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Genetic and non-genetic sex determination in plants

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Abstract

Sexual reproduction arose at the dawn of the evolution of living beings and is a defining moment for Darwinian evolution and fitness. Its primary significance lies in the mixing of genes in a population and the creation of new genomic complexes in each new generation. From this perspective, the separation of individuals in a population by sex and the control of this separation are important attributes of sexual reproduction. Despite extensive research on the determination and control of sex expression in plants, this field of research remains relevant and less studied than in animals. This review discusses the current research and views on genetic and non-genetic sex determination in plants; the presence and role of sex chromosomes in dioecious species; sex-determining genes and downstream regulators; hormonal and epigenetic factors regulating sex expression; the influence of external and environmental factors; plasticity of plant sex expression and the transition from bisexual individuals to female and male and vice versa. The influence of sex-determining genes on the conserved floral meristem identity genes *A, B, C, D* and *E*, which ultimately express sex, is also considered.

Keywords: *plant sex determination, sex chromosomes, dioecy, monoecy, hermaphroditic flowers*

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1. Introduction

Sexual reproduction in plants originated well before the transition to terrestrial habitats, which took place during the Ordovician Period around 470 million years ago [1]. By that time, the ancestors of land plants had already differentiated female and male gametes and the reproductive structures for their production, archegonia and antheridia, respectively. Over the course of evolution, land plants developed an alternation of haploid and diploid generations (gametophytes and sporophytes), with the development of the reproductive organs that produce egg and sperm cells occurring in the gametophyte phase [2–4]. However, control of sexual development varies among representatives of different taxonomic groups and can be carried out by the sporophyte, the gametophyte, or both phases [5, 6]. Sex determination in plants involves a dynamic interaction of genetic, epigenetic, and hormonal regulation, and environmental factors. The separation of males and females in plants, called dioecy, has evolved independently and repeatedly in different plant groups, involving a variety of molecular and genetic strategies [7]. The presence of dioecy, due to the existence of male and female chromosomes, even in such a relict gymnosperm as *Ginkgo biloba*, testifies to its very ancient origins [8]. In angiosperms, the diversity of inflorescences—the whimsical shapes, colors, scents, and ways of attracting pollinators—has continually amazed humans since ancient times. Most species of angiosperms found on Earth bear bisexual, that is, hermaphroditic flowers, containing both female (carpels) and male (stamens) structures in a single flower. Hermaphroditism is much more widespread among plants than among animals. According to research, approximately 65% of gymnosperm species are dioecious [9], while dioecy in angiosperms is a much rarer phenomenon, observed in only 5–6% of all species. However, its presence has been recorded in a fairly large number of phylogenetic taxa, including about 15,600 species belonging to 175 families [10, 11]. Around 10% of angiosperms have unisexual flowers, located either on the same individual in monoecious plants or on different individuals in dioecious plants [12, 13]. Dioecious plants may exhibit gynodioecy, or female dioecy, when specimens bearing both female (pistillate) and bisexual flowers are present, and androdioecy, or male dioecy, when plants with both male (staminate) and bisexual flowers are observed [14, 15]. Gynodioecy is often maintained by nuclear–cytoplasmic genetic interactions and is observed in plants such as wild thyme, *Thymus vulgaris*; bladder wedge, *Silene vulgaris*; *Silene acaulis* (with cytoplasmic male sterility (CMS) observed in *S. vulgaris*); plantain, *Plantago lanceolata*; North American geranium, *Geranium maculatum*; *Beta vulgaris* ssp. maritima (sea beet); common lobelia, *Lobelia siphilitica*; *Daphne kamtschatica* and others [16–21]. From an adaptive perspective, dioecy represents an ecologically risky strategy for sessile organisms such as plants and is possible only in environments with certain favorable pollination conditions for dioecious species [22]. Nevertheless, in such plants, a significant number of individuals remain unpollinated, which may explain the repeated reversion of dioecious plants to hermaphroditism during reproductive evolution [23–25]. Androdioecy is a relatively rare system of sexual reproduction and is found in the annual plant *Mercurialis annua* [26], *Fraxinus lanuginosa* (Japanese ash) [27], *Ulmus minor* [28], and some other plant species. Many populations of “androdioecious” plants are actually functionally monoecious or partially dioecious, so the true cases are a matter of debate. Androdioecy, like gynodioecy, is considered not very common and is a kind of transitional reproductive system. Evolutionary models suggest that androdioecy

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is stable only under strict conditions—for example, with a high rate of self-pollination and strong reproductive benefits from pollen abundance [29].

Historically, two categories of unisexual flowers have been recognized: type I flowers have vestigial structures of the opposite sex (for example, male flowers retain a rudimentary gynoecium and female flowers retain a rudimentary androecium), while type II flowers completely lack vestiges of the opposite sex, meaning that the flowers are strictly unisexual and do not exhibit signs of bisexual origin [13, 30]. The evolutionary significance of this division may lie in the fact that type I suggests that dioecy arose from a hermaphroditic ancestor relatively recently, with vestiges of the organs of the opposite sex retained. Type II, however, indicates a more specialized dioecy, where evolution has eliminated all traces of the opposite sex. The dynamics of the development and evolution of unisexuality followed much more complex scenarios and different paths in representatives of different plant groups, which is also confirmed by the diverse modes of genetic, hormonal, and external regulation of sex determination in different plant species and genera [15, 31].

In most angiosperms and in gymnosperms, the gametophyte phase is greatly reduced compared to spore-forming plants, and the gametophytes consist of only a few cells—usually seven in the female gametophyte of angiosperms (the embryo sac) and three in the male gametophyte (pollen) embedded within the sporophyte tissues [2]. Sex is determined by the diploid sporophyte. Sporophytes can be hermaphroditic, producing both anthers and ovules, or they can be exclusively male, producing only pollen, or exclusively female, producing only ovules containing female gametophytes in monoecious plant species. That is, in seed plants, especially in angiosperms, the sporophyte determines sex by controlling the arrangement and number of female and male reproductive structures within it. Sex determination can occur through genetic factors (GSD = genetic sex determination) or by non-genetic components mediated by the environment (ESD = environmental sex determination), such as the position of the inflorescence on the stem, temperature, plant density, and other factors [32].

Despite extensive research and analysis of the causes of sex determination in plants, this topic remains relevant and less studied in plants than in animals. This review discusses genetic and non-genetic sex determination in plants; the internal and external factors influencing sexual identity in dioecious, monoecious, and hermaphroditic plants; and their occasional interconversion.

