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Evolution of Sex Chromosomes and Dosage Compensation in Plants

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Abstract

Sex chromosomes are the chromosomes involved in sex determination and are characterized by reduced recombination, specialized gene content and dosage compensation. These are also called as **allosomes**[1]. Plants based on sexuality can be broadly classified into two classes namely, monomorphic species and polymorphic species. There are three sex chromosome systems in plants, (*a*) XY: male heterogamety (*b*) ZW: female heterogamety and (*c*) UV: haplo-diploid system. There are two important models to explain evolution of sex chromosomes in plants *viz.*, two mutational model and sexual antagonism model[2]. With SNR (sex specific non recombining region) degeneration, the heterogametic sex in ZW and XY systems has lower levels of expression than the homogametic sex, which can be deleterious. A mechanism called **dosage compensation** has evolved in some species that allows for similar male and female expression levels. There are three different dosage compensation mechanisms, namely random inactivation of female X-chromosome, hyper-activation of male X -chromosome and hypo-activation of female X- chromosomes. An advanced genetic and molecular study on the plant sex chromosomes will help to develop markers for sex determination of dioecious plants before flowering, so this in turn increase the proportion of desired sex types like females in case of grapevines, kiwi fruit, date palms, strawberries and *Cannabis sativa*. Males in asparagus and hermaphrodites in case of papaya and also early sex determination of young seedlings could enhance the breeding programme and also lowers the cost of production.

Key words: -Allosomes, Markers, Gene

Introduction

Sex chromosomes are the chromosomes involved in sex determination and are characterized by reduced recombination, specialized gene content and dosage compensation. These are also called as **allosomes**[1]. Around 200 BC, the Nordic tribes devised rune symbols to represent the forces of nature. These symbols were **X-GEBA,-"**the rune of love and sexuality, and Y-FEOH,-"the rune of success". Later it turns out that in biology, X and Y symbols were used to denote female and male sex chromosomes respectively. The two standard sex symbols are the Mars symbol ♂ (often considered to represent a shield and spear) for male and Venus symbol ♀ (often considered to represent a bronze mirror with a handle) for female, derived from astrological symbols, denoting the classical planets Mars and Venus, respectively. Plants based on sexuality can be broadly classified into two classes namely, monomorphic species and polymorphic species. There are three sex chromosome systems in plants, (*a*) XY: male heterogamety (*b*) ZW: female heterogamety and (*c*) UV: haplo-diploid system. There are two important models to explain evolution of sex chromosomes in plants *viz.*, 1. **Sexual antagonism model 2. two mutational**.

1. **Sexual antagonism model of sex chromosome evolution**: The model was proposed by the scientist W.R. Rice in the year 1987. According to this model, the evolution of heteromorphic chromosomes starts with the separated sex system, that is called as Gonochorism in animals and Dioecy in plants. The model also assumes that the process of sex chromosome evolution necessitates halting recombination between the nascent X and Y in males, or Z and in **females,** and this recombination suppression is brought about by sex antagonistic alleles
2. **Two mutational model of sex chromosome evolution in plants**: The theory is given by Charlsworth *et al* in the year 1978.According to the theory, dioecy in flowering plants must often have evolved through at least two mutations, a male-sterility mutation (creating females; it should be recessive sterility mutation in XY system and dominant mutation in ZW system) and one or more female-sterility mutations (creating males; it should be dominant in case of XY and recessive in case of ZW system).

The study of sex chromosomes is restricted to dioecious plants because monoecious plants don't have sex chromosomes. In monoecious species, genes are, of course, involved in the sex-determining developmental pathway, but there are no sex-determining loci. So all individuals are capable of developing flowers of either sex, depending on the environment experienced in a given flowering season. In contrast to monoecious plants, many dioecious species have a genetic polymorphism involving sex-determining genes and particular sex determining loci, which control whether a plant as a whole develops as a male or female. Dioecious plant species are reported to occur in 38% (167) of angiosperm families. Among the estimated 2,50,000 angiosperm species, 6% (14,620) are dioecious. (**Ming *et al.*, 2011**).

