



REVIEW ARTICLE

# Sex evolution path involved in flowering plant family Cucurbitaceae: A review

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## Abstract

The predominant sexual system in the plant kingdom is hermaphroditism, where both female and male reproductive organs coexist within a single flower. The major parameters that influence the sexual systems are genetic variation, pollinator availability and type, mating system, ecological factors, geographical isolation, selective pressures, evolutionary history, polyploidy, hybridization and sexual conflict. These factors all play significant roles. Plants may evolve self-fertilization or outcrossing mechanisms based on their specific environmental conditions, reproductive strategies and evolutionary history. The interplay of these factors shapes the diverse range of sexual systems observed in plant species worldwide. The Cucurbitaceae family exhibits a highly specialized sex chromosome differentiation scheme with three major sexual patterns (monoecy, dioecy and hermaphroditism). In the present review, we focus on the evolution of gender in flowering plants of the Cucurbitaceae family, exploring the various paths and drivers involved in the evolution of dioecy. We also shed light on the sex chromosomes and phytohormones that contribute to gender diversification. Several molecular and genomic approaches have been recently applied to uncover the genetic basis of gender differentiation in different flowering plant species.

## Keywords

flowering plant; evolution; multiple pathways; major plant types; sex determination

## Introduction

Understanding the complexities of sexual expression is vital for both theoretical and classical research. Hermaphroditism, the most common sexual system in plants, is characterized by the coexistence of male and female sexual structures in a single flower. In contrast to animals, which frequently exhibit the XY or WZ sex determination systems, plants have rarely developed such mechanisms and these systems are recognized in only a few genera of flowering plants (1). Furthermore, only about 7 % of all angiosperms possess separate sexes, or dioecy, which are usually thought to evolve from complete-flowered or monoecious progenitors (2, 3). However, plants that have distinct sexual systems often rely on outcrossing, which is essential for improving the species' innate variability and adaptability. It is not yet known if all dioecious organisms have a distinctive sexual morphology (4). However, theoretical data indicates that sex-linked genes typically cluster in

gonosome regions where recombination is reduced. The differentiation of male and female sex chromosomes is thought to be resulted from the accumulation of these gonosome-specific genes (5, 6). In particular, the activation of sex-linked genes in the recombination-suppressed loci of a chromosome is believed to be marked the beginning of the evolution of sexual patterns (7). The primary factors influencing sexual systems include genetic variation, pollinator availability and type, mating system, ecological factors, geographical isolation, selective pressures, evolutionary history, polyploidy, hybridization and sexual conflict (8-10). Plants may evolve mechanisms for self-fertilization or outcrossing based on their specific environmental conditions, reproductive strategies, and evolutionary history (11, 12). The interaction of these factors shapes the diverse range of sexual systems observed in plant species worldwide.

Members of the Cucurbitaceae family have played a significant role in the food economies of tropical countries since the dawn of human civilization. After the Solanaceae family, Cucurbitaceae contributes the second highest amount of vegetables in our country. The Cucurbitaceae family consists of about 800 species spread within 120 genera, such as the watermelon (*Citrullus melo* L.), pumpkin, squash and cucumber (*Cucumis sativus* L.), etc. Seventeen percent of the total Cucurbit species, encompassing 108 species from 34 genera, are found in India, which has been recognized as one of the 3 primary centers of origin for cultivated Cucurbits (13). The importance of the family Cucurbitaceae in agriculture and medicine is well established. While the limited hereditary base of the cultivated cucurbits poses a challenge for their genetic improvement, wild species are highly diversified and possess the genetic variations and agriculturally useful traits necessary for the genetic enhancement of existing crops. The Cucurbitaceae family exhibits all three major angiosperm sexual patterns—bisexuality, monoecy and dioecy—among its members. It has also been observed that species with exclusively unisexual flowers can be either monoecious or dioecious (14). Specifically, 67 species within this family are dioecious, spanning across 19 genera (15). Due to the aforementioned significance, the Cucurbitaceae family is an ideal choice for analyzing sexual dimorphism and evolu-

tion. Therefore, the aim of this study is to understand the evolution of sex in flowering plants within the Cucurbitaceae family, exploring the multiple paths and drivers involved in the evolution, the role of phytohormones in sexual expression and sex determination and the involvement of sex chromosomes in gender diversification.