2. Floral organ identity determined by gene expression in the floral meristem

The transition from the shoot apical meristem to the floral meristem requires the activation of genes responsible for floral meristem identity, which promote the cessation of stem cell formation and determine the formation of floral organs. It has been shown that the interaction of the *AGAMOUS* (*AG*), *LEAFY* (*LFY*), and *WUSCHEL* (*WUS*) genes is important for maintaining floral identity and specificity. *AGAMOUS* (*AG*) is a homeotic gene necessary for maintaining floral meristem function and for the proper development of stamens and carpels [33]. *AG* prevents the reversion of the floral meristem to a shoot meristem but is not directly involved in the transition from shoot to floral meristem [34]. *AG* is activated by two other floral meristem genes, *LFY* and *WUS*, and is restricted to the center of the floral meristem or the two inner whorls [35]. *WUS* activates *AG* by binding to a consensus sequence in the second intron of *AG*, and *LFY* binds to adjacent recognition sites. Activated *AG* suppresses *WUS* expression, leading to the cessation of meristem development [36].

The genetics of hermaphroditic flower development has been well characterized using the *ABC* model, which explains the identity of floral organs formed in the four whorls of the floral meristem through the overlapping expression of three classes of regulatory homeotic genes, encoding transcription factors [37]. Later, genes determining the identity of floral organs were cloned in *Arabidopsis* and several other species; they were homologous across species and can be roughly divided into three gene groups depending on the floral meristem whorl in which they are expressed. In *Arabidopsis,* these genes are as follows: *A* (*APETALA1* and *APETALA2*), *B* (*APETALA3* and *PISTILLATA*), and *C* (*AGAMOUS*) [38, 39]. The development of sex-specific organs depends on the combinatorial and differential expression of homeotic genes in time and space. These genes are responsible for coordinating the formation of all floral organs, which are formed in four floral meristem circles: sepals, petals, carpels, and stamens. Thus, it was shown that sepal formation is encoded by gene *A*, petals by the coexpression of gene *A* and gene *B*, stamens by the coexpression of gene *B* and gene *C*, and carpels by gene *C* (**Figure 1**; **Table 1**). Mutations in these genes cause homeotic transformations and the ectopic formation of floral organs, such as the transformation of stamens into petals. Loss of gene *A* results in expansion of gene *C* activity in flower whorls 1 and 2, such that stamens and carpels replace sepals and petals. Loss of gene *C* results in expansion of gene *A* activity in flower whorls 3 and 4, such that sepals and petals replace stamens and carpels. These mutations were particularly well studied in the cruciferous plant *Arabidopsis thaliana* and the distantly related snapdragon *Antirrhinum majus*. Mutations in each of these genes result in a characteristic phenotype with a disrupted pattern of floral organ formation. For example, in the *apetala2* mutant, sepals are transformed into carpels and petals into stamens, while in the *apetala3* mutant, petals are transformed into sepals and stamens into carpels [40]. Based on these observations, it was concluded that the rows of modified leaves corresponding to specific flower-forming organs arise from the corresponding four whorls. The whorls are equivalent to segments in animal body patterning. Their development is controlled by homeotic genes, just as the sequences of segments in animal body patterns are controlled [40].

Later, an expanded model was introduced that added the *D* and *E* genes to the original *ABC* model proposed earlier (**Table 1**). *D*-class genes (*SEEDSTICK* (*STK*)) in *Arabidopsis* specify and control placenta and ovule development in carpels [41–44]. *E*-class genes (*SEPALLATA1-4*) form complexes with proteins A, B, C, and D and are essential for the identity of all floral organs [42, 44, 45]. Loss of gene *E* results in floral organs transforming into leaf-like structures because the organ identity complex cannot form.

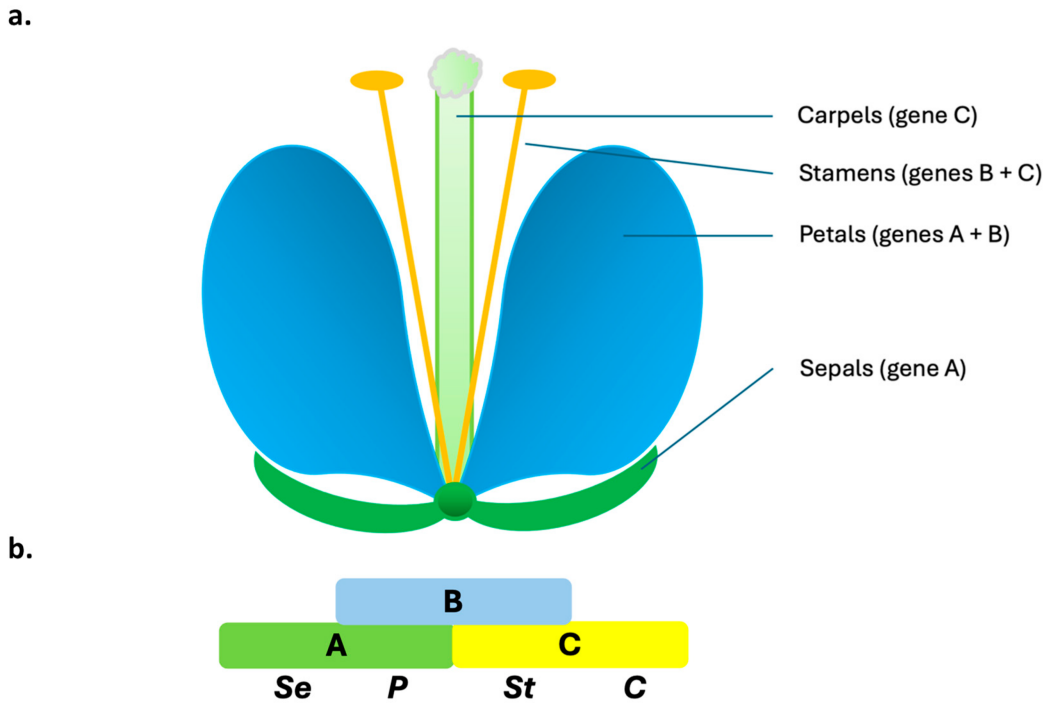

Figure 1 • Model of floral organ regulation by homeotic genes *ABC*: (**a**) Schematic representation of floral organs formed in four whorls of the floral meristem and the genes responsible for their identity. (**b**) Block diagram demonstrating the overlap of homeotic gene expression in the second and third whorls of the floral meristem—*AB* and *BC*, where petals and stamens are formed, respectively, and the activity of single genes *A* in the first whorl and *C* in the fourth whorl, where sepals and carpels are formed, respectively. *Se*—sepals; *P*—petals; *St*—stamens; *C*—carpels.

