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Review

Sex determination in flowering plants: Papaya as a model system

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ABSTRACT

Unisexuality in flowering plants evolved from a hermaphrodite ancestor. Transition from hermaphrodite to unisexual flowers has occurred multiple times across the different lineages of the angiosperms. Sexuality in plants is regulated by genetic, epigenetic and physiological mechanisms. The most specialized mechanism of sex determination is sex chromosomes. The sex chromosomes ensure the stable segregation of sexual phenotypes by preventing the recombination of sex determining genes. Despite continuous efforts, sex determining genes of dioecious plants have not yet been cloned. Concerted efforts with various model systems are necessary to understand the complex mechanism of sex determination in plants. Papaya (*Carica papaya* L.) is a tropical fruit tree with three sex forms, male, hermaphrodite, and female. Sexuality in papaya is determined by an XY chromosome system that is in an early evolutionary stage. The male and hermaphrodite of papaya are controlled by two different types of Y chromosomes: Y and Y^h. Large amounts of information in the area of genetics, genomics, and epigenetics of papaya have been accumulated over the last few decades. Relatively short lifecycle, small genome size, and readily available genetic and genomic resources render papaya an excellent model system to study sex determination and sex chromosomes in flowering plants.

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1. Background

Most angiosperms produce hermaphrodite flowers with functional male and female sex organs within the same flower. However, unisexuality is widely spread in plant kingdom and evolved independently along multiple lineages. About 5% of flowering plants are monoecious with separate male and female flowers on the same plant and about 6% are dioecious with separate male and female individuals [1,2]. Unisexuality in plants is derived from hermaphrodite ancestors. On the transition from hermaphroditism to unisexuality, plants acquire various mechanisms to suppress the development of one of the sex organ (stamen or carpel) depending on the sex of the flowers or plants.

Genetic control of flower development is one of the most extensively studied areas in plant developmental biology. It is now well established that three classes of floral homeotic genes namely A, B, and C coordinately regulate the development of four floral whorls of hermaphrodite flowers. According to the ABC model, the A class genes are essential for proper development of two outer whorls, calyx and corolla; the B class genes regulate the development two middle whorls, corolla and androecium; and the C class gene regulates the development of the innermost whorls androecium and gynoecium [3,4]. Although the ABC model of flower development elegantly explains the genetic network regulating the individual whorls in hermaphrodite flowers, development of unisexual flowers cannot be explained by the this model alone. Intensive studies on complex floral gene networks and flower developmental pathways are necessary to understand the evolution of unisexual flowers from their bisexual ancestor. Significant achievements have been made over the past few decades towards understanding sex determination mechanisms and evolution of dioecy in various plant systems. Here we review the recent advances in the understanding of sex determination from different plant systems. We further review the achievements made in a trioecious tropical plant, papaya, and discuss its relevance as a model system to study the sex determination mechanisms in plants.

2. Evolution of plant sexuality

Angiosperms are predominantly hermaphrodite with both stamens and carpels in the same flower. The unisexual flowers are derived from ancestral hermaphrodite flowers [2,5]. Transition from hermaphrodite to unisexual forms may have occurred more than 100 times in angiospermic lineages [1]. Two possible routes have been proposed for the evolution of dioecious plants from hermaphrodite ancestors, via monoecious or gynodioecious plants (Fig. 1). The androdioecious condition is rare in the plant kingdom, and may have evolved from dioecious plants by reverse mutation on female plants by gaining the male function [6]. Conversely, androdioecious condition may provide an intermediate stage in the evolution of dioecious species with ZW (female heterogametic) sex chromosome system whereas the XY (male heterogametic) system may have evolved through gynodioecious intermediate. Androdioecious intermediate is found in wild strawberry, *Fragaria virginiana*, a subdioecious species with incipient ZW chromosomes [7]. The androdioecious intermediate on the evolution of dioecy also fits well with the theoretical model of evolution of ZW sex chromosome system. In ZW system, female sterile mutation on Z chromosome produces male individuals having ZZ chromosomes while ZW is hermaphrodite. Later, gain of stamen suppressor function on the W chromosome renders ZW individuals as female giving rise to a complete dioecious condition. Rare occurrence of both, androdioecy and ZW sex chromosomes system in nature further supports the hypothesis that the ZW chromosome system evolves through androdioecious intermediate. Collectively, the androdioecious species may have evolved from both dioecious species by reverse mutation on female plants and from hermaphrodite ancestors by female sterile mutation. Trioecy (functional male, female and hermaphrodite individuals are present within a species) in plants is also rare. Investigation of the evolution of trioecy is underway in papaya. Preliminary evidence suggests that trioecy is derived from a dioecious ancestor by the loss of carpel suppressor function.

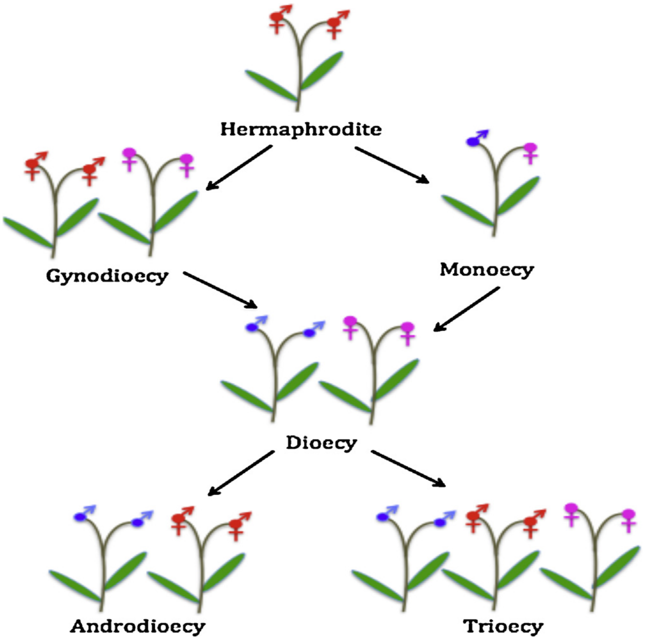

Fig. 1. Evolution of plant sexuality. Dioecy evolves from a hermaphrodite ancestor through gynodioecy and monoecy, while androdioecious and trioecious conditions are derived from dioecious ancestors.

Unisexual flowers in a species arise by arresting the development of one of the sex organs, carpel or stamen. In some species, the arrest occurs at the cell specification stage of the floral meristem, failing to produce the organ primordia (stamen or carpel). Whereas in some species, the arrest occurs later during the development leaving the vestige of the opposite sex organ. The first condition is called unisexual by inception and the latter is called unisexual by abortion [5]. The arrest of opposite sex organs in unisexual flowers is achieved in different stages in different plants (Fig. 2). Hemp (*Cannabis sativa*) and mercury (*Mercurialis annua*) flowers are completely unisexual and do not develop any vestige of the opposite sex organs, while unisexuality in *Fragaria* occurs later during the gamete development [8]. In some plants, the vestiges of a carpel is left in the male flower while the female flower shows no trace of stamens (papaya), while the opposite is true in other plant species (*Rumex acetosa*). In *Silene latifolia*, vestiges of the opposite sex are present in both male and female flowers (see [9] for more reviews).

3. Plant sex determination systems

Sex determination in flowering plants is regulated at several points on the intricate network of genes involved in flower development. Here we categorize the mechanisms of sex differentiation in flowers into three main categories: genetic control by sex determining genes and sex chromosomes, epigenetic control by DNA methylation and small RNAs, and physiological regulation by phytohormones.