### Sex evolution in flowering plants

The sex determination system based on heteromorphic sex chromosomes, X and Y, is an interesting study from both developmental and evolutionary perspectives. In animal systems, the labiality in the sex-determining systems was laid down by Charlesworth and Mank, 2010 (16). Basically, sex changes are possible due to fluctuation in heterogamety and sex-linkage (17). Several attempts have been made by different groups of researchers to find out the pathways leading to such modifications (18). The evolutionary transitions in the sexual systems of flowering plants involve 2 key phenomena. The first is the shift from predominant outcrossing to predominant selfing and the second is the evolution of separate sexes from combined sexes (19). A comprehensive review of mixed mating systems provided theoretical explanations and empirical evidence for the evolution of selfing (20). An earlier study had explored the evolution of dioecy in flowering plants, examining ecological and genetic correlates (21). Another study discussed the recent advances in understanding plant sexual diversity, including transitions between outcrossing and selfing as well as the evolution of separate sexes, integrating genetic, ecological and evolutionary factors (22). A report has provided valuable insights into the genomic basis of reproductive isolation and the evolution of selfing in dandelions (23), highlighting the genetic changes associated with transitions in the sexual system. These references collectively provided a comprehensive understanding of the evolutionary dynamics shaping sexual systems in flowering plants. A major conclusion drawn from these studies is that differentiated sex chromosomes and sexually incompatible alleles can obstruct the modification of sexual differentiation in animals (24). In contrast, plants consist of multiple sexual forms, regulated by environmental, evolutionary and hereditary events (1) (Fig. 1). Hermaphroditism is the most prevalent sexual form making up for 94 % of plant species. Deviations from this general



**Fig. 1.** Three major angiosperm sexual systems in the family of Cucurbitaceae.

pattern lead to dioecy, observed in only 6 % of the 24000 angiospermic plant species (25). Although dioecy is rare in plant systems, its evolution from hermaphrodites ancestors is quite common (21). According to a study, approximately 15600 dioecious species likely developed through 5000 sovereign transitions from bisexual ancestors (25). This suggests that dioecy can form a completely isolated lineage (21, 25). However, recent studies challenge the idea that dioecy represents the culmination of sexual evolution. One study suggests that divergence may occur more rapidly in some dioecious lineages compared to their hermaphrodite ancestries (26). Another study suggested that dioecy does not universally influence diversification rates, even in many genera that include both dioecious and non-dioecious species (27). These findings suggest that different lineages may exhibit different patterns. Although the development of dioecy is often considered irreversible, based on the comparison with gonochorism in the animal system (28), recent evidence suggests that dioecy in plants can revert to other sexual forms (21, 25). The evolution of dioecy in flowering plants is controlled by multiple pathways and influenced by different evolutionary forces across various lineages (29).

#### **Multiple paths and drivers in the evolution of dioecy in cucurbits**

Among the most evolved taxa of angiosperms, dioecy is not only widely distributed but also associated with a variety of diverse characteristics (25). Most dioecious species are trees, shrubs and herbs, commonly found in tropical regions and islands rather than in temperate or continent regions. Pollination occurs through wind, water and animal-mediated seed dispersal. Dioecious plants typically have small, whitish or greenish flowers arranged in large inflorescences. The evolution of dioecy is highly complex due to the involvement of multiple interdependent traits (29). There are various theories put forth to explain the complex phenomenon of dioecy, or the evolution of separate sexes in plants. Two reports on the selective advantage theory argues that dioecy arises when natural selection favors distinct sexes due to factors such as reduced resource competition between the sexes or increased outcrossing rates (30, 31). According to the genetic burden theory, dioecy develops as a means to isolate harmful mutations on non-recombining segments of sex chromosomes, thereby reducing the genetic load caused by inbreeding (28). A study explaining the sexual conflict theory, suggest that dioecy emerges from conflicts between the reproductive objectives of males and females, which are resolved through the evolution of distinct sexes (32). Another study discussing the environmental determinism theory, argue that environmental factors such as stress and habitat heterogeneity drive the evolution of dioecy as a strategy to maximize reproductive success in unpredictable or challenging conditions (33). Together, these theories illuminate the various mechanisms that have contributed to the evolution of distinct sexes in plants.