Table 1 • Role of each class of *MADS*-box genes.

Class	Function	Active	Essential genes in *Arabidopsis*	Reference
A	Defines sepals (with B → petals)	whorls 1 and 2	*APETALA1 (AP1), APETALA2 (AP2)*	[38, 39, 46]
B	Defines petals (with A) and stamens (with C)	whorls 2 and 3	*APETALA3 (AP3), PISTILLATA (PI)*	[38, 39, 46]
C	Defines carpels (together with B → stamens)	whorls 3 and 4	*AGAMOUS (AG)*	[38, 39, 46]
D	Defines ovules within carpels	whorl 4 (ovules)	*SEEDSTICK (STK)*	[41–44]
E	Acts as a cofactor for all organs (required everywhere)	all whorls	*SEPALLATA1-4 (SEP1-4)*	[42, 44, 45]

Despite the conservation of the *A-, B-, C-, D-* and *E-* class genes, they play virtually no role in determining the sex in dioecious plants, i.e., whether the plant will become male or female; although, being activated by genes that determine sex, they do influence reproductive traits. In animals, mammals and some insects, males are the heterogametic sex, i.e., they carry two different sex chromosomes, designated X and Y, while females are the homogametic sex, carrying two X chromosomes. Insects may have an Xo system, where females carry two X chromosomes and males only one. In birds and some reptiles, the female is the heterogametic sex, as the female karyotype contains ZW chromosomes, while the male karyotype contains identical ZZ chromosomes [11]. Plants also exhibit XY and ZW types of heterogametic sex determination systems. However, unlike in animals, heteromorphic sex chromosomes in plants have only been identified in some species to date [10, 11, 47, 48]. In nature, plants with homomorphic sex chromosomes are more common. These chromosomes are similar or nearly identical in size and structure, except for the presence of a male-linked factor on the proto-Y chromosome, which is always heterozygous in male plants. They recombine readily. One cannot easily tell them apart cytologically.

3. Sex chromosomes and genetic systems of plants

Understanding the evolutionary patterns in the emergence of separate sexes and dioecious plants is perhaps even more relevant for the latter than for animals, as unlike in animals where most lineages share ancient sex-chromosome systems, accumulating evidence indicates that dioecy and sex chromosomes originated independently at least 40–50 times in flowering plants

from hermaphroditic ancestors lacking sex-determining genetic polymorphism, with sex-determining regions arising in a lineage-specific manner rather than from a shared ancestral SDR [10, 25, 49–52]. In some dioecious plants, the sex-determining regions (SDRs) of the genome are physically small, while in others, loci that do not recombine during meiosis sometimes form large regions with properties very similar to those of animal sex chromosomes. Studies show that up to 10% of flowering plants have genetic sex determination [25, 47], which is consistent with the proportion of plants that have unisexual flowers. In some dioecious angiosperms, sex chromosomes have evolved from autosomes to XY or ZW systems (**Table 2**). The mechanism behind the XY sex determination system in plants has been extensively studied, particularly in species like *Silene latifolia* [50, 53], where the Y chromosome carries male-specific genes responsible for triggering male development. The presence of a male-specific region of the Y chromosome (MSY) and a female-specific region on the X chromosome plays a crucial role in the determination of sex [47]. **Figure 2** schematically depicts the putative origin of the Y chromosome from the X chromosome through the gradual appearance on the homologous chromosome of a homomorphic and then heteromorphic non-recombining locus, which increases to the size of a separate Y chromosome. The regions in which the pair of sex chromosomes recombine are called "pseudoautosomal regions" or PARs [25, 54].

Empirical studies document male heterogamety (XY) in many plant systems (*Silene, Cannabis, Populus,* asparagus and others) [55–63]; female heterogamety (ZW) in willows (*Salix viminalis, S. purpurea*) [64, 65], some species of *Fragaria* [66, 67], and pistachio [68, 69]; and complex systems such as XY_1Y_2 in *Rumex acetosa* (**Table 2**). The ZW system is notably less studied in comparison to XY systems, but remains critical in certain plant families. Comparative genomic and mapping studies confirm patterns of chromosome systems origin in some plant species [70–72]. In campion (e.g., *Silena latifolia*), sorrel (*Rumex*) and date palm, sex chromosome differentiation follows patterns of recombinational suppression, Y chromosome degeneration, gene loss, and DNA repeat accumulation [31]. *Rumex acetosa* has a multiple sex system with 2n = 12 + XX in females and 2n = 12 + XY_1Y_2 in males. Depending on the ratio of X chromosomes to autosomes, female, male, bisexual, or intersex flowers are formed. Thus, sex in *Rumex* is determined not only by the presence of X and Y chromosomes, but also by the ratio of X chromosomes to autosomes [73, 74].

During the evolution of many dioecious species, the recombinant regions on one Y (or W) chromosome were significantly or completely removed, and the heteromorphic region accumulated genes that were hemizygous, that is, lacking their allelic pair on the homologous X (or Z) chromosome. Thus, heterogamety gradually evolved in dioecious species from hermaphroditic ancestors. Examples of some heterogametic dioecious plant species are shown in **Table 2**. In various taxa of dioecious plants in which sex chromosomes have been found, male heterogamety occurs five times more often than female heterogamety [75].

Table 2 • Examples of plant species with sex chromosomes.

Species	Family	Sex-chromosome system	Sex determination	Notes	Reference
Silene latifolia (White campion)	Caryophyllaceae	XY	Male heterogametic	Model for early sex-chromosome evolution; Y is larger and heterochromatic.	[50, 53, 70]
Rumex acetosa (Common sorrel)	Polygonaceae	XY_1Y_2	Male heterogametic (two Y's)	Complex system with two Y chromosomes; females are XX.	[73, 74]
Populus trichocarpa (Black cottonwood)	Salicaceae	XY	Male heterogametic	Poplars show both XY and ZW systems in different species.	[44, 76, 77]
Salix viminalis (Common osier, basket willow)	Salicaceae	ZW	Female heterogametic	Willows typically have a ZW system (opposite to poplars).	[64, 65]
Carica papaya (Papaya)	Caricaceae	XY	Male heterogametic	Hermaphroditic forms arise from mutations in the Y chromosome.	[78]
Coccinia grandis (Ivy gourd)	Cucurbitaceae	XY	Male heterogametic	Clear differentiation between X and Y; good dioecious model.	[79]
Diospyros kaki (persimmon, date plum)	Ebenaceae	XY	Male heterogametic	The OGI gene on the Y suppresses female development.	[11, 76, 77, 80]
Mercurialis annua	Euphorbiaceae	XY	Male heterogametic	Young sex chromosomes; studied for the evolution of dioecy.	[81]
Fragaria chiloensis, F. virginiana (wild strawberry)	Rosaceae	ZW	Female heterogametic	Edible berries; octoploid, homomorphic, female heterogametic (ZW) inheritance, short SDR in females but not in males.	[66, 67]

