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Review

The genomics of plant sex chromosomes

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ABSTRACT

Around six percent of flowering species are dioecious, with separate female and male individuals. Sex determination is mostly based on genetics, but morphologically distinct sex chromosomes have only evolved in a few species. Of these, heteromorphic sex chromosomes have been most clearly described in the two model species – *Silene latifolia* and *Rumex acetosa*. In both species, the sex chromosomes are the largest chromosomes in the genome. They are hence easily distinguished, can be physically separated and analyzed. This review discusses some recent experimental data on selected model dioecious species, with a focus on *S. latifolia*. Phylogenetic analyses show that dioecy in plants originated independently and repeatedly even within individual genera. A cogent question is whether there is genetic degeneration of the non-recombining part of the plant Y chromosome, as in mammals, and, if so, whether reduced levels of gene expression in the heterogametic sex are equalized by dosage compensation. Current data provide no clear conclusion. We speculate that although some transcriptome analyses indicate the first signs of degeneration, especially in *S. latifolia*, the evolutionary processes forming plant sex chromosomes in plants may, to some extent, differ from those in animals.

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1. Introduction

Genetic recombination is a key process in the variation achieved during meiosis when paternal and maternal chromosomes are combined and exchanged. Random combination of male and female gametes completes the variation necessary for evolution. However, there are exceptions demonstrating other mechanisms for ensuring genetic variation. For example, bdelloid rotifers reproduce asexually and are propagated by parthenogenesis without meiosis. Their genome is totally restructured during anhydrobiosis, including the integration of foreign DNA sequences from adjacent organisms (horizontal gene transfer). Mechanisms like this appear to be functionally equivalent to genetic exchange and allow a large divergence and speciation [1].

The flowers of angiosperms are largely bisexual, i.e., they contain both pistils and stamens. These develop differently from most animals. Briefly, they do not possess a true germline, and sexual organs are formed in flowers after transition from the vegetative to the generative state from somatic axillary meristems late in development. This enables them to partially maintain the environmentally induced epigenetic changes occurring during development. The products of meiosis are not gametes, as in animals, but haploid spores which require gene expression for differentiation. Finally, there are two fertilization events between sperms produced by the male gametophyte (the pollen tube) and the embryo sac: one fertilization event leads to the formation of a zygote, and the other

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leads to (usually triploid) endosperm, which is critical for embryo nutrition and viability. Plant bisexuality may result in inbreeding depression, and dioecy (the separation of the sexes into different individuals) may have evolved in many plant species in response to selection to avoid inbreeding.

The separation of male and female organs in different flowers occurs either as dioecy (pistillate or staminate flowers in different individuals) or monoecy (pistillate or staminate flowers on the same individual). Either way, unisexuality in flowers is achieved in floral development as an arrest of sex organ formation (either the pistil or the stamen). In dioecious species, sex is most often determined by genotype, but environmental, hormonal, and epigenetic cues are also used in determination [2–4]. Sexual differentiation includes not only floral differentiation and the formation of male and female gametes. It is also responsible for gender dimorphism, and, in some groups of organisms, dosage compensation of X-linked genes and genomic imprinting. Sex-determining genes are often clustered in heteromorphic sex chromosomes, which are more common in animals, and less relevant in plants. Heteromorphic sex chromosomes are defined by being distinguishable under a microscope [3–5].

Similar to animal species, sex determination systems in plants can be classified with respect to whether each sex forms different gametes: in X/Y systems males (XY) are heterogametic and females (XX) are homogametic (e.g., *Silene latifolia*, *Rumex acetosa*, and *Carica papaya*). By contrast, in Z/W systems males (ZZ) are homogametic and females (ZW) are heterogametic (e.g., *Populus trichocarpa*, *Fragaria chiloensis*, *Silene ottites*). In X/Y species, there are two basic systems of sex determination, the mammalian type with the dominant Y chromosome (e.g., *S. latifolia*) and the *Drosophila* type with the critical X/A ratio (e.g., *R. acetosa*).

2. Evolution of sex chromosomes

According to evolutionary theories [6,7], the sex chromosomes originated from an ordinary pair of chromosomes (autosomes), usually in lineages derived from hermaphrodite plants. For dioecy to evolve from hermaphroditism, two mutations are needed, a male-sterility (usually the first to occur) and a female-sterility mutation. These loci had to be linked at one chromosome pair (the sex chromosomes) for the stability of the sexes. Later, selection for alleles advantageous to males and disadvantageous to females is hypothesized to bring about further genetic differences between the X and Y chromosomes and sometimes suppression of recombination between them in further regions [8]. In discussing sex determination mechanisms and specific features of sex chromosome evolution (especially degeneration of non-recombining regions of Y or W), one should bear in mind the variety of sex-determining mechanisms (genetic, environmental, hormonal, and epigenetic), sex determination genes and pathways. Further, ageing and degeneration of Y (or W) sex chromosomes make generalizations difficult [9].