Dioecious species have 2 major advantages. The first is the evolution of outcrossing mechanisms, which are

crucial for the reproductive success of most plant species (34). Outcrossing serves as a major driving force in the evolution of plant reproductive systems, with more than 50 % of the flowering plants adopting this strategy to evade selfing (35). Consequently, dioecy, which inherently prevents selfing, can restore genetic self-incompatibility (SI) under definite conditions, as observed in cucurbits like *Coccinia grandis* (Fig. 2). In such plants, pollen transfer may be less efficient, leading to an increased rate of self-pollination (36). Further, SI can prevent self-fertilization, it does not completely eliminate selfing and pollen discounting. Overall, the loss of pollen to selfing can compromise the chances of outcrossing in the dioecious plants. It is generally easier to lose self-incompatibility than to evolve it over time (18).

The loss of Self-incompatibility (SI) can create a platform for the development of separate sexes through polyploidization by alternative outcrossing (37). In some cases, SI may be lost to enhance reproductive success when species colonize isolated areas, such as oceanic islands, which could explain the high frequency of separate sexes in these environments (38). The second major advantage of dioecy is the optimized allocation of resources between male and female functions, which is essential for the evolution of gonochorism in dioecious cucurbit species. Hermaphroditism tends to evolve only when the fitness of male or female is compromised by increased investment in either sex. Furthermore, it is true that attractive flowers can benefit from both sexual functions, while the temporal separation of male and female roles often favours hermaphroditism. This has been a long debate over the past few decades regarding whether dioecy primarily serves to optimize sex allocation or to avoid selfing (39). However, recent survey and different modeling studies suggest that interplay of several forces, including the sexual specialization and inbreeding avoidance, likely contributes to the development of dioecy in cucurbit (Fig. 3) (40, 41).

There are 2 possible evolutionary pathways for the development of dioecy: one involves the emergence of one sexual phenotype followed by the other and the other involves the transition from hermaphrodite to monoecy, wherein species initially produce unisexual flowers before developing distinct unisexual characteristics (29). However, the exact pathway contributing most significantly to the prevalence of dioecious individuals is yet to be ascertained in different plants along the evolutionary pathway. In reality, dioecious cucurbit species exhibit variable sex expression, with male individuals frequently developing female flowers or female organs. This suggests that males may have evolved after females, possibly through an intermediate gynodioecious state (42). Additionally, studies of gynodioecious species indicate significant differences in the male characteristics of hermaphrodites, suggesting that various intermediate stages may be present in different plants along the evolutionary pathway (43).

To become fully dioecious, gynodioecy may not always provide a direct evolutionary pathway (44). Comparisons between the two attributes have shown that