Table 2 • *Cont.*

Species	Family	Sex-chromosome system	Sex determination	Notes	Reference
Asparagus officinalis (Garden asparagus)	Asparagaceae	XY	Male heterogametic	Sex determined by a small Y-linked region (M locus).	
Humulus lupulus (Hop)	Cannabaceae	XY	Male heterogametic	Used in brewing; Y chromosome carries sex-determining genes.	[63, 82, 83]
Cannabis sativa (Hemp)	Cannabaceae	XY	Male heterogametic	Well-studied XY system; males XY, females XX.	[58, 59]

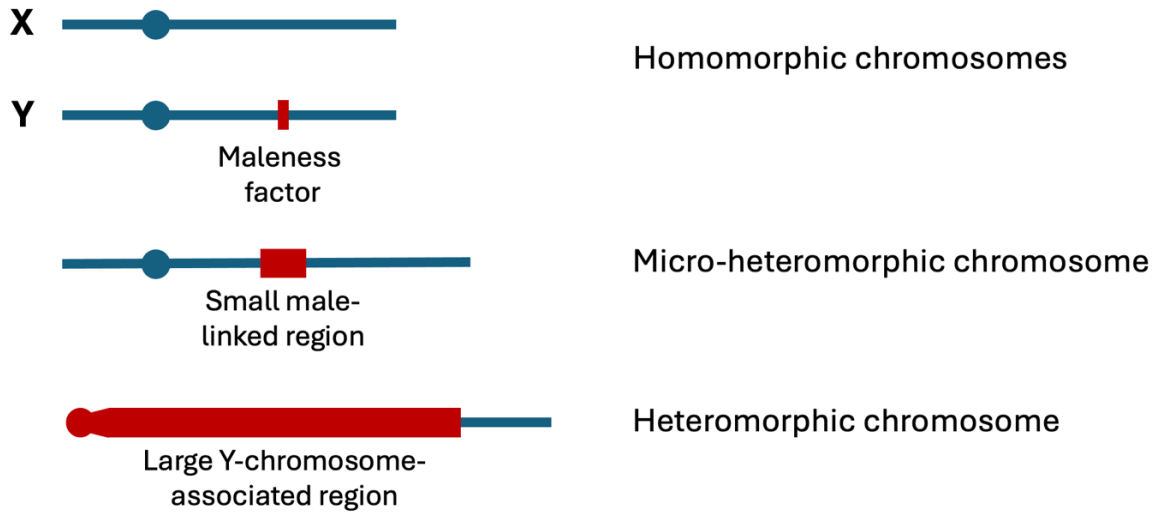

Figure 2 • Examples of 3 different types of Y-linked regions observed in male heterogametic angiosperms, which appear to reflect the evolution of the Y chromosome. The top diagram depicts an X chromosome that resembles the ancestral state before genetic sex determination evolved; its centromere is indicated by a circle. The 3 diagrams below show the different types of "Y chromosomes", with thin horizontal lines indicating recombining pseudoautosomal regions (PARs) and thick boxes, highlighted in red, indicating non-recombining regions. The upper Y chromosome is identical to the X chromosome, i.e., homomorphic, except for the presence of the male-linked factor, which is always heterozygous in male individuals. In the second diagram, the male locus is located within a small, completely non-recombining region that may include several genes that are always heterozygous relative to the X chromosome in males; this condition could also likely be classified as either relatively homomorphic or micro-heteromorphic, since the distinctive region is a small part of the chromosome. The lower diagram shows a pronounced heteromorphic situation in which the male sex-determining locus is in a large, completely non-recombining region spanning most of the chromosome arm, including the centromere, and has a larger arm size than the homologous arm of the X. Adapted from [25].

To summarize the above, the early stages of the evolutionary transition from bisexuality to dioecy and sex chromosomes occurred according to the following scheme: hermaphroditism → mutations causing male/female sterility → dioecy → linkage of sex-determining factors → suppression of local recombination → formation of SDRs and subsequent degeneration [25, 51]. The evolutionary history of the sex chromosomes of *Silene latifolia*, revealed by genetic mapping of four genes, shows that the sex chromosomes of *S. latifolia* are approximately 10–20 million years old, and divergence of X/Y homologs is observed; this confirms evolutionary strata in which recombination suppression expanded stepwise. Rapid Y chromosome degeneration and dosage compensation in *Silene latifolia* indicate that many Y-linked genes have become dysfunctional or are not expressed; *Silene latifolia* shows loss of gene expression and pseudogenization in the Y chromosome [48, 70]. Two sex-determining genes located on the same chromosome become linked. Recombination is suppressed around these genes, indicating the beginning of sex chromosome formation. Over time, the Y or W chromosome degenerates, accumulating mutations and repetitive DNA [84–86]. One example of evidence that sex chromosomes in plants have evolved multiple times and independently comes from the evolutionary studies of sex chromosomes in willow (*Salix viminalis*) and poplar (*Populus*). Although these plants belong to the sister genera within the same family, their sex chromosomes originate from different autosomes, the number of which varies in these species, suggesting an independent origin for the sex chromosomes [62, 87].

However, many species of dioecious angiosperms lack heteromorphic sex chromosomes with pronounced differentiation, and their sex-linked regions are relatively small. They perhaps are at different stages of evolutionary development along the path to sex chromosome formation, during which homomorphic, non-recombining regions will be transformed via heteromorphic regions into fully functional sex chromosomes. However, this hypothesis requires confirmation.

4. Sex-determining genes and downstream regulators

Sex-determining regions (SDRs) of chromosomes have been studied in many dioecious plants, from algae and ancient gymnosperms such as ginkgo to fruit and ornamental flowering plants [8, 11, 51, 88–90].

Currently, two conceptual genetic models of sex determination are recognized in plants. The first is a two-factor (two-gene) model, in which sex determination is controlled by two tightly linked genes located within a non-recombining sex-determining region (SDR), as described in species such as asparagus and kiwi. In this model, sex chromosome evolution involves two sequential mutations within a recombination-suppressed region: one gene acting as a suppressor of femaleness (SuF), often encoding a cytokinin regulator or transcription factor, and a second gene functioning as a male-promoting factor (M), typically expressed in the anther tapetum and required for male fertility; both genes are usually localized on the Y chromosome. The second model involves single-gene sex determination, in which a master regulator acts as a key determinant of sex, exemplified by persimmon and poplar (*ARR17* gene) [11, 76].

