Plant sex chromosome evolution in the phylogenomic era

Mark S. Hibbins[1,2*] and Stephen I. Wright[2]

[1]Department of Biology, University of Rochester, Rochester, NY, USA 14620

[2]Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, CA M5S 3B2

[*]Corresponding author

Email: mark.hibbins@rochester.edu

Abstract

Plants harbor a tremendous diversity of sexual systems, including various forms of chromosomal sex determination that have arisen repeatedly across major clades, especially in angiosperms. The causes and consequences of sex chromosome evolution are far-reaching, with implications for sexual system, mating system, and life history evolution, genome architecture, and speciation, extinction, and diversification across lineages. With advances in sequencing, it is now possible to generate high-quality, chromosome-scale genome assemblies for many non-model plant species, ushering in a "golden age" for phylogenomic research. In this review, we argue that the time is ripe for a phylogenomic perspective on the evolution of plant sex chromosomes; the repeated origins of these systems, availability of hermaphroditic close relatives, and access to high quality genomic data will enable new approaches to testing classic models for the initiation, progression, and consequences of sex chromosome evolution. We conduct a clade-level survey of documented plant sex chromosome systems, revealing remarkable variation in the size, age, and degree of differentiation across sex-linked regions, revealing the need for renewed consideration of alternate models. Identifying key questions for future research, we highlight how phylogenomic approaches can be used to test hypotheses across a wide range of models, paving the way for a more robust understanding of how sex chromosomes arise and persist across lineages.

1. Introduction

Sex chromosomes have long been of interest to evolutionary biologists, owing to their distinct hemizygous mode of inheritance and their association with the mechanisms of sex determination in many groups. Much of the early work on sex chromosome evolution focused on animal groups with ancient and highly differentiated sex chromosomes, such as mammals and *Drosophila* (Bachtrog et al. 2011). It was later realized, however, that the age and characteristics of sex chromosomes vary widely across groups, with some having much more recent origins (Bull 1983, Charlesworth 1996, Bachtrog et al. 2014). Plants are one such group. Plants are of particular interest because most species are hermaphroditic (male and female reproductive organs in the same

individual), and dioecy (separate male and female individuals) has evolved repeatedly across different groups, often in the recent evolutionary past (Charlesworth 2002, Ming et al. 2007, Ming et al. 2011, Charlesworth 2013, Charlesworth 2015, Charlesworth 2016). These repeated origins provide independent evolutionary replicates of the transition from hermaphroditism to dioecy and the subsequent evolution of chromosomal sex determination, a powerful framework for testing fundamental evolutionary hypotheses (Figure 1). The relatively young age of many plant sex chromosomes additionally provides valuable insights into the early stages of sex chromosome evolution and the progenitors of sex chromosomes.

Broadly speaking, sex chromosome systems can be grouped into one of three categories, defined by their mode of inheritance in relation to sex determination. The two most commonly studied are heterogametic systems, with males being heterogametic in XY systems and females being heterogametic in ZW systems. A less studied system called UV exists in species with a haploid-dominated life cycle, such as the mosses and liverworts; in this system each sex inherits a distinct haploid chromosome, U or V (Coelho et al. 2018). Regardless of the exact configuration, the canonical model for how sex chromosomes evolve remains similar, beginning with the evolution of a sex-determining locus or region (SDR) on a pair of autosomes. Once established, this SDR provides an avenue for the resolution of sexually antagonistic variation, by selecting for the co-inheritance of mutations with sex-specific benefits and the region of the chromosome determining that sex (Charlesworth & Charlesworth 1980, Rice 1987). This ultimately promotes the suppression of recombination on the chromosome containing the SDR. This process is often envisioned as occurring in a stepwise fashion, starting close to the SDR and extending outward along the chromosome as more sexually antagonistic variation is captured. This is predicted to lead to the formation of "evolutionary strata" on sex chromosomes, where recombination is suppressed more recently in regions more distant from the SDR (Lahn & Page 1999, Handley et al. 2004, Bergero et al. 2007).

This process of linkage and recombination suppression leads to sex chromosomes having several features that are distinct from autosomes, and interesting from a fundamental evolutionary genetic perspective. The heterogametic nature of XY and ZW systems mean that these chromosomes have sex-biased inheritance; as opposed to autosomes which have equal inheritance across sexes, Y and W chromosomes are only inherited in males and females, respectively, while the X and Z chromosomes are inherited 2/3 of the time in females and males, respectively. This means these chromosomes typically have reduced effective population sizes compared to autosomes and experience differing strengths of selection related to sex-specific functions. The suppression of recombination in the sex-linked region often promotes the degeneration of the Y and W chromosomes via selective interference, leading to losses of synteny and gene function and the proliferation of repetitive genetic elements (Rice 1994, Charlesworth & Charlesworth 2000, Bachtrog 2013). Lastly, the number of X and Z chromosome copies differs between sexes, posing a challenge for the regulation of expression of X and Z-linked genes experiencing degeneration on the Y and W chromosomes respectively; this often results in the evolution of dosage compensation mechanisms (Charlesworth 1978, Charlesworth 1996, Vicoso & Bachtrog 2009, Graves 2016).

The sexual antagonism framework has been powerful for understanding the general processes leading to the formation and evolution of sex chromosomes. Despite this, there are many aspects of sex chromosome evolution that it cannot explain in isolation, and empirical evidence for a role of sexual antagonism is equivocal (Ponnikas et al. 2018). In plants and other groups, the degree of differentiation and degeneration seems to differ across sex chromosome systems of comparable ages, as well as the extent or even presence of dosage compensation (Charlesworth 2013, Charlesworth 2015, Muyle et al. 2017, Renner & Müller 2021). The factors promoting the evolution of an XY vs. ZW system in diploid organisms remain unclear, and some systems turn over liberally between these two configurations while others appear to remain stable for many millions of years (Charlesworth 2019, Vicoso 2019, Palmer et al. 2019). Significant variation in sexual systems and sex determination often exists among closely related plants, and the role, if any, this plays in the long-term maintenance of species barriers and the process of speciation over macroevolutionary timescales is not well understood. Given these gaps, alternate models for the origin and differentiation of sex chromosomes should be given renewed consideration.

In this review, we argue that combining modern whole-genome sequencing with explicit phylogenetic approaches will be necessary in the future to address many of these conceptual challenges. Recent advances in whole-genome sequencing technology are making it easier than ever before to sequence and assemble high-quality genomes in non-model species (Amarasinghe et al. 2020, Coster et al. 2021). Improvements in long-read sequencing technology in particular are enabling assemblies of traditionally challenging genomic regions, such as the centromeric and telomeric regions of autosomes, and the sex-linked regions of sex chromosomes, which are often highly repetitive. These advances are ushering in a golden age for phylogenomics research, as high quality genome assemblies are now increasingly obtainable for whole clades of organisms for the first time, particularly in plants which often have large, repeat-rich genomes and experience high rates of polyploidy (Jung et al. 2019, Michael & VanBuren 2020, Pucker et al. 2022). To highlight the use of these datasets, we present an updated literature survey of documented sex chromosome systems in plants and their relatives, with an emphasis on clade-level variation and genome-scale datasets (Figure 2). We use this survey to explore the patterns of variation within and between clades, and to highlight the opportunities for hypothesis testing using phylogenomics (Figure 2).

We see phylogenomics providing four key advantages for sex chromosome research (Figure 1); first, it allows for the identification of repeated origins of sexual system and sex chromosome transitions, providing statistically independent replicates of the process (Figure 1A). Applying phylogenetic comparative methods in such cases will yield new insights into the macroevolutionary drivers of sexual system transitions and sex chromosome evolution. Second, through ancestral state reconstructions and synteny analyses, it will be possible in many systems to identify the ancestral homologs of sex chromosomes and SDRs in hermaphroditic relatives (Figure 1B). This will enable a more direct understanding of the features of chromosomes that are sex chromosome progenitors, including the landscape of recombination, the distribution and function of genes, and the regulation of their expression. Third, inferences of historical hybridization and introgression across taxa will allow for new insights into the role of sex chromosome formation and variation in the long-term maintenance of species barriers (Figure 1A). Finally, comparative analyses of life history characteristics such as mating system or generation

time will enable macroevolutionary tests of many models of sex chromosome formation and evolution (Figure 1C). The plants are a group that is particularly well-suited to these approaches, owing to their repeated origins of sex chromosomes from hermaphroditic ancestors, often in the recent past. Overall, we argue that phylogenomics will produce valuable new insights into the processes by which autosomes become sex chromosomes and how and why sex-linked regions evolve and turn over.