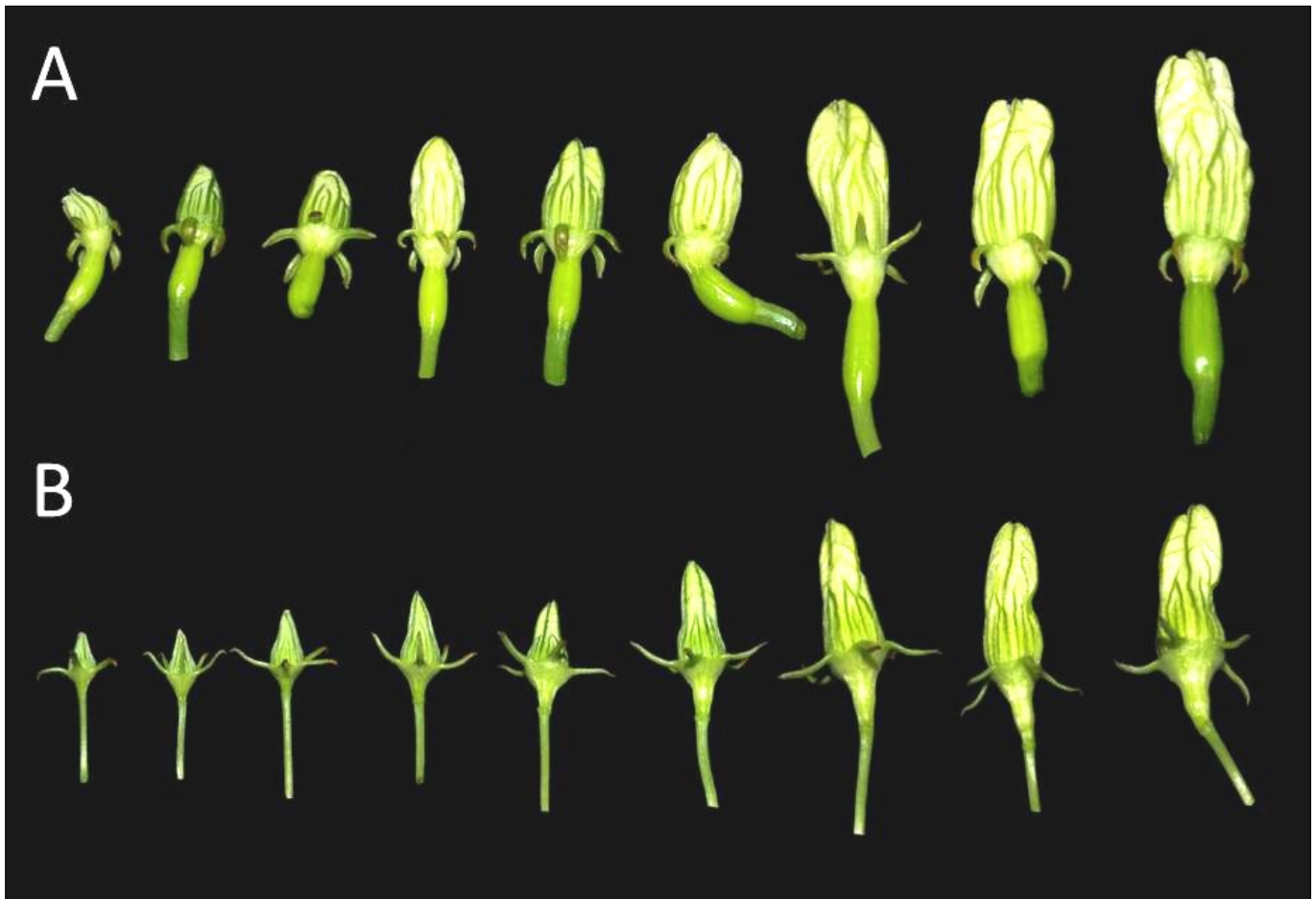
**Fig. 2.** Sex evolution pattern of dioecious cucurbit: (A) Evolution of male flower from three different budding stages to flower formation with anther, (B) Evolution of female flower from three different budding stages to flower formation with stigma in dioecious cucurbit *C. grandis*.

while gynodioecy is primarily found in temperate herbs (45), dioecy is more common in tropical woods (24). On the other hand, monoecy is found linked with dioecy traits (5, 25), suggesting that monoecious conditions are more likely to favor the evolution of dioecy than those that promote gynodioecy. Therefore, the evolutionary development of dioecy from hermaphrodite is not bound to follow 2 distinct steps but may instead be a gradual process with multiple steps and pathways (44). For instance, in the case of *Sagittaria latifolia*, a dioecious species, the progression appears to have occurred from monoecy through gynodioecy (46). In this scenario, male and female flowers are

fully developed and separate, while hermaphroditic individuals possess incomplete floral structures. Contrary to this assumption, a recent report suggests that the gynodioecious nature of *Sagittaria latifolia* may be the outcome of monoecious and dioecious hybridization (47). This might be one of the reasons why there have not been direct steps for evolution from monoecy to dioecy.

#### **Evolution of sex chromosomes in cucurbits**

Most angiosperms exhibit hermaphroditism characterised by the presence of bisexual flowers. Only around 10 % of flowering plants have the ability to produce unisexual



**Fig. 3.** Developmental stages of bud in dioecious flowering plant: **A.** Nine different stages of female buds, **B.** Nine different stages of male bud.

flowers (48). Among these, only about 6 % of angiosperms have separate male and female flowers on different plants, a condition known as dioecy (24) (Table 1). Based on existing data, it is suggested that dioecious plants have independently evolved from their bisexual progenitors (49). The evolution of sex chromosomes in angiosperms is a recent concept compared to the animal system. In studying sex chromosomes, dioecious plants are particularly valuable due to the presence of fertile bisexual relatives in some species. Unlike animal dioecy, dioecious plants rarely possess sex chromosomes; only 19 species have been identified with heteromorphic sex chromosomes (50). Dioecy results from 2 simultaneous modifications, leading to male and female sterility within the hermaphroditic