One of the well-studied two-factor models is kiwi (*Actinidia deliciosa*), in which sex is determined by two Y-linked genes, *SHY GIRL* (*SyGI*) and *Friendly Boy* (*FrBy*), which suppress gynoecium development and promote androecium formation [31, 91, 92]. The *SyGI* gene stands for *Suppressor of Gynoecium Development in Kiwifruit*, a male-specific gene that influences cytokinin profiles and regulation: this gene plays a key role in the mechanism of dioecy by suppressing the development of the gynoecium (female reproductive organs) in male flowers, while the *FrBy* is responsible for the development of male organs (androecium) and their functionality. *FrBy* is associated with the Microspore and Tapetum Regulator1 (MTR1) protein family, which influences tapetum development and male fertility [91, 92]. In female plants, the sex chromosomes (XX) do not contain either the *SyGI* or *FrBy* gene; accordingly, they develop a gynoecium (pistil), resulting in the formation of a female flower.

Asparagus (*Asparagus officinalis*) also has XX/XY sex chromosomes and a two-gene sex regulation system represented by the *SOFF* (*Suppressor of Female Function*) gene and the *aspTDF1* (*Defective in Tapetum Development and Function 1*) gene, both localized on the Y chromosome in an ~1 Mb SDR [82].

Two-gene sex determination systems have been discovered in grapes (*Vitis vinifera*), date palms (*Phoenix dactylifera*), and other dioecious plants. Interestingly, dioecy was artificially created in melon (*Cucumis melo*) and maize (*Zea mays*) from monoecious species by manipulating the genes responsible for the development of female floral organs and their suppressors [93, 94]. The creation of dioecious melon and maize plants can be seen as an illustration of a potential pathway for the evolution of dioecy through the fixation of one mutation and one segregating mutation controlling sex determination [11]. Moreover, both genes in the "two-gene model" of sex regulation are combined within the sex-determining region (SDR).

In persimmon (*Diospyros lotus*), a single-factor or single-gene sex determination system has been described, whereby male plants carry the Y-chromosome-linked *OGI* gene located in the SDR (~1 Mb). It forms a hairpin RNA that promotes the formation of a 21-nucleotide-long small RNA (sRNA) and, through RNA interference (RNAi), targets and suppresses the expression of the autosomal feminizing gene *MALE GROWTH INHIBITOR* (*MeGI*), which is a homeodomain transcription factor that stimulates the development of female plants, allowing the development of the male sex [95]. It has been shown that the expression levels of cytokinin-related genes during gynoecium differentiation correlate with the expression levels of *MeGI* [96]. The *OGI* gene is an inverted duplication of the autosomal *MeGI* gene. Thus, the sex determination system in persimmon represents a classical epigenetic cis-regulatory switch [31]. It is quite possible that such a regulatory system could have evolved from hermaphroditic ancestors who developed mutations of male and female sterility that were distributed on different chromosomes due to the duplication of a single gene.

A similar single-factor sex determination system has been found in poplar (*Populus deltoides*), which has female X and male Y chromosomes. Moreover, male plants carry the Y-linked *FERR-R* gene, which suppresses the development of female structures through small interfering RNA-mediated silencing of the *FERR* (homologue of *ARR17—ARABIDOPSIS RESPONSE REGULATOR17*) gene, which is a regulator of the type A cytokinin response [77], acting as a suppressor of female fate [76]. The *FERR-R* is a partial duplicate of the *ARR17* gene in a male-specific region of the Y chromosome [77]. Long-read sequencing revealed that the partial duplicates of the *ARR17* gene on the Y chromosome are inverted repeats of the gene, which leads to the formation of small RNAs and, apparently, causes DNA methylation and silencing of the *ARR17*, similar to the *OGI/MeGI* system in persimmon [77, 80]. Knockout experiments of the *ARR17* gene converted female poplar trees into males, confirming its role as a single-gene sex switch [76]. Thus, in the "one-gene model" of sex regulation, as in the "two-gene model," two genes are involved, but only one single gene located in the SDR is crucial for sex determination through epistatic interactions between genes, rather than physical association with downstream genes [97].

Single-gene sex determination systems have been found in willow (*Salix purpurea* L. and *Salix viminalis* L.), ficus (*Ficus hispida* L.), spinach (*Spinacia oleracea*), and even in the gymnosperm cycad (*Cycas panzhihuaensis*) [97].

In many diverse dioecious plant species, sex determination is mediated by class *B* floral organ development regulator genes (*MADS*, e.g., *AP3* and *PI*), which are the final effectors determining the development of stamens or carpels. These genes play a key role in the development of unisexual flowers in dioecious plants. Although the upstream regulators vary among species, many modulate the expression of these floral organ identity genes in a similar manner [97]. For example, the *B*-class genes *AP3* and *PI* in dioecious spinach were found to be expressed in stamen primordia, but their expression was absent in carpel primordia [98]. In several dioecious plants, it was demonstrated that suppression of *B*-class gene expression converted male flowers into female flowers, indicating that *B*-class genes are associated with the emergence of dioecy, at least in some dioecious plants, such as *Thalictrum dioicum, Silene latifolia*, poplar, persimmon, and other plants, where *B*-class genes are expressed only in male flowers [97], whereas in other dioecious plants, feminizing genes, for example, *MeGI* in persimmon, were negatively regulated by the class *B PI* gene [77].

To conclude, the sex-determining genes in different dioecious plant species using both the "two-gene" and "single-gene" models between different taxa are functionally convergent, despite the lack of obvious homology, and these pathways largely determine sex [97]. Though the divergence of mechanisms operating at the initial stage of development—single master genes (*ARR17* and *OGI*), dual factors (*SyGI* + *FrBy*), and hormone-mediated regulators—the downward convergence toward the *B*-class *MADS*-box genes in flowers is striking. This pattern is repeatedly observed across different dioecious taxa, suggesting that functional constraints lead to similar regulatory strategies. Typically, in a two-gene system, one gene determines male fertility and is involved in pollen development, while the other suppresses gynoecium development, usually by affecting cytokinin regulation. Both genes are located in the SDR associated with the Y or Z chromosome in species with sex chromosomes. In a single-gene system, the pseudogene located in the SDR is associated with the male sex chromosome and activates a sex-reversal regulator not localized in the SDR. This effect occurs through epigenetic regulation, such as RNA interference or RNA-directed DNA methylation (RdDM) [76, 77]. In addition, the feminizing factor often acts through negative regulation of *B*-class genes (*AP3/PI*) either directly, but more often through floral meristem genes [97, 99]. For example, *ARR17* controls dioecy in *Populus* by repressing *B*-class *MADS*-box gene expression [77, 81]. It is likely that *MADS*-box genes affecting important reproductive traits can also be regulated by sex-determining genes. Apparently, the evolution of dioecy from monoeciousness was carried out using the "one gene model", while the evolution of dioecy from hermaphroditeness was probably carried out using the "two gene model" [7].