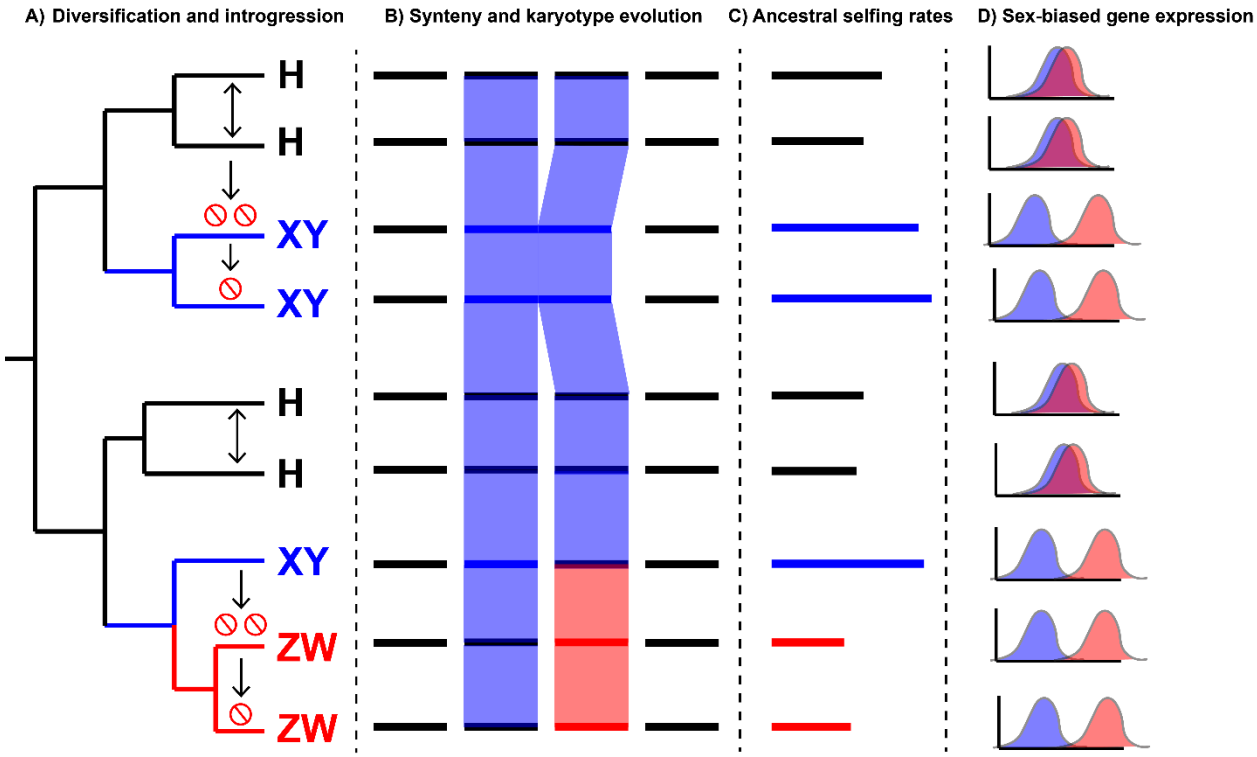

***Figure 1*:** Phylogenetic approaches to the study of sex chromosomes. A) Phylogenetic reconstruction allows for identification of independent origins of sex chromosome systems and turnovers, and for testing of rates of introgression among species with varying degrees of sexual system differentiation. B) Ancestral reconstruction and comparative approaches applied to synteny data can uncover the ancestral autosomal homologs of sex chromosome systems, whether certain autosomes repeatedly become sex chromosomes, and properties of those autosomes. C) Analyses like phylogenetic regression can help test models of sex chromosome evolution; for example, some models predict that higher ancestral rates of selfing should promote the formation of XY over ZW systems. D) Comparative approaches to the study of gene expression could help identify sexually antagonistic gene candidates, by identifying genes that rapidly evolve sex-biased expression in taxa with sex chromosomes. They may also provide new insights into the evolution of dosage compensation by enabling estimation of ancestral expression levels for sex-linked genes.

2. Sexual system transitions in plants

2.1 Transitions to dioecy and initial sex chromosome formation

Since most major plant lineages are ancestrally hermaphroditic (with the possible exception of liverworts, which may be ancestrally dioecious; Laenen et al. 2016, Singh et al. 2023), the first

step in the evolution of plant sex chromosomes is the evolution of separate male and female individual plants. This system is called dioecy when separate male and female sporophytes exist, like in vascular plants, and dioicy when separate male and female gametophytes exist, like in non-vascular plants (referred to hereafter only as "dioecy" for simplicity's sake). Two models are often considered for the evolution of dioecy from hermaphroditic ancestors. The first involves the successive fixation of male-sterility and female-sterility mutations, leading to female and then male individual plants (Charlesworth & Charlesworth 1978a, Charlesworth and Charlesworth 1978b); this is the referred to as the "gynodioecy pathway", referring to the intermediate state in which both female and hermaphroditic plants exist in a population. In the second model, selection drives plants to differentially allocate resources to one sexual function over the other, eventually resulting in sexual specialization (Charnov et al. 1976, Lloyd 1980). This is known as the "monoecy pathway", referring to the intermediate state where separate male and female flowers exist on the same plant, with genetic variation in the resource allocation between them. In both models, the accumulation of genetic changes enabling sex-biased and eventually sex-specific expression paves the way for the evolution of sex chromosome systems.

Dioecy has evolved independently numerous times in plants, currently constituting 40-60% of bryophytes (Villarreal & Renner 2013) and 65% of gymnosperms (Walas et al. 2018), but only 5-6% of angiosperms (Renner et al. 2014). Each independent origin of dioecy provides an opportunity to study the evolution of genetic sex determination. However, the mechanisms of sex determination have not been elucidated in most dioecious plants. Once dioecy evolves, multiple paths to sex determination are possible, including not just sex chromosomes but alternate mechanisms like environmental sex determination, haplo-diploidy, and paternal genome elimination. The latter three mechanisms are common in animals but rare or non-existent in plants (Bachtrog et al. 2014) and so will not be a focus of this review. Dioicous species are limited to UV systems by their haploid nature, but diploid plants can evolve either an XY or ZW system following the transition to dioecy. In our literature survey, we took a clade-level perspective on plant sex chromosome systems, aiming to identify phylogenetically independent origins of each system. Out of 34 dioecious clades documented, we find at least 38 independent origins of sex chromosomes, of which 27 (71%) are XY sex determination and 8 (21%) are ZW sex determination (Figure 2A, Table S1). Note that these estimates are likely conservative, since most of these inferences are based on parsimony, and some systems may share the same system of heterogamety but on non-homologous chromosomes. This asymmetry in favor of XY systems is consistent with previous surveys (Ming et al. 2011, Baránková et al. 2020). We found at least 3 independent origins of UV systems in bryophytes, brown algae, and green algae (Figure 2A, Table S1).