**Table 1.** Some selected angiosperms and their chromosome numbers with references

Plant species	Chromosome sex chromosome number	Reference
<i>Spinacia oleracea</i>	Dioecious (2n=12)	(62)
<i>Silene latifolia</i>	Dioecious (2n=24)	(63)
<i>Carica papaya</i>	Dioecious (2n=18)	(64)
<i>Mercurialis annua</i>	Dioecious (2n=14)	(65)
<i>Rumex acetosa</i>	Dioecious (2n=14)	(29)
<i>Salix</i> spp.	Dioecious (2n=38-156)	(66)
<i>Humulus lupulus</i>	Dioecious (2n=20)	(67)
<i>Asparagus officinalis</i>	Dioecious (2n=20)	(68)
<i>Dioscorea bulbifera</i>	Dioecious (2n=20)	(69)
<i>Actinidia chinensis</i>	Dioecious (2n=29)	(70)
<i>Cannabis sativa</i>	Dioecious (2n=20)	(71)

developmental program. A close genetic linkage between the mutant genes is crucial for maintaining dioecy, as it prevents genetic recombination and the reversion to hermaphroditism (49). Likewise, dioecy co-evolve with monoecy in many plant systems, serving as a viable alternative pathway to the evolution of dioecious plants (51).

A well-studied example of sex chromosomes in plant is *Silene latifolia*, (family Caryophyllaceae), which exhibits distinct male and female plants with XY and XX sex chromosomes respectively. Another example is *Rumex acetosa*, which is well known for its ZW sex determination system (52). In *Carica papaya* (Papaya), sexual variation is controlled by a homologous set of sex chromosomes, where the Y chromosome controls male development and YH chromosome controls hermaphroditism (53). The Cucurbitaceae is particularly notable for encompassing three angiospermic sexual systems i. e. monoecy, dioecy and bisexuality. This diversity makes it an ideal group for studying the evolution of sex and sexual dimorphism. Various investigations have led to the understanding of the mechanism of sexual segregation in different genera of Cucurbitaceae, including *Bryonia*, *Trichoxanthes* and *Coccinia* (48, 54, 55). Chromosomal sex determination mechanism was first commenced in *Bryonia*, resulting in the development of the X-Y sex determination system. The genus is represented by a basic chromosome number of  $x=10$  and *B. dioica* exhibits homomorphic sex chromosomes (56). In contrast, the chromosome number in *Ecballium* is 9 and 12 (56). Chromosome counting has also been demonstrated in other species of this genus, such as *Bryoniaalba* (2n=20),

*B. aspera* (2n=40), *B. cretica* (2n=60), *B. marmorata* (2n=40), *B. multiflora* (2n = 20), *B. syriaca* (2n =20) and *B. verrucosa* (2n=20) (56). Development of a male specific marker *BdY1* in *Bryoniadioica* supports the past agreement of an X–Y sexual system (54, 55). Another genus in the Cucurbitaceae family, *Momordica*, provides a wide range of sexual expressions. *M. Dioica* is represented by an asymmetric karyotype with n=14 and possesses homomorphic sex chromosome (X and Y of approximately the same length) (57). Similarly, *M. charantia* has a confirmed set of 22 chromosomes (58). Among other species in this genus, *M. sahyadrica*, *M. subangulata*, *M. cochinchinensis* and *M. denudata* have 14 pairs of chromosomes (59), while *M. rostrata* has 11 pairs (n=11) (60). The monoecious *M. cymbalaria* has 9 pairs of chromosome (59). Interestingly, all dioecious species of this genus exhibit chromosomal homomorphism. Two other important genera in the Cucurbitaceae family are *Luffa* and *Trichosanthes*. Unisexual species like *L. cylindrica*, *L. Hermaphrodita*, and *L. acutangula* have 13 pairs of chromosomes, while the bisexual *L. Echinata* exhibits gonosomal homomorphism. *Trichosanthes* is a model genus for studying sex determination due to its high level of speciation among all members in the family of the Cucurbitaceae family. The cucurbit *Trichosanthes* possesses x=11 in both diploids and polyploids. *T. dioica* has homomorphic sex chromosomes but also exhibit irregularities in meiotic behaviour (61). However, *T. kirilowii* var. *japonica* and *T. ovigera* are reported to have heteromorphic sex chromosomes.