5. Hormonal level of sex determination

Hormones such as ethylene, cytokinins (CKs), auxin, and gibberellins (GA) also influence the sex expression of plant flowers. For example, the pumpkin family (Cucurbitaceae) is primarily monoecious, with the development of different-sex flowers on a single plant. In pumpkins, during the development of the floral meristem, the floral organs—sepals, petals, stamens, and carpels—are sequentially initiated in its four whorls. Subsequently, the hermaphroditic rudimentary flower develops into a female or male flower, with a corresponding cessation of stamen or carpel development. Stimulating the development of female flowers and the corresponding fruit formation is an important factor in increasing pumpkin yield. The morphogenesis of female and male flower buds from a bisexual meristem is determined, among other things, by environmental factors such as temperature, daylength, the use of phytohormones, and, to some extent, mineral nutrition [81, 100–103]. It has been shown that under short-day (SD) conditions, female flowers are predominantly formed, whereas under long-day (LD) conditions, male flowers develop [104, 105]. Stimulation of female sexual differentiation, dependent on a short photoperiod and low temperatures, occurs due to the influence of these factors on the levels of endogenous hormones such as ethylene, auxin, and gibberellins. Studies have found that sexual determination in pumpkin is mediated by the coordinated regulation of multiple signaling pathways. This regulation involves flowering regulator genes such as *PRR9, CONSTANS*, and the NF-Y transcription factors, and the gibberellin signaling pathway, which includes the core proteins of the GRAS family, SCL and DELLA [106, 107]. Furthermore, the ethylene synthesis genes *ACO* and the ethylene signaling response factors, encoded by the *ERF* (*Ethylene Response Factor*) genes, play a key role in this process [107].

It has been shown that under short-day conditions, ethylene production in cucumber (*Cucumis*) increases due to accelerated expression of the *ACS2* gene (encoding 1-aminocyclopropane-1-carboxylate synthase), which contributes to an increase in the formation of female flowers in cucumber. Furthermore, under these conditions, the expression of the ethylene production-related genes *ERF1* (*Ethylene Response Factor 1*) and *CaN* (*Calcium-Dependent Nuclease*) is increased; these genes are dependent on the photoperiod and further influence the formation of female flowers [108–110]. Ethylene plays an important role in the regulation of sexual differentiation in cucurbits. It arrests the development of stamens and promotes the formation of carpels, controlling the transition from the male to the female phase of development. Studies revealed no significant difference in the expression of ethylene receptor genes with changing daylength, but significant differences in the expression of ethylene synthesis genes were found [108]. In asparagus (*Asparagus officinalis*), gibberellins have a masculinizing effect [83]. Exogenous application of gibberellins in maize plants inhibits the development of stamen primordia but has no significant effect on the development of pistil primordia. In cucumber plants, ethylene both stimulates pistil primordia development and inhibits the formation of stamen primordia, leading to female induction. Both plant hormones, gibberellins and ethylene, induce primordial stamen arrest in maize and cucumber, respectively. Also in melon (*Cucumis melo*), ethylene leads to the formation of female flowers, while in watermelon (*Citrullus lanatus*), ethylene plays the opposite role [110, 111].

In *Mercurialis annua*, a type II dioecious species, the floral meristem has three distinct whorls of primordia and no whorl of opposite-sex primordia [13]. High cytokinin/auxin hormone ratios promote female flower formation through the activation of class *D* genes (*AGL1, AGL3*), while high auxin levels induce male flower development through the activation of class *B* genes (*PI* and *AP3*) and the suppression of class *D* genes [112]. The authors conclude that the ability of hormones to induce sex reversal suggests the presence of sexual bipotency in *M. annua*, and that both sexes possess genes necessary for the development of both sexes, but their activity may be limited by various factors, including epigenetic regulation influencing the initiation of primordia in the meristem, leading to dioecy. Differential expression of homeotic genes (*A, B, C, D, E*) in the floral meristem is associated with sexual dimorphism, and cytokinin is involved in the regulation of their transcription. Feminization of male flowers induced by cytokinin was accompanied by significant changes in the content and activity of nuclear proteins involved in the structure and function of chromatin and transcription factors (**Figure 3**) [112]. It can be assumed that sexual bipotency of dioecious plants is one of the reasons for multiple transitions from dioecy to monoeciousness in the process of plant evolution [112].