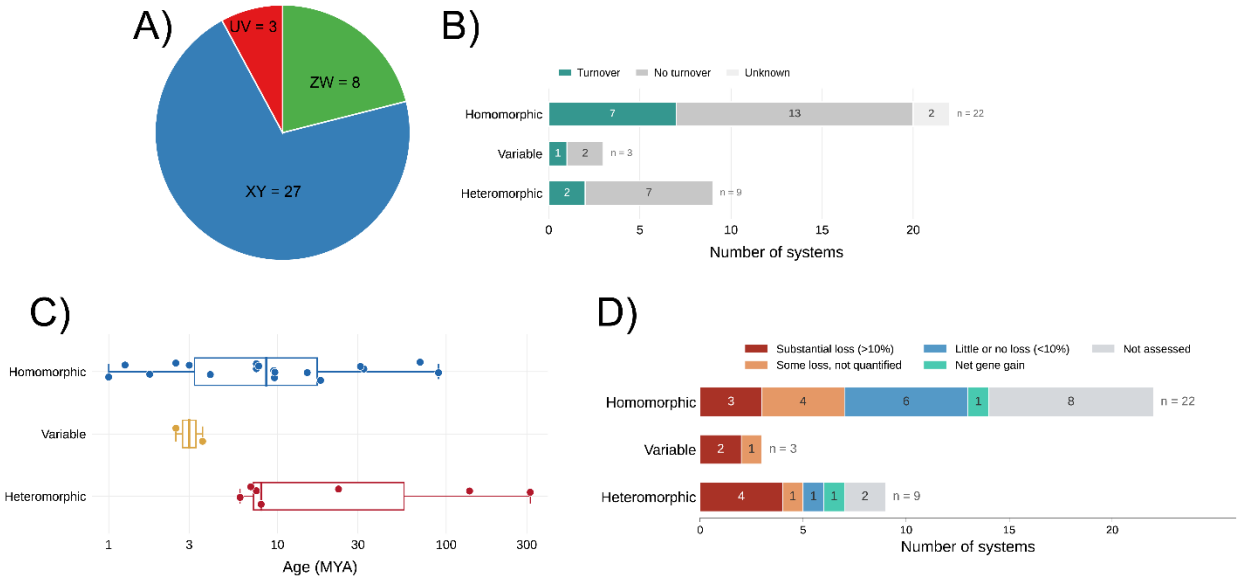

***Figure 2*:** Summary of our literature survey of plant sex chromosome systems. A) Breakdown of sex chromosome systems across clades. Each instance corresponds roughly to an independent origin of the sex chromosome system based on parsimony. B) Breakdown of sex chromosome turnover rates in systems with homomorphic vs. heteromorphic sex chromosomes. Note that the "no turnover" category simply denotes instances where turnover was not observed, rather than cases where it was strictly ruled out using evidence-based criteria. C) Age in millions of years for sex chromosome systems labelled as homomorphic vs. heteromorphic, plotted on a log scale. D) Degree of gene loss in sex chromosome systems labelled as homomorphic vs. heteromorphic. Panels B through D of this figure were generated by Claude Cowork using our survey data.

Why XY is more common than ZW in plants remains unclear, although several models have been proposed. Under the gynodioecy pathway, an XY system arises if the initial male-inactivating mutation is recessive, while a ZW system arises if it is dominant (Charlesworth & Charlesworth 1978a, Charlesworth and Charlesworth 1978b). One simple explanation, then, is that the gynodioecy pathway is common and such loss-of-function mutations are more likely to be recessive, with the production of homozygous females facilitated by selfing (Charlesworth 2016). A recent model integrating the resource allocation / monoecy pathway with the evolution of genetic architecture also found that high selfing and inbreeding depression promotes the evolution of XY over ZW systems (Lesaffre et al. 2024). This occurs for two reasons: 1) because female flowers can receive both self and outcrossed pollen, reproductive competition through female function is increased; 2) when inbreeding depression is high, selfed offspring produced through female flowers have less reproductive value. Under these conditions, hermaphrodites will gain a fitness advantage if they allocate more resources towards male function. This selects for the dominance of male-determining alleles, resulting in an XY system (Lesaffre et al. 2024). Both models suppose a major role for selfing and inbreeding depression in the evolution of dioecy; this could be consistent with the higher prevalence of dioecy in abiotically pollinated plants, including bryophytes, gymnosperms, and wind-pollinated angiosperms (Renner 2014), where the promotion of outcrossing in selfing hermaphrodites is more difficult.

Phylogenomic approaches could be valuable for testing these ideas in multiple ways (Figure 3). Currently there is some evidence for both pathways to dioecy; gynodioecy and dioecy co-occur in plant phylogenies more than expected (Dufay et al. 2014), and monoecy and dioecy also co-occur in many groups (Renner 2014). Phylogenetic comparative approaches that explicitly estimate rates of transition from each of these states into dioecy, as well as correlating dioecy with other phylogenetically distributed characters such as selfing rates or proxies for selfing, will be valuable (Figure 1C). However, given the expected transience of monoecy and gynodioecy as intermediate sexual systems, their presence in extant taxa may not be fully representative of ancestral states. Likewise for sex chromosomes, further characterization of the independent origins of these systems in a phylogenetic context will be helpful for testing theories of initial sex chromosome formation. Estimation of syntenic regions and genealogical patterns of gene orthologs among close hermaphroditic relatives (e.g. Hou et al. 2015, Hibbins et al. 2025a, Hibbins et al. 2025b) will allow for highly accurate characterization of independent sex chromosome origins in many plant clades (Figure 1B). Finally, comparative genomic and transcriptomic approaches will help understand the molecular basis of sexual system transitions, for example, by identifying genes involved in genetic variation in sex allocation in hermaphroditic relatives and testing for selection on their sequences or expression levels and the evolutionary fate of these genes in species with sex chromosomes (Figure 1D).

2.2 Sex chromosome stability and turnover

Once a sex chromosome system is established, the evolutionary stability of that system is not guaranteed. Sex chromosomes can turn over, which we define here as any karyotypically significant shift in the physical location of a sex-determining region and/or the genetic mechanism of sex determination. In our survey (Table S1), we documented tremendous variation in the stability of sex chromosome systems across plants and their relatives. Outside of the angiosperms, while not as well-characterized, sex chromosomes appear to be ancient and relatively evolutionary stable. The XY systems of *Gingko* (Liao et al. 2020, Gong & Filatov 2022) and cycads (*Cycas*; Abraham & Mathew 1962, Liu et al. 2022), in addition to the UV systems of bryophytes (Iwasaki et al. 2021, Carey et al. 2021, Healey et al. 2023) and algae (Ferris et al. 2010, Luthringer et al. 2015, Avia et al. 2018, Yamamoto et al. 2021), may be on the order of hundreds of millions of years old, with some evidence of derived loss and re-evolution of UV sex determination in liverworts (Fu et al. 2025). In contrast, the angiosperms have much younger and less stable sex chromosomes, with the oldest documented systems on the order of 25-50 million years in date palms (*Phoenix*, Siljak-Yakovlev et al. 1996, Cherif et al. 2016), pitcher plants (*Nepenthes*, Scharmann et al. 2019), and the sex chromosome system shared by hops (*Humulus*) / *Cannabis* (Prentout et al. 2020, Prentout et al. 2021).

In the angiosperms, sex chromosome turnovers appear to be common in systems where the genetic basis of sex determination has been studied across multiple species. These turnover processes can be highly variable, including the formation of neo-sex chromosomes, the translocation of sex-determining genes to different chromosomes, and even shifts in the system of heterogamety (i.e. from XY to ZW and vice-versa). Perhaps the most dynamic of these known systems is the Salicaceae, the willows (*Salix*; Wang et al. 2022, Hu et al. 2023) and poplars

(*Populus*; Geraldes et al. 2015, Yang et al. 2020, Li et al. 2022). Despite a common origin of dioecy inferred using phylogenetics, genetic sex determination evolved independently in these sister genera (Geraldes et al. 2015, Huo et al. 2015), and sex chromosomes have turned over multiple times within each group, including translocations of the sex-determining locus and shifts from XY to ZW systems. Another highly labile system is *Rumex*, where sex chromosome-autosome fusions have resulted in XYY karyotypes with neo-X chromosomes at least twice, including a within-species XY/XYY polymorphism and population-specific translocations of the Y chromosomes in *Rumex hastatulus* (Grant et al. 2022, Sacchi et al. 2024, Hibbins et al. 2025a, Hibbins et al. 2025b). Several other angiosperm groups have documented turnovers, including *Silene* (Martin et al. 2019, Bačovský et al. 2020), kiwifruit (*Actinidia*; Akagi et al. 2023), and strawberry (*Fragaria*; Tennessen et al. 2018). Finally, we note that the derived loss of dioecy altogether has been observed in several groups, including the Caricaceae (papaya and its relatives; Wu et al. 2010), persimmon (*Diospyros*; Horiuchu et al. 2023), domestic grapevine (*Vitis vinifera*; Picq et al. 2014), and *Mercurialis* (Obbard et al. 2006).