Reason for existence of sex chromosomes only in few species of plants remain unclear. But One of the predicted reasons is the **recent origin** of dioecy, from a hermaphrodite progenitor. Another possible reason could be the fact that plants don't move and hence hermaphrodite plants have an advantage in ensuring **successful reproduction.**

The Differentiation of Sex Chromosomes

Once proto-sex chromosomes have established, they can continue to differentiate into sex chromosomes through a number of different mechanisms like accumulation of repetitive sequences, recombination suppression between the two sex chromosomes and degeneration of non- recombining sex chromosome. Several species of plants and algae have sex chromosomes that show varying degrees of differentiation, each of which could represent different stages of sex chromosome evolution.

Chromosomal rearrangements involving sex chromosomes and autosomes are common and have been observed for example in *Silene latifolia* where autosomal regions have been translocated to the sex chromosomes and are now non-recombining (**Bergero *et al*. 2013).** Another example comes from the plant *Silene diclinis*, where a reciprocal translocation between an autosome and the ancestral Y chromosome led to two Xs and two Ys with a chain quadrivalent at meiosis metaphase I. In *Rumex hastatulus* some populations have a XY_1Y_2 system due to an X- autosome fusion. These chromosomal rearrangements make it possible for genes that were autosomal to become sex-linked.

The Evolution of Dosage Compensation in Plants

With SNR degeneration, the heterogametic sex in ZW and XY systems has lower levels of expression than the homogametic sex, most of all after SNR gene losses that make the heterogametic sex partially aneuploid, which can be deleterious. A mechanism called dosage compensation has evolved in some species that allows for similar male and female expression levels (Charlesworth 1996), but more importantly, similar expression levels between sex chromosomes and their ancestral autosomal pair. **Susumu Ohno** was the first to hypothesize that potential haplo-insufficiencies unveiled by male monosomy were counteracted by increased expression from the single X chromosome. First discovered by **H. Muller (1947)** in *D. melanogaster*. It is a form of adaptation involving selection that must often generate sexual antagonism is the evolution of dosage compensation, which acts when genes on the Y chromosome in XY systems (or the W in ZW systems) lose functions, so that males (in XY systems) are equivalent to loss-of-function mutants for those genes. The ideal genes for studying whether dosage compensation has evolved are those that have been lost from the Y, but are still present on the X chromosome, which will have the largest difference in dosage

Why chromosome dosage matters??

Dosage of a chromosome (or a gene) refers to its genomic copy number. Dosage differences may lead to **Polyploidy, Aneuploidy, Partial aneuploidy.**

- Polyploidies refer to an increase in the dosage of all chromosomes, and are well tolerated.
- Aneuploidies refer to a change in the dosage of one chromosome with respect to the rest of the genome, and are generally detrimental to the organism
- Partial aneuploidies, due to duplication or deletion of a chromosomal segment, can also be harmful.

In some cases, changes in the copy number of a single gene cause problems (e.g. haplo-insufficiency). Thus, maintenance of correct gene dosage at multiple scales (single genes to whole chromosomes) is important for an organism's fitness. Proper chromosome dosage is Integral part of the transcriptional regulatory networks.

Dosage Compensation in Plants

In plants dosage compensation is studied only in 2 main plant species viz., *Silene latifolia* and *Rumex hastatulus* but the mechanism is not clearly understood. There are **three steps in the evolution of dosage compensation in plants**:

- Recombination between the X and Y chromosomes is suppressed,
- The Y degenerates, and
- This massive loss of Y chromosome genes is balanced by dosage compensation of the X chromosome.

Conclusion

An advanced genetic and molecular study on the plant sex chromosomes will help to develop markers for sex determination of dioecious plants before flowering, so this in turn increase the proportion of desired sex types like females in case of grapevines, kiwi fruit, date palms, strawberries and *Cannabis sativa*. Males in asparagus and hermaphrodites in case of papaya and also early sex determination of young seedlings could enhance the breeding programme and also lowers the cost of production.

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