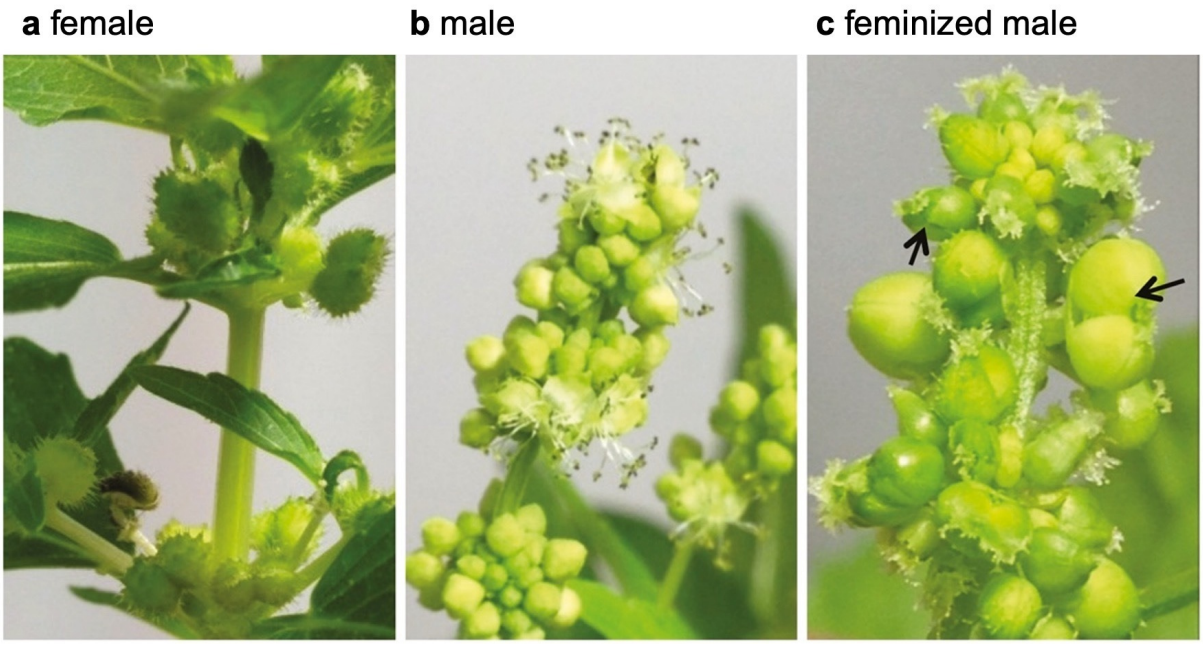

Figure 3 • Inflorescences of the dioecious plant *Mercurialis annua*: (**a**) female plant, (**b**) male inflorescence, and (**c**) feminized male inflorescence obtained by spraying plants with 6-benzylaminopurine three times a day for 4 weeks. Feminized male plants produced flowers with two carpels, a couple of which are indicated by arrows. Reproduced from [112].

6. Epigenetic regulation influences sex determination

Plants exhibit remarkable plasticity in sex determination, involving not only genetic but also epigenetic components, including DNA methylation, small RNA-mediated silencing, and histone-modified chromatin remodeling, which play important roles in determining and stabilizing sexual phenotypes [113]. Sex expression through epigenetic regulation has been observed in many species [114]. Furthermore, switching on or off the activity of sex-determining loci (SDRs) can occur reversibly, sometimes in a tissue- or developmental-stage-specific manner.

As mentioned above, small RNAs can influence sex determination by mediating RNA-directed methylation of the promoters of feminization-regulating genes, which causes the suppression of feminizing genes, determining the male phenotype in poplar, and the suppression of the feminizing gene *MeGI* in persimmon by the Y-linked pseudogene *OGI*, which produces sRNAs [96, 115]. miRNAs can also regulate sex determination and floral morphogenesis. For example, in maize, miRNA172, encoded by the *tasselseed4* (*ts4*) gene, determines normal panicle formation and regulates carpel abortion by controlling the activity of the *IDS1* (*INDETERMINATE-SPIKLELET1*) gene, a floral homeotic transcription factor similar to *APETALA2*, the differential expression of which determines differences in primordial cell initiation and thus regulates sexual differentiation [116, 117].

Comparative analysis of unisexual flowers in melon (*Cucumis melo*) revealed sex-specific epigenetic states of transcription factors involved in the ethylene response and flower development. Histone modifications (H3K9ac—active chromatin and H3K27me3—repressive chromatin) modulate organ-specific expression of ethylene and *MADS*-box genes, which correlates with the transcription of sex-determining genes. It has been demonstrated that the female feminizing gene *CmACS11* represses the expression of the musculinizing gene *CmWIP1* through the formation of closed chromatin (H3K27me3), suggesting coordinated chromatin control of development and organ abortion during unisexual flower formation [118]. Transposon insertions into the *WIP* promoter in melon cause its methylation, which leads to the formation of female flowers [119].

Papaya exhibits DNA methylation differences in sex-determination regions (SDRs) and promoters, such as the *CpHUA1* gene, which correlate with different sex types (male, female, and hermaphroditic) [120]. This gene encodes an RNA-binding protein that plays a role in regulating floral organ identity in *Arabidopsis thaliana* by influencing the processing of the *AGAMOUS* (*AG*) gene pre-mRNA [121].

In the dioecious species *Silene latifolia*, in which the Y chromosome is present only in male plants, DNA methylation is required to maintain unisexuality in male plants, and genome demethylation causes partial reversion from male to hermaphroditic flowers [122].

7. Transcription factors

Transcription factors appear to be hormonal integrators, playing a crucial role in sexual determination in plants. Members of the WRKY, ERF/AP2, and MYB transcription factor families respond to hormonal treatment by influencing downstream genes that determine sexual identity. For example, in horse chestnut (*Castanea henryi*), exogenous cytokinin induced male-to-female flower shifts accompanied by differential expression of *WRKY47, ERF021, MYB4*, and the sexual identity genes *DEF, SEP1*, and *AGL11/15* [123]. In *Arabidopsis*, the *WRKY34* gene influences pollen development under stress by linking environmental signals to male gametogenesis, and phenotypic analysis revealed that the WRKY2 and WRKY34 transcription factors are crucial for plant male gametogenesis. [124].

8. Sex determination in non-seed plants depends on environmental conditions

Environmental sex determination (ESD), similar to temperature-dependent sex determination in some reptiles, is characteristic of some plants. For example, in homosporous ferns, sex is determined not by chromosomes, but by environmental factors like crowding and nutrient availability. Also, female gametophytes secrete antheridiogens, which are gibberellin derivatives that stimulate the development of neighboring gametophytes into males, promoting outcrossing. Nutrient stress or crowding also promotes the development of males, and under favorable conditions, female or bisexual individuals are formed. Although sex chromosomes have not been described in ferns and club mosses, they have been found in some mosses such as *Sphagnum* and some liverworts. [125–127]. In heterosporous ferns, gametophytes are differentiated, and gametophyte sex is controlled by the sporophyte, acting on sporangia that produce either small "microspores" that develop into male (micro-) gametophytes or larger "megaspores" that develop into female (mega-) gametophytes [128].

9. Plasticity in sex determination

Plasticity in sex determination is reflected in a quantitative genetic architecture rather than a discrete Mendelian state, with sex expression within populations governed by the cumulative, dosage-dependent effects of multiple interacting loci that contribute to male or female function [129, 130]. In such systems, sex behaves as a polygenic, threshold-dependent trait, and individuals may reversibly alter their sexual phenotype in response to physiological state and environmental conditions, a phenomenon known as sexual diphasy. This plasticity indicates that sex is not necessarily determined by fixed genetic dimorphism but instead emerges from the differential regulation of genes shared by all individuals, whose expression balance is modulated by environmental cues [5, 131, 132]. In this framework, sex phenotype emerges from the combined, dosage-dependent effects of multiple interacting loci, each contributing incrementally to male- or female-promoting pathways. The "quantitative distribution" of these genes refers both to (i) allelic variation within individuals and (ii) frequency distributions of alleles across populations, which together shape population-level sex ratios and individual sex expression.