A growing body of models seeks to understand what forces may drive or inhibit the turnover of sex chromosomes. In the absence of selection acting on genetic variants, turnover can be favored by the interaction of dominance with selection to maintain an equal sex ratio (Bull & Charnov 1977, Veller et al. 2017, Saunders et al. 2018). While relatively weak, this "drift-induced selection" effect can promote both heterogametic and non-heterogametic turnover both within and between chromosomes, but favors turnovers that preserve the system of heterogamety (Saunders et al. 2018). When deleterious mutations are introduced, shifts in the heterogametic system (XY → ZW and vice-versa) become disfavored, as they require the fixation of unfit YY / WW genotypes (Veller et al. 2017, Saunders et al. 2019). However, turnovers that shift the existing heterogametic system to a new chromosome may be favored, as they enable the loaded ancestral Y / W chromosome to be lost; this has been dubbed the "hot potato" effect (Blaser et al. 2013, Blaser et al. 2014). Finally, turnovers to new chromosomes may be favored by the buildup of sexual antagonism at new loci that outstrips the existing antagonism in the sex-determining region (van Doorn & Kirkpatrick 2007, van Doorn & Kirkpatrick 2010). Sexual antagonism can also promote the formation of neo-sex chromosomes via chromosomal fusions and translocations that link antagonistic variation to the existing sex chromosome system (Charlesworth & Charlesworth 1980, Rice 1987, Charlesworth et al. 2005).

Which of these evolutionary forces drive or inhibit sex chromosome turnover across plants remains unclear. Qualitatively, these models predict that, on net, turnovers that preserve the heterogametic system but move it to a new chromosome should be most common; however, the relative strengths of drift and selection play an important role. In systems with low effective population size and/or small and undifferentiated sex-determining regions, heterogametic turnovers may be tolerated or even promoted via sex-ratio selection. This may explain why systems like the willows and poplars, which are generally long-lived perennials with homomorphic sex chromosome systems, are so labile to turnover. However, several groups with similar life histories, such as date palms and pitcher plants, appear to have stable sex chromosome systems. Importantly, these systems also typically have long generation times, which may confound analyses that correlate sex chromosome properties with units of absolute time. Coalescent-based dating of sex-

linked regions using phylogenomic approaches may provide a more accurate picture of the age of sex-linked regions and how it relates to the stage of degeneration.

When sex chromosomes become highly differentiated, turnovers may be inhibited by the high cost of disrupting the existing sex-determining mechanism; the "evolutionary trap" hypothesis (Pokorná & Kratochvíl 2009, Vicoso 2019). In our literature survey, we found preliminary evidence for a slightly higher occurrence of turnovers in homomorphic systems compared to heteromorphic ones, consistent with this idea. However, ascertainment bias in the detection of turnover events may confound this pattern, so it should be treated with caution. Nevertheless, the evolutionary trap hypothesis this does not explain what might maintain the initial stability of sex chromosome systems, and some groups such as *Ginkgo biloba* and *Nepenthes* appear to have stable configurations despite relatively small and undifferentiated sex-linked regions. One recently proposed mechanism is that turnovers disrupt the balance of chromosome-specific drift that maintains stable trait values under stabilizing selection (Muralidhar 2026). Overall, phylogenomic approaches will help elucidate these mechanisms by (Figure 3) 1) uncovering new cases of sex chromosome turnover (Figure 1A); 2) identifying the selective forces acting on ancestral and derived sex-determining regions by detecting selective sweeps and the recurrent movement of sex-linked genes and syntenic regions (Figure 1B, D); 3) associating turnover rates with ecological and life history traits that may shape selective forces (Figure 1C).

2.3 Sex chromosome evolution and polyploidy

A major question in plant biology concerns why polyploidy is much more common in angiosperms than in animals. One long-standing idea is that the more widespread presence of sex chromosomes in animals inhibits whole-genome duplications, which may disrupt sex determination and the dosage balance of X-linked genes, particularly in back-crossed hybrids (Muller 1925, Orr 1990). Hemizygous systems are also more common in animals, resulting in exposed recessive incompatibilities in allopolyploids (i.e. Haldane's rule, Haldane 1922). In our literature survey, we found multiple instances of polyploid plants with sex chromosomes, including the decaploid pitcher plant *Nepenthes gracilis* (Saul et al. 2023), the tetraploid kiwifruit *Actinidia arguta* (Akagi et al. 2023, Lu et al. 2024), both triploids and tetraploids in *Ginkgo biloba* (Šmarda et al. 2018), the octoploid wild strawberry *Fragaria virginiana* (Spigler et al. 2008), tetra/hexaploid *Mercurialis* (Russell & Pannell 2015, Gerchen et al. 2022), hexaploid *Rumex acetosella* (Cuñado et al. 2007) variable ploidy in yams (*Dioscorea*; Cormier et al. 2019, Ngwe & Siljak-Yakovlev 2023) and tetraploid *Salix polyclona* (He et al. 2023). In many other groups, we observed the coexistence of polyploidy and sex chromosomes, though not necessarily in the same species (Table S1).

Robust investigations into an inhibitory relationship between polyploidy and sex chromosome evolution should consider three important factors. First, the genetic mechanism of sex determination, namely X:autosome balance vs Y-presence (and vice-versa in ZW systems). While not known for most plants, whole-genome duplications should be more disruptive in systems with X-autosome balance because they directly alter the balance of X chromosomes to autosomes. Genotypes containing multiple duplicated Y chromosomes may be less fit if the Y is degraded, so the most stable sex chromosome systems in polyploids may contain a single dominant

Y chromosome (He & Hörandl 2022), consistent with experiments in *Silene* (Warmke & Blakeslee 1939) and the karyotype of *Nepenthes* (Saul et al. 2023). A second factor is whether the duplication event is autopolyploidization or allopolyploidization. While the simple autopolyploid duplication of an existing sex chromosome system may be tolerated, especially under a Y-presence system, allopolyploids may be more inhibitory to sex chromosome evolution, as they would require both parent species to have a homologous sex-determination mechanism and for backcrosses to these parents to maintain functional sex determination. However, viable diploid hybrids between XYY and XY cytotypes of *Rumex hastatulus* have been observed (Beaudry et al. 2022), and the allotetraploid weeping willow appears to have arisen from allopolyploidization of two lineages with non-homologous sex chromosomes (He et al. 2024), indicating that such differences might not present complete barriers to the formation of allopolyploids among closely related populations or species.

Finally, the relative timing of these two events matters; if sex chromosomes evolve first, and especially if they have time to establish and begin to differentiate, then we might expect polyploidy to be inhibited, due to higher costs associated with disrupting the genetic architecture of sex determination. The sex chromosome systems of many animal groups are evolutionarily ancient, consistent with this idea. However, if the whole-genome duplication occurs first, we might not expect the subsequent evolution of sex chromosomes to be inhibited, as long as the karyotype remains stable thereafter. While few studies have explicitly dated sex chromosome evolution and polyploidy on the same plant phylogeny, preliminary inferences based on parsimony of phylogenetic characters suggest mixed results. In *Nepenthes*, decaploidization appears to have preceded the evolution of dioecy and chromosomal sex determination (Saul et al. 2023), in line with our predictions. However, in *Mercurialis* (Gerchen et al. 2022), *Actinidia* (Akagi et al. 2023), and *Rumex* (Cuñado et al. 2007, Hibbins et al. 2025a, Hibbins et al. 2025b), individual polyploid lineages have arisen inside clades with shared sex chromosome systems. *Mercurialis* is an especially striking case, as the sex chromosome system has remained stable despite recurrent allopolyploidization and Y-chromosome introgression, which should be highly disruptive to sex-determining mechanisms. Experimental work resolving sex-determining mechanisms in plants, in combination with phylogenomic approaches to resolve the timing of whole-genome duplications and sex chromosome evolution, will open new avenues to investigating this old question and understanding the drivers of polyploid evolution (Figure 3).