*Coccinia* represents the most important genus in Cucurbitaceae characterized by a highly specialized sex chromosome and sex differentiation scheme. Although there are a large number of *Coccinia* species in Africa, *C. grandis* from India has been reported to demonstrate X–Y sex-determination system and possesses chromosomal heteromorphism. Based on cytogenetic analysis, *Coccinia* is dioecious with diploid chromosome number (2n=24) and an X–Y sexual system, characterized by a large Y chromosome in males (Fig. 2). The large Y chromosome is mainly due to tremendous accretion of repeat sequences in the newly evolved large male Y chromosome structures (72). A distinctive heteromorphy of 45S rDNA signals has been reported in the homologous chromosomes found in the 2 genders of *C. grandis* (73). Furthermore, the genome sizes of the male and female plants differ by at least 10 %. The male genome size ranges from 0.92 to 0.94 picograms/2 coulombs (pg/2C), whereas the female genome measures between 0.75 and 0.85 pg/2C (72, 44). The Y chromosome of *C. grandis* is extensively pseudo-autosomal and highly heterochromatinized, as demonstrated by genomic in situ hybridization (GISH) and C-banding analysis (72). The significant retrotransposon accumulation in the Y chromosome from the Ty1/copia and T3/gypsy superfamilies, is another variable causing gonosomal heteromorphism (73). Intriguingly, the Y chromosome in *C. grandis* does not respond to rDNA signals and chromomycin A3 stains (74). Recent report suggests that the Y chromosome possesses specific genes related to stamen development, gynoeceum suppression and male fertility (48, 75).

#### Role of phytohormones on plant sexual expression and

#### sex determination in cucurbits

Phytohormone biosynthesis and signal transduction are crucial factors in floral development, sexual expression and sex determination (76). According to the previous studies, auxin plays a vital role in floral organ development (77). Anthers are the primary sites of auxin deposition, where it accumulates in high concentrations, inhibiting the development of adjacent whorls in both acropetal and besipetal directions. AUX/IAA proteins, auxin response factors (ARFs), auxin-induced proteins and auxin efflux carriers are the major constituents of the auxin signaling pathway (78). ARF1, ARF6, small auxin up RNA (SAUR) gene and auxin responsive Gretchen hagen 3 (GH3) have been implicated in stamen elongation, anther dehiscence and flower bud opening (79). In contrast, low-level expression of IAA/AUX proteins could result in higher expression of secondary auxin-responsive genes which in turn induces sex differentiation (80) (Fig. 4). Additionally, multiple ARFs and transport inhibitor response 1 (TIR1) correlate auxin synthesis with carpel differentiation and stigma maturation (77).

Auxin-induced ethylene biosynthesis plays a sub-

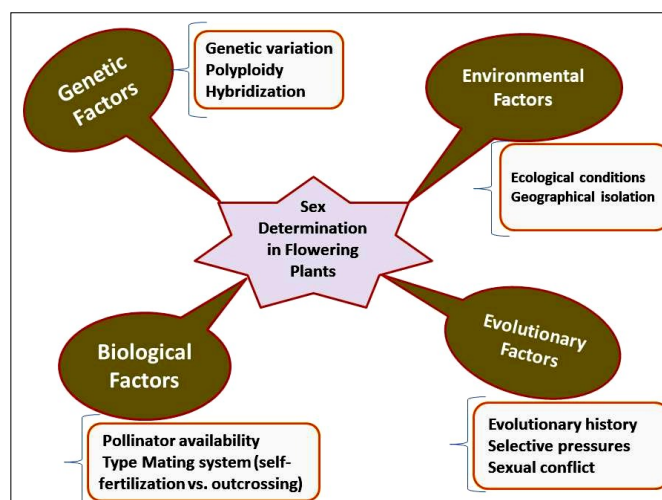


Fig. 4. Factors affecting sex determination in flowering plants.

