS

The monoecious and dioecious systems described here illustrate the difficulty in distinguishing the factors that influence sex determination from the factors that carry out the resulting floral differentiation programs. The focus of many studies on the effects of growth regulators such as auxins, cytokinins, and GAs has demonstrated the ability of these substances to influence sex differentiation but has not demonstrated that they are involved in decisions during normal development. In both types of system, maleness and femaleness appear to be achieved through the suppression of the differentiation program for the opposite sex. This suggests that sex determination acts through genes regulating the relative activities of the male and female differentiation pathways, possibly using known growth regulators as messengers. The genetic approach used in the maize and *Mercurialis* systems has identified a number of loci of demonstrated importance to the male/female switches in these species. The molecular genetic study of genes such as the *tassel seeds* in maize and the cytokinin-responsiveness genes in *Mercurialis* is likely to identify the pivotal genes, if they exist.

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