3. The genomic architecture of sex chromosome evolution

3.1 The evolution of recombination in sex-linked regions

The key hallmark of a chromosomal sex-determination system is the presence of a region of suppressed recombination surrounding the sex-determining locus. Importantly, this region must evolve from an ancestral pair of recombining autosomes. This means that, regardless of the exact mechanism promoting recombination suppression (discussed in 3.2), sex chromosome evolution requires the introduction of mutations that modify the landscape of recombination. In plants, the landscape of recombination is highly variable and correlated with a variety of genomic features, including chromosome size and number, the size and distribution of telomeric and centromeric regions, and the density of genes and transposable elements (Tiley & Burleigh 2015, Stapley et al.

2017, Haenel et al. 2018, Brazier & Glémin 2022). Modifiers of recombination can act at both small and large genomic scales. Like in other eukaryotes, double strand-breaks in plants are concentrated in genomic "hotspots" of a few kb in length, with methylation and chromatin state playing important roles in determining their locations (He et al. 2017, Choi et al. 2018). In addition to these smaller-scale shifts in recombination rate, larger-scale changes involving significant proportions of chromosomes, or even whole chromosomes, can be generated by structural rearrangements, including both intrachromosomal (e.g. inversions) and interchromosomal (e.g. fissions and fusions) mutations. These mutations affect recombination by inhibiting homologous chromosome pairing (i.e. heterozygous inversions and translocations; Kirkpatrick & Barton 2006) or physically bringing together previously unlinked chromosomal regions.

Classic theories place a particular importance on chromosomal rearrangements for the evolution of sex chromosomes, by enabling rapid extension of suppressed recombination surrounding the sex-linked region (Charlesworth & Charlesworth 1980, Rice 1987, Charlesworth et al. 2005). Studies in old sex chromosome systems generally find that divergence between gametologs decreases with distance from the sex-determining locus (Lahn & Page 1999, Handley et al. 2004, Bergero et al. 2007, Moraga et al. 2025), but distinguishing the contributions of stepwise successive rearrangements (i.e. evolutionary strata) from the gradual accumulation of smaller-scale modifications to the recombination landscape has proven difficult. In addition, additional rearrangements within the sex-linked region may erode the initial signal of strata.. Large-scale rearrangements involving sex chromosomes have been found in some plant systems, such as *Silene* and *Rumex* (Bačovský et al. 2020, Beaudry et al. 2020, Sacchi et al. 2024, Moraga et al. 2025), but it remains unclear whether they were selected for their sex chromosome association or are simply part of the "background" input of rearrangement mutations across the genome (Hibbins et al. 2025a, Hibbins et al. 2025b). In general, outside of *Silene*, the evidence for evolutionary strata on plant sex chromosomes remains weak. One possibility is that the initial stages involve large-scale rearrangements that generate regions of suppressed recombination, which are then followed by smaller-scale modifications that fine-tune the boundary of the sex-linked region with the pseudoautosomal region. Phylogenomic approaches in plant systems could prove extremely valuable here, by allowing for the direct identification of ancestral autosomes that are homologous to existing sex chromosome systems in the many plant clades where dioecious and hermaphroditic species coexist (Figure 1B). Synteny analysis in a phylogenetic framework should allow for much more detailed inference of the contribution of rearrangements to the expansion of recombination suppression in these groups, especially in young sex chromosome systems (Hibbins et al. 2025b).

In classic models of sex chromosome evolution, recombination suppression evolves as a consequence of selection to link sexually antagonistic alleles to sex-determining loci. However, in many eukaryotic systems, including plants, large regions of suppressed recombination already exist on autosomes (Sardell & Kirkpatrick 2020, Brazier & Glémin 2022, Rifkin et al. 2022, Guo et al. 2022). If sexually antagonistic variation accumulates in these nonrecombining tracts, these autosomes may be "primed" to become large, heteromorphic sex chromosomes, allowing the easier establishment and/or expansion of a novel sex-determining region (Charlesworth 2019, Otto 2019, Rifkin et al. 2022, Guo et al. 2022). Additionally, in dioecious species, the landscape of

recombination often differs between the sexes (heterochiasmy), with male recombination more biased towards the telomeric ends of chromosomes (Sardell & Kirkpatrick 2020, Brazier & Glémin 2022, Rifkin et al. 2022). The presence of larger regions of suppressed recombination in males could enable the stronger linkage of male-beneficial mutations once a male sex-determining gene arises, contributing to the higher prevalence of XY over ZW sex chromosome systems in plants. Taken together, these hypotheses predict that certain kinds of autosomes should be more likely to become sex chromosomes; particularly, those that are large, highly heterochromatic, and where male recombination is more tip-biased. Phylogenomic approaches to synteny data studying the autosomal progenitors of sex chromosomes will be invaluable for testing these ideas (Figure 1B, Figure 3).

3.2 Sexual antagonism, sex chromosome differentiation and degeneration

Sexual antagonism has broad explanatory power when considering the initial formation, differentiation, and degeneration of sex chromosomes. However, despite the preponderance of sexual conflict at the phenotypic level, not all sex chromosome systems clearly harbor sexually antagonistic variation, and demonstrating that sexually antagonistic genetic variants drive the evolution of sex chromosomes remains challenging (Rice 1992, Gibson et al. 2002, Ironside 2010, Ponnikas et al. 2018, Lund-Hansen et al. 2021, Dagilis et al. 2022). In addition, in our own survey and in past work (Figure 2C, Renner & Müller 2021), the size and degree of degeneration (Figure 2D) of sex-determining regions does not appear to be strongly correlated with their age, as would be expected if the recurrent suppression of recombination and expansion of sex-linked regions are generally driven by ongoing sexual conflict. More generally, it remains poorly understood why some sex-determining regions remain relatively small and undifferentiated, while others expand to fill most of the chromosome and undergo significant degeneration (Figure 2D). These findings have led to increased interest in alternate models for the expansion and degeneration of sex-linked regions that do not rely on classic models of sexual antagonism. A variety of these alternate models exist, based on processes such as heterozygote advantage (Charlesworth & Wall 1999), meiotic drive (Úbeda et al. 2015), neutrality (Kent et al. 2017, Jeffries et al. 2021), regulatory evolution (Lenormand et al. 2020, Lenormand & Roze 2022), and/or sheltering of deleterious mutations (Jay et al. 2025).

Under inbreeding depression, mutations that increase the average genome-wide heterozygosity may become favored. Translocations or fusions involving a sex chromosome and an autosome allow for the long-term maintenance of heterozygosity of the rearrangement, promoting the expansion of sex-linked regions in inbred populations (De Waal Malefijt & Charlesworth 1979, Charlesworth & Wall 1999). This model does not explain how sex chromosomes could initially establish in the absence of sexual antagonism, but provides a mechanism for their ongoing expansion under certain conditions. Alternatively, a new sex-determining allele may be favored in a population if it becomes linked to a sex-biased meiotic driver; compensatory mutations to restore an equal sex ratio can result in the evolution of a sex chromosome system (Hall 2004, Kozielska et al. 2010, Úbeda et al. 2015). In contrast to the heterozygote advantage model, a meiotic driver may promote the initial establishment of sex chromosomes, but not necessarily their ongoing expansion and degeneration.