stantial role in sex determination by inhibiting stamen development and inducing pistillate flowers (77). 1-aminocyclopropane, 1-carboxylate synthase (ACC synthase) is primarily associated with ethylene biosynthesis and has been previously implicated in the development of female flowers (81). ACS-7 and ACS-11 are increasingly expressed in the female primordia of both melon and cucumber and a loss in their enzymatic activity directs stamen development (81). These 2 genes have also been found to be conserved in other cucurbits, such as watermelon and *M. charantia* (81). The *Ethylene insensitive 3 (EIN3)* gene and serine threonine protein kinase CTR1 are negative regulators in the ethylene response pathway. The response to ethylene signaling was reported to be highly deformed in the *ein3* insensitive mutant of *Arabidopsis thaliana* (82). Cytokines play an important role in sex determination of *Vitis vinifera* and *Spinacea oleracea*. Giberellins (GAs) is required for male flower promotion in *Cucumis sativus* and *A. officinalis* (83). High concentrations of GA abort the development of male sexual structures in female flowers of maize. In con-

trast, abscisic acid (ABA) promotes the development of femaleness by decreasing the activity of GAs (84).

ABA is a major promoter of flower senescence. In *Arabidopsis*, *ABSCISIC ACID-INSENSITIVE 4 (ABI4)* gene adversely control's floral transition by directly endorsing the transcription of *FLOWERING LOCUS C (FLC)* (85). ABA delays the flowering transition mediated by DELLA transcription factors, although the precise mechanism is yet to be explored. According to a study, ABA negatively affects floral transition by activating *FLC* transcription through the transcription factor *ABSCISIC ACID INSENSITIVE MUTANT 5 (ABI5)* (86). In contrast to these findings, ABA also stimulates floral development through *LcAP1* expression in *Litchi chinensis* Sonn. The study showed that the number of panicles in the ABA induced plants was higher as compared to the control (86). Jasmonic acid (JA) and salicylic acid (SA) also play crucial roles in plant reproductive development. Male sterility is often found in JA mutants lines (*fad378*, *dad1*, *opr3* and *acx1/5*) of *Arabidopsis thaliana* (82). High concentration of JA activates a complex network of bHLH-MYB and MYC transcription factors (TFs) guided by JAZ repressors (87). JAZ repressors are known for directing appropriate development of stamen in plants (88). In maize, mutation in JA biosynthetic pathway resulted in early floral developmental flaws including poor development of male propagative organs (89). A different scenario was found in tomato, where the *jai1* mutant resulted in female sterility. Similarly in *Arabidopsis thaliana*, the coordinated action of CONSTANS and jasmonate signaling was found controlling flower senescence (90, 91). Similarly, SA has been reported to be involved in the regulation of flower senescence, but there is no clear information about its role in floral differentiation (92). Overall, these reports suggest that phytohormones and their associated signaling pathways are essential for reproductive development and sex differentiation in a wide range of angiosperms.

## Conclusion and future prospects

The review has shed light on the complex process of sex evolution in flowering plants and demonstrated the variety of factors that have shaped the development of sexual systems in cucurbit. From studying the evolution of sex in flowering plants, it is clear that multiple routes have led to the development of dioecy as a common sexual system. Numerous factors, including as sexual conflict, genetic load, selective advantage and environmental determinism, have influenced the evolution of dioecy. Furthermore, the evolution of angiosperm sex chromosomes provides insight into the genetic foundations of sexual differentiation, with various phytohormones playing crucial roles in floral whorl differentiation, as seen in cucurbits.

As research continues to uncover the complexities of sex determination and sexual systems in plants, it is clear that the story of sex evolution in flowering plants is rich and multifaceted, offering fertile ground for future exploration and discovery. There is a pressing need for additional research on the mechanisms determining sex, the effects of dioecy on genome structure, the epigenetic

aspects of sex chromosome evolution and the interactions between TE regulation and non-recombining region formation.

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## Authors' contributions

AP, PKP and MB, RM, JNM designed the study and drafted the manuscript. PKP, JNM and AP addressed all the reviewers' queries. All authors read and approved the final manuscript.

## Compliance with ethical standards

**Conflict of interest:** Authors do not have any conflict of interests to declare.

**Ethical issues:** None

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