The early steps in Y-chromosome evolution have been revealed through experimental interspecific hybrids created between dioecious and non-dioecious species [2]. In the genus *Silene*, hybrids between *S. latifolia* and the closely related *S. viscosa* have given insights into the dominance of Y-linked alleles [10]. In these hybrids, there is only one sex chromosome (X) inherited from the *S. latifolia* seed parent. Its counterpart (an autosome) originates from the *S. viscosa* pollen donor. Despite the absence of the Y chromosome, the hybrid plants should form bisexual flowers. Indeed, in these hybrids, anthers developed far beyond the early bilobal stage characteristic of XX *S. latifolia* female plants. The *S. viscosa* genome can thus replace the Y-linked sex determination gene(s) whose
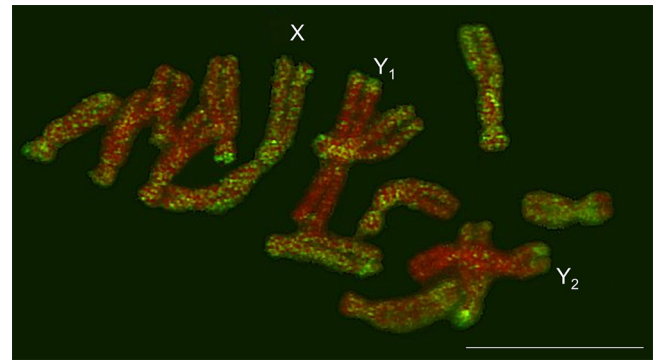

Fig. 1. Immunostaining of male mitotic metaphase chromosomes of *R. acetosa*. Chromosomes were mild denatured with formaldehyde and stained with anti-acetyl-lysine5-H4 histone antibody (green) and counterstained with DAPI (red). The sex chromosomes are indicated. The bar indicates 10 μm.

absence, or lack of function, in females abolishes early stamen development.

3. Case studies: recent advances through genomic studies

Here we provide some recent genomic data on the most commonly studied dioecious species (Table 1). The following section is focused on the classical model of dioecy, *S. latifolia*.

Various types of reproductive systems occur in *Rumex*: hermaphroditism, polygamy, gynodioecy, monoecy and dioecy. Phylogenetic analysis of ITS rDNA sequences suggest that dioecy appeared in *Rumex* between 15–16 million years ago [11]. Two different sex-chromosomal systems and sex-determining mechanisms have been described in dioecious *Rumex* species: XX/XY with an active Y chromosome (e.g., *R. acetosella*) and XX/XY$_1$Y$_2$ with sex determination based on the X/A ratio (e.g., *R. acetosa*). There is one exceptional species, *R. hastatulus*, which has two chromosomal "races": the Texas race possesses an XX/XY system, while the North Carolina race has an XX/XY$_1$Y$_2$ system. In this species, the X/A ratio controls sex determination, but the presence of the Y chromosome is necessary for male fertility [12]. The two Y chromosomes of *R. acetosa* are large, full of repetitive satellites, and cytologically heterochromatic [13,14]. Their epigenetic analysis reveals that they are depleted in acetylated H4 histones, which is a clear marker of heterochromatin (Fig. 1). In somatic cells of some male tissues, these Y chromosomes form heterochromatic interphase bodies that are typically located in the nuclear periphery [15]. *R. acetosa* is an ideal subject for cytogenetic studies: its genome is huge (C ∼ 7.0 Gb), and it is divided into seven pairs of acrocentric autosomes and larger metacentric sex chromosomes (XX in females and XY$_1$Y$_2$ in males). In *R. acetosa*, similar repetitive sequences in both Y chromosomes suggest that they might originate from one Y chromosome that underwent centromere fission and gave rise to a pair of metacentric chromosomes possessing identical chromosomal arms (isochromosomes). These isochromosomes have been subsequently modified by deletions. One view suggests evolution of the XX–XY$_1$Y$_2$ system through autosomal translocation to the original X chromosome. A phylogenetic study indicates that all dioecious *Rumex* species evolved from a common hermaphroditic ancestor [11]. The switch from a sex-determining mechanism based on the active role of the Y chromosome to a mechanism based on the X/A ratio occurred at least twice [16]. The dynamics of microsatellite expansion vary between closely related *Rumex* species [17] and the abundance of microsatellites within the individual genomes differs with higher frequency in the neighbourhood of transposable elements. This fact suggests that microsatellites are probably targets for transposon insertions and that microsatellite expansion is an