Even without selection, the sufficient accumulation of neutral divergence near an existing sex-determining locus could promote the expansion of recombination suppression by reducing the recognition of homologous sequences (Ironside 2010, Jeffries et al. 2021). Additionally, the elevated rate of accumulation of transposable elements on degenerating sex chromosomes (Bachtrog 2013) may promote the neutral spread of recombination suppression as a byproduct of TE silencing, by reducing regions of open chromatin (Kent et al. 2017). Accumulating cis-regulatory divergence between X/Y gametologs may promote the fixation of nascent inversions to fix compensatory mutations, promoting recombination suppression and degeneration of Y-linked genes (Lenormand et al. 2020, Lenormand & Roze 2022). Finally, recombination-suppressing rearrangements that capture less loaded haplotypes may be more likely to fix around established Y-linked regions, as their hemizygous nature enables permanent masking of the effects of recessive deleterious mutations (Jay et al. 2025). However, unless mutations are highly recessive and strongly selected against, this process may be unlikely to fully explain the elevated fixation of Y-linked inversions, especially considering the low N_e of Y/W chromosomes and the potential reversibility of such inversions (Charlesworth & Olito 2024).

Many of these processes may act in concert, painting a complex picture of the forces shaping the expansion or stability of sex-linked regions. While recent phylogenomic analyses in *Rumex* found evidence for elevated rates of chromosomal rearrangement associated with sex chromosomes (Hibbins et al. 2025b), more explicit models are necessary to distinguish among hypotheses (Figure 3). Variation in the size and age of sex-determining regions in plants presents opportunities for phylogenomic approaches to distinguish among these many hypotheses. Testing for associations between inbreeding (or proxies for inbreeding) and chromosomal fusions / translocations in clades with sex chromosomes could provide evidence for a role of heterozygote advantage (Figure 1B, C). In less degenerated systems, evaluating signatures of selection near the sex-linked region in comparison to autosomal homologs in related species could help distinguish between neutral and sexual antagonism / meiotic drive hypotheses, provided the timing is recent enough to detect such signals. Identifying homologs of known meiotic drivers on sex chromosomes could additionally help distinguish among hypotheses. Lastly, applying phylogenetic comparative methods to estimate the tempo and mode of evolution of gene expression evolution relative to the origin of sex chromosomes will help distinguish whether cis-regulatory divergence is a cause or a consequence of recombination suppression on the sex chromosomes (Figure 1D). Generally, many models exist to explain the expansion of existing sex-linked regions, but fewer can explain the initial formation of such regions in the absence of sexual antagonism; studies in plant systems with very young sex-determining regions will be invaluable for understanding this process.

3.3 Sex chromosomes and the evolution of gene regulation

Heteromorphic sex chromosomes pose a challenge for the regulation of gene expression: the heterogametic sex has half the number of X/Z-linked gene copies as the homogametic sex. This is expected to promote the evolution of dosage compensation, a set of mechanisms that restore the expression balance of X/Z-linked genes between the sexes. The mechanisms and extent of dosage compensation are highly variable across the tree of life, ranging from a small set of genes

to the entire X/Z chromosome, including both global and gene-level mechanisms, and promoting upregulation in the heterogametic sex or downregulation in the homogametic sex (Charlesworth 1996, Marín et al. 2000, Vicoso & Bachtrog 2009, Muyle et al. 2017, Muyle et al. 2022). At the same time, genes on the sex chromosomes with important sexual functions must maintain sex-biased gene expression levels. While traditional models propose that dosage compensation evolves in response to ongoing gene loss and degeneration on the Y/W chromosome (Charlesworth 1978), more recent work proposes that it may be an early contributor to sex chromosome evolution (Lenormand et al. 2020, Lenormand & Roze 2022), and new evidence from young sex chromosome systems suggests that dosage compensation can evolve rapidly (see below). Broadly, much remains to be understood about the early stages of dosage compensation evolution, and what promotes the evolution of different compensation mechanisms, especially in plants.

Dosage compensation is common in plants where it has been investigated, but it is often incomplete. *Silene latifolia* is the most-studied plant system on the subject, and to our knowledge, the only one where mechanisms of dosage compensation have been investigated. The Y-chromosome of *S. latifolia* exhibits significant degeneration and gene loss, and a significant proportion of X-linked genes have equal expression in males and females (Muyle et al. 2012, Papadopulos et al. 2015). While the mechanism is not fully understood, it appears to involve upregulated expression of X-linked genes that can be triggered immediately upon deletion of Y genes, suggesting a global mechanism targeting specific chromosomal regions (Krasovec et al. 2019). Some evidence also suggests genomic imprinting to upregulate the maternal X chromosome specifically (Muyle et al. 2018, Krasovec et al. 2019). While dosage compensation has been observed in a handful of other plant systems, including *Rumex rothschildianus* (Crowson et al. 2017), *Coccinia grandis* (Fruchard et al. 2020), *Carica papaya* (Liu et al. 2021), and cannabis and hops (Prentout et al. 2021), much less is understood about how dosage compensation evolved in these systems and via what mechanisms. Additionally, dosage compensation appears to be absent in the XY cytotype of *Rumex hastatulus* despite ongoing Y-chromosome degeneration and loss of expression (Sacchi et al. 2025), highlighting that dosage compensation may not strictly be necessary even in older sex chromosome systems.

Phylogenomics can help resolve these questions in three primary ways (Figure 3). First, by applying ancestral state reconstructions to gene expression values, it will be possible to estimate the direction of regulatory evolution, i.e. whether expression is upregulated or downregulated on the sex chromosomes relative to ancestral levels (Figure 1D). This will yield new insights into what mechanisms tend to be involved in the evolution of dosage compensation and why. Second, using evolutionary rate estimates of expression levels, it should be possible to resolve the timescale of dosage compensation evolution relative to the suppression of recombination on sex chromosomes. If dosage compensation begins to evolve long after the establishment of suppressed recombination, it would lend support to traditional frameworks. Alternatively, if dosage compensation precedes or coincides with the suppression of recombination, more recent alternative models based on compensatory cis-regulatory evolution should receive increased consideration (Lenormand et al. 2020, Lenormand & Roze 2022). Finally, phylogenetic analysis of gene expression could provide a powerful tool for investigating the role of sexual antagonism in transitions to dioecy and the evolution of sex chromosomes. Genes undergoing sexually

antagonistic selection should be constrained in their ability to evolve sex-biased expression in hermaphroditic species. Therefore, if genes with ancestrally sex-equal expression rapidly evolve sex-biased expression in association with transitions to dioecy, that would provide compelling evidence for a role of sexual antagonism in shaping those transitions (Figure 1D). These approaches will provide new insights into the complex processes of regulatory evolution that accompany sexual system and sex determination shifts in plants.

4. Revisiting the "two rules of speciation" with a macroevolutionary lens

4.1 Sex chromosome barriers to hybridization and introgression

It has long been understood that sex chromosomes introduce post-zygotic barriers to hybridization. These effects manifest primarily in two ways, which have been dubbed the "two rules of speciation" (Coyne and Orr 1989). First is Haldane's rule, which states that the heterogametic sex (XY/ZW) is more often inviable/infertile in interspecific hybrids (Haldane 1922), and second is the large-X effect, which proposes a disproportionate role of the X/Z chromosome in contributing to hybrid compatibility as compared to autosomes (Coyne 1992). While several models exist to explain these patterns, their near-ubiquity has been confirmed by a large body of experimental and observational evidence in contemporary and early-generation hybrids, as well as genomic data from closely related populations or species (Presgraves 2018, Cowell 2023). It is less understood, however, whether these effects persist over macroevolutionary timescales and contribute to the long-term maintenance of species barriers. Such investigations would provide invaluable insights into the forces that shape species diversification over time. As for other questions discussed in this review, the many independent origins of sex chromosome systems and generally high variation in sexual systems observed in plants provide valuable evolutionary replicates for addressing this question.