A striking example of such quantitative and reversible sex determination is found in *Arisaema* (Araceae), where young, resource-limited individuals typically express male function, while larger or older plants transition to female or hermaphroditic states. In this system, sex expression is tightly correlated with plant size, resource availability, and hormonal status, consistent with a developmental threshold model rather than discrete genetic sex determination [133–135]. Comparable polygenic and environmentally responsive architectures have been described in *Mercurialis annua*, where sex expression varies continuously and responds to nutrient availability, population density, and hormonal manipulation, despite underlying genetic predispositions toward dioecy [26, 81, 112]. Similarly, in Cucurbitaceae species such as cucumber and melon, sex expression is regulated by quantitative variation in interacting genes controlling ethylene biosynthesis and signaling, producing a continuum of male, female, and hermaphroditic phenotypes that are highly sensitive to environmental conditions [81, 100–102, 104–107, 111].

At the population level, allelic variation across multiple loci generates a continuous distribution of sex propensities, allowing sex ratios to shift rapidly in response to environmental heterogeneity without changes in underlying genotype frequencies. Such quantitative genetic architectures are frequently modified by epigenetic regulation, including DNA methylation and histone modifications that respond to photoperiod, temperature, and light conditions. These epigenetic states influence the activity of conserved floral developmental networks, including the *A, B, C, D*, and *E* classes of floral identity genes, thereby integrating genetic, hormonal, and environmental signals into sex-specific developmental outcomes [44, 112]. **Table 3** presents examples of some species regarding their different sex determination systems.

Table 3 • Plant sex determination systems—examples and mechanisms.

Species	Sex determination system	Primary mechanism(s)	Reference(s)
Silene latifolia	Sex chromosomes (XY)	Y carries male promoters and suppresses female traits; male sex-linked genes: *SlAP3, SlSTM,* and *SlCUC;* DNA methylation required	[15, 50, 53, 71, 122]
Spinacia oleracea (Spinach)	Sex chromosomes (XY)	Single-gene sex determination system; the sex-determining region is located on the LG4 locus, which is associated with a Male-Specific Region (MSR)	[15, 54, 98]
Phoenix dactylifera (Date palm)	Sex chromosomes (XY)	Two-gene sex determination system; male determination with sex-linked genes *CYP703, GPAT3* located on the Y chromosome; also, sexual phenotypes are not merely determined by sex chromosomes, but by the ratio of sex chromosomes and autosomes	[11, 15]
Coccinia grandis (Ivy gourd)	Sex chromosomes (XY)	The highest level of X/Y heteromorphy; exhibits sex chromosome dosage compensation; >1300 sex-linked genes known	[79, 136]
Ginkgo biloba	Sex chromosomes (XY)	Male determination region, in SLR 200 genes (including four *MADS*-box genes and two PPR genes) are specifically expressed in males	[8, 15]

Table 3 • *Cont.*

Species	Sex determination system	Primary mechanism(s)	Reference(s)
Fragaria virginiana (Wild strawberry)	Sex chromosomes (ZW)	ZW female heterogamety; W-linked female determinants; sex-lined genes *GMEW, RPPoW*	[15, 66, 67]
Carica papaya (Papaya)	Sex chromosomes (XY) with epigenetic	Trioecious species: female XX, male XY, and hermaphrodite XY^h; nine genes involved in stamen and carpel development; sex expression influenced by hormones (ABA and auxins)	[15, 78, 137, 138]
Diospyros kaki (Persimmon)	Sex chromosomes (XY) with genic/epigenetic	Y-linked noncoding RNA OGI suppresses MeGI; epigenetic regulation influences sex	[11, 15, 76, 77, 80]
Populus deltoides (Poplar)	Sex chromosomes (XY) with gene master regulator and epigenetic	Single feminizing gene (FERR or popARR17) acts as master regulator; two Y-specific genes, FERR-R and MSL, trigger the sex determination	[15, 44, 51, 76, 77, 139]
Asparagus officinalis	Sex chromosomes (XY) and hormone regulators	Two gene (*SOFF* and *aspTDF*) sex-regulating system, both localized in an SDR on the Y chromosome; gibberellins show a masculinizing effect	[63, 82, 83]
Mercurialis annua (Annual mercury)	Sex chromosomes (XY) with Genic and hormonal regulators	Multiple loci with hormonal control (auxins/cytokinins) influence sex	[81, 112]
Cucumis sativus (Cucumber)	Genic, hormonal and environmental regulators	Multiple sex genes with strong ethylene/hormone effects modulated by the environment	[104, 105, 108, 109, 140]
Cucumis melo (Melon)	Genetic, epigenetic and hormonal regulators	Sex genes *CmACS11* and *CmWIP1* interact and are modulated by epigenetic marks that regulate primordia arrest; epigenetic methylation affects promoters	[15, 94, 118, 119, 140]
Zea mays (Maize)	Genetic, epigenetic and hormonal regulators	Monecious, multiple genes (*tasselseed1-4*, etc.) regulate floral organ arrest via hormone (GA and JA) pathways and microRNA	[93, 116, 140]
Eucommia ulmoides	Gene-biased expression	Sex-biased MADS box TFs (*EuAP3* and *EuAG*) determine male vs female tissues	[139]
Arabidopsis thaliana	Genetic and hormonal	Hermaphrodite with sex-biased gene expression; no separate chromosomes	[33, 34, 38, 121]
Arisaema triphyllum (Jack-in-the-pulpit)	Environmental and physiological	Sex is determined by the environment and may change during an individual's lifetime, influenced by nutrients and plant size	[131, 133, 135]
Acer pensylvanicum (Striped maple)	Environmental and physiological	Changes sex with stress/branch loss; size and condition-based	[141]
Lilium concolor var. megalanthum	Environmental	Resource availability affects sex expression; nutrient levels influence allocation to male vs hermaphrodite flower traits	[142]

10. Conclusions

At the end, it can be concluded that sex determination in plants arises through a multilayered regulatory network: 1. Genetic switches on sex chromosomes or autosomes initiate the development of male or female structures in the floral meristem. 2. Propagating hormonal signals reinforces decisions regarding the type of sexual development. 3. Epigenetic marks such as DNA methylation, histone code, and non-coding RNAs determine sex specification in the context of chromatin. 4. Transcriptional networks, particularly through floral identity genes, determine organ formation.

The convergent model proposes that diverse genetic mechanisms ultimately regulate common downstream effector modules: the floral *B*-class genes. Future studies, particularly those incorporating long-read sequencing-based genomics, CRISPR gene editing, and broad phylogenetic studies, will deepen our understanding of how plant sexual systems have independently and repeatedly evolved.

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Conflict of interest

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