There is surprisingly little work on sex chromosomes and speciation in plant systems. Haldane's rule has only been experimentally confirmed in *Silene* (Brothers and Delph 2010) and *Rumex* (Kasjaniuk et al. 2019), and only in *Silene* has evidence been presented that is consistent with a large-X effect (Hu & Filatov 2016). Unlike in ancient animal systems, the size and degree of differentiation of sex-linked regions is highly variable in plants (Table S1), particularly angiosperms. As such, plant systems may be invaluable for distinguishing the contributions of recessive hybrid incompatibility alleles from other factors that could contribute to the large-X effect, including higher rates of molecular evolution of the X chromosome (i.e. the faster-X effect; Mank et al. 2010, Meisel & Connallon 2013, Charlesworth et al. 2018), or suppressed recombination leading to stronger selection against introgressed haplotypes (Kim et al. 2018, Martin et al. 2019). In *Silene,* rather than unmasking of recessive incompatibilities, recombination suppression has been hypothesized to be the primary driver of reduced gene flow involving the X (Wong & Filatov 2023). In general, phylogenomic approaches in plants could provide new insights into these questions by estimating the rate of accumulation of incompatibility alleles or formation of gene flow-poor regions on X chromosomes as compared to their ancestral autosomal homologs (Figure 1A, B, Figure 3).

The significant variation of sexual systems across angiosperms may present additional barriers to speciation beyond the classic two rules, which to date have been applied primarily to closely related species or populations that share a homologous sex chromosome system. Closely related species can vary in sexual system (e.g. hermaphroditism vs dioecy) or in sex chromosome configuration (e.g. XY vs. ZW), presenting opportunities for significant disruption of sex determination and function in potential hybrids. From this, we may predict that plant clades containing greater sexual system variation will exhibit reduced rates of post-speciation introgression and potentially higher rates of diversification (Figure 1A, red circles). In *Rumex hastatulus*, cytotype differences (XY vs. XYY) between populations separated by the Mississippi River contribute disproportionately to barriers to gene flow, potentially driving the formation of incipient species (Beaudry et al. 2020, Beaudry et al. 2022). On longer timescales, patterns of post-speciation introgression in *Rumex* are most consistent with ancient introgression events that predate the formation of sex chromosomes, consistent with their formation playing a role in reinforcing species barriers (Hibbins et al. 2025a). Finally, among a clade of willows (*Salix*) with three different sex chromosome systems (dubbed 15XY, 15ZW, and 7XY), introgression occurs more frequently among species that share a system than between species with different systems, with no introgression among 15ZW and 7XY species (Xue et al. 2024). These results highlight how increasing levels of divergence and reduced homology among sex determination systems can generate additional barriers to hybridization among species.

4.2 Sexual system variation and plant diversification

The evolution of dioecy in plant systems may have consequences for macroevolutionary patterns of species diversification. In angiosperms, observations that dioecy is rare and broadly phylogenetically distributed, rather than concentrated in large speciose clades (Heilbuth 2000, Renner 2014), contributed to the common view that dioecy represented an evolutionary "dead end" in plants (Heilbuth 2000), with dioecious lineages either going extinct more frequently or being less likely to speciate. Possible reasons for this may include more limited mating opportunities, reduced colonization ability (i.e. Baker's Law), or genetic constraints introduced by degeneration of sex-linked regions. However, Baker's Law / mating opportunity costs cannot fully explain this pattern, since it does not also hold true for self-incompatible hermaphroditic species, which share the same limitations (Heilbuth 2000). Alternatively, the evolution of dioecy may promote diversification via the generation of genetic diversity by obligate outcrossing. More recent analyses using improved methods and broader taxonomic sampling have found that dioecy has a slightly positive (Käfer et al. 2014, Meyer et al. 2026) or inconsistent (Sabath et al. 2015) effect on diversification rates in angiosperms. Diversification is not related to sexual system in hornworts (Villarreal & Renner 2013), and dioecious mosses appear to have lower diversification rates (McDaniel et al. 2012). Given the lack of a strong diversification signal for sexual systems, one alternate explanation for the rarity of dioecy in angiosperms is recurrent reversion to hermaphroditism, as discussed in 2.2 (Käfer et al. 2017).

Distinguishing the effects of sex chromosomes from the effects of dioecy on diversification may prove difficult, as non-chromosomal sex determination is very rare in plants (Bachtrog et al. 2014). Approaches comparing sex chromosome systems with different degrees of degeneration and

homology may prove valuable (Figure 3). If sex chromosomes promote speciation in plants, clades that contain more hetermorphic and/or variable sex chromosome systems should exhibit higher rates of diversification than clades with younger, more homomorphic systems and hermaphroditic clades. Testing these approaches will require new and more standardized approaches for mapping characters like the degree of heteromorphicity and the tempo and mode of sex chromosome turnover to phylogenetic datasets. Overall, these approaches will provide valuable new insights into the mechanisms driving speciation in plants.

Model	Testable prediction	Phylogenomic test
1 Canonical model		
Sexual antagonism	Antagonistic variation selects for linkage to the SDR; suppression then spreads stepwise.	Identify SA genes based on gene expression and tests for selection, test if strata boundaries contain candidate genes
2.1 Transitions to dioecy		
Gynodioecy pathway	Dioecy arises from gynodioecious ancestors; recessive male sterility gives XY, dominant gives ZW.	Fit state-dependent rates for gynodioecy → dioecy against monoecy → dioecy.
Monoecy / allocation pathway	Selfing and inbreeding depression favor dominant male-determining alleles, and hence XY.	Regress heterogamety on reconstructed selfing rate and proxies such as pollination mode.
2.2 Stability and turnover		
Drift-induced selection and load	Heterogamety-preserving turnovers predominate; XY ↔ ZW shifts require unfit YY/WW.	Map turnover type against coalescent N_e and SDR age across clades.
"Hot potato" escape	Same-heterogamety moves to a new chromosome are favored, discarding a loaded Y/W.	Compare load and gene loss between ancestral and derived sex-linked regions.
Antagonism at new loci	Turnover targets chromosomes whose antagonistic variation outstrips the current SDR.	Test if derived SDRs are enriched for genes rapidly gaining sex-biased expression.
Evolutionary trap vs. drift balance	The trap predicts stability only once differentiated; drift disruption predicts it even for small SDRs.	Regress turnover rate on heteromorphy and gene loss
Reversion to hermaphroditism	Recurrent loss of dioecy, not reduced diversification, explains its rarity.	Estimate reversal rates under asymmetric transition models.
2.3 Polyploidy		
Sex determination inhibits duplication	Duplication is depleted where sex chromosomes exist, most strongly under X:autosome balance.	Date duplications and sex chromosome origins on one phylogeny; test branch depletion.
Relative timing and allopolyploidy	Polyploidy before sex chromosomes is tolerated; the reverse order is inhibited.	Reconstruct ancestral ploidy and sex-determining mechanism to order events per clade.
3.1 Recombination and progenitors		
Stepwise rearrangement and strata	Suppression expands in steps, giving strata of decreasing gametolog divergence.	Date rearrangements by phylogenetic synteny against ancestral autosomal homologs.
"Primed" autosomes	Large, heterochromatic autosomes with non-recombining tracts become sex chromosomes.	Test if reconstructed autosomal progenitors are atypical in recombination and repeats.
Heterochiasmy	Male tip-biased recombination links male-beneficial alleles to a nascent male SDR, favoring XY.	Test if heterochiasmy in hermaphroditic relatives predicts XY vs. ZW across origins.

Model	Testable prediction	Phylogenomic test
3.2 Expansion and degeneration		
Sexual antagonism	SDR size and degeneration scale with the age of the sex-linked region.	Regress SDR size and gene loss on coalescent-dated SDR age.
Heterozygote advantage	Inbreeding favors fusions that maintain heterozygosity, expanding but not founding an SDR.	Test association between selfing rate and rates of sex chromosome–autosome fusion.
Meiotic drive	Linkage to a driver can establish an SDR, but predicts no ongoing expansion.	Search for driver homologs near SDRs; test if they occur mainly in young systems.
Neutral divergence and TE silencing	Divergence and TE silencing spread suppression, leaving no selective signature.	Test if suppression tracks TE and methylation density rather than sex-biased genes.
Compensatory cis-regulatory evolution	Regulatory divergence between gametologs precedes suppression and drives inversion fixation.	Time expression evolution against dated suppression to separate cause from consequence.
Sheltering of deleterious mutations	Inversions capturing less-loaded haplotypes fix around Y-linked regions; contested.	Compare rearrangement rates on sex chromosomes against autosomal homologs, correlate with estimates of load
3.3 Gene regulation		
Degeneration-driven compensation	Dosage compensation evolves after, and in proportion to, Y/W gene loss.	Reconstruct ancestral expression to test whether compensation postdates degeneration.
Regulatory-first compensation	Compensation coincides with or precedes suppression, arising in young systems.	Date compensation from expression rates relative to dated suppression.
Antagonism in expression evolution	Antagonistic genes gain sex-biased expression rapidly at transitions to dioecy.	Test for accelerated gains of sex bias on branches where dioecy originates.
4.1 Barriers to hybridization		
Haldane's rule and large-X effect	Incompatibilities concentrate on the X/Z; recessivity, faster-X and low recombination	Compare rates of introgression on on X against ancestral autosomal homologs; correlate with factors
Sexual system divergence	Introgression is reduced between species with non-homologous sex chromosome systems.	Test introgression rates against degree of sex chromosome homology / similarity in system of heterogamety
4.2 Diversification		
Dioecy as a dead end	Dioecious lineages speciate less or go extinct more, but not self-incompatible ones.	Fit state-dependent diversification models, allowing reversion to hermaphroditism.
Outcrossing promotes diversification	Obligate outcrossing generates genetic diversity, raising diversification rates.	Compare rates across independent origins and across land plant groups.
Sex chromosomes promote diversification	Clades with heteromorphic and variable systems diversify faster.	Map standardized heteromorphy and turnover characters onto phylogenies fit SSEs.

***Figure 3*:** A summary of models of sex chromosome evolution discussed in this review, and predictions from these models that are testable using phylogenomic approaches. An initial draft of this figure was generated by Claude Cowork from the manuscript text and was then manually vetted and edited.

5. Conclusions

The tremendous variation of reproductive and sexual systems in plants has long served as a valuable resource for addressing fundamental questions in evolution. With high-quality genome sequencing and assembly now available for non-model organisms, this variation can now serve to

answer questions that require genome-scale datasets, particularly relating to the evolution of dioecy and chromosomal sex determination. By pairing these phylogenomic datasets with new methodological advances that can reconstruct the history of genetic processes like recombination, introgression, chromosomal rearrangement, and gene regulation, plant biologists will gain an unprecedented understanding of what forces shape speciation, phenotypic diversification, and the evolution of sex determination.

Literature Survey Materials & Methods

To better understand the current state of research into plant sex chromosome systems, we conducted a literature survey. Our survey was focused on 1) clade-level relationships, such that individual entries correspond to at least one independent origin of sex chromosomes 2) systems in which some form of published genome-scale data is available. Our survey is intended primarily as qualitative examination of trends in the literature, rather than an explicit statistically rigorous meta-analysis, and reports information with variable levels of data quality and precision.

For each system, we recorded the name of the clade and the reported sex chromosome systems within that clade. For age estimates, we reported explicit estimates of the age of the sex-determining region (SDR) when they were available. When not available, we used the estimated age of the parent and daughter nodes of the branch from which the sex chromosome system was most likely to have arisen, based on parsimony, to place upper and lower bounds on the age of the system. For gene loss, we used estimates of percent gene loss when provided, and also included qualitative descriptions of the degree of degeneration of sex chromosomes.

For structure (heteromorphic vs. homomorphic), we used explicit descriptions of sex chromosome systems as one of these types when available, but also assigned some of these systems to categories ourselves, based on descriptions of the size of the sex-determining region and degree of differentiation between sex chromosomes. Systems with approximately equal-sized X/Y or Z/W chromosomes, and/or with sex-determining regions that span a relatively small proportion of the chromosome, were generally described as homomorphic. For turnovers, we applied the definition described in the main text of the manuscript: any karyotypically significant shift in the size and/or configuration of an existing sex chromosome system.

Life history and ploidy information was obtained from a combination of horticultural / agricultural sources and peer-reviewed manuscripts.

Acknowledgements

This work was supported by an NSERC Postdoctoral Fellowship awarded to M.S.H., and by startup funds provided to M.S.H. by the University of Rochester.

Generative AI statement: Claude Cowork with Opus 5 was used to aid the creation of Figures 2B-D and 3. Claude Cowork was also used to help identify some of the sources for our literature review, which were then verified manually and from which survey data was collected manually. None of the manuscript text was generated with AI, with the exception of the table text in Figure 3, which was generated directly from the original manuscript text using Claude Cowork and then manually vetted and edited.

References

Abraham, A., Mathew, P.M. 1962. Cytological studies in the cycads: sex chromosomes in *Cycas*. *Annals of Botany* 26(2): 261-266. https://doi.org/10.1093/oxfordjournals.aob.a083792

Ahmed, S., Cock, J.M., Pessia, E., Luthringer, R., Cormier, A., Robuchon, M., … Coelho, S.M. 2014. A haploid system of sex determination in the brown alga *Ectocarpus sp. Current Biology* 24(17): 1945-1957. https://doi.org/10.1016/j.cub.2014.07.042

Akagi, T., Henry, I.M., Tao, R., Comai, L. 2014. A Y-chromosome-encoded small RNA acts as a sex determinant in persimmons. *Science* 346(6209): 646-650. https://doi.org/10.1126/science.1257225

Akagi, T., Pilkington, S.M., Varkonyi-Gasic, E., Henry, I.M., Sugano, S.S., Sonoda, M., … Tao, R. 2019. Two Y-chromosome-encoded genes determine sex in kiwifruit. *Nature Plants* 5(8): 801-809. https://doi.org/10.1038/s41477-019-0489-6

Akagi, T., Shirasawa, K., Nagasaki, H., Hirakawa, H., Tao, R., Comai, L., Henry, I.M. 2020. The persimmon genome reveals clues to the evolution of a lineage-specific sex determination system in plants. *PLoS Genetics* 16(2): e1008566. https://doi.org/10.1371/journal.pgen.1008566

Akagi, T, Varkonyi-Gasic, E., Shirasawa, K., Catanach, A., Henry, I.M., Mertten, D., … Kataoka, I. 2023. Recurrent neo-sex chromosome evolution in kiwifruit. *Nature Plants* 9: 393-402. https://doi.org/10.1038/s41477-023-01361-9

Al-Dossary, O., Alsubaie, B., Kharabian-Masouleh, A., Al-Mssallem, I., Furtado, A., Henry, R.J. 2021. The jojoba genome reveals wide divergence of the sex chromosomes in a dioecious plant. *The Plant Journal* 108(5): 1283-1294. https://doi.org/10.1111/tpj.15509

Amarasinghe, S.L., Su, S., Dong, X., Zappia, L., Ritchie, M.E., Gouil, Q. 2020. Opportunities and challenges in long-read sequencing data analysis. *Genome Biology* 21(30). https://doi.org/10.1186/s13059-020-1935-5

Avia, K., Lipinska, A.P., Mignerot, L., Montecinos, A.E., Jamy, M., Ahmed, S., … Coelho, S.M. 2018. Genetic diversity in the UV sex chromosomes of the brown alga *Ectocarpus*. *Genes* 9(6): 286. https://doi.org/10.3390/genes9060286

Bachtrog, D. 2013. Y-chromosome evolution: emerging insights into processes of Y-chromosome degeneration. *Nature Reviews Genetics* 14: 113-124. https://doi.org/10.1038/nrg3366

Bachtrog, D., Kirkpatrick, M., Mank, J.E., McDaniel, S.F., Pires, J.C., Rice, W., Valenzuela, N. 2011. Are all sex chromosomes created equal? *Trends in Genetics* 27(9): 350-357. https://doi.org/10.1016/j.tig.2011.05.005.

Bachtrog, D., Mank, J.E., Peichel, C.L., Kirkpatrick, M., Otto, S.P., Ashman, T.L., … Vamosi, J.C. 2014. Sex determination: why so many ways of doing it? *PLoS Biology* 12(7): e1001899. https://doi.org/10.1371/journal.pbio.1001899

Bačovský, V., Čegan, R., Šimoníková, D., Hřibová, E., Hobza, R. 2020. The formation of sex chromosomes in *Silene latifolia* and *S. dioica* was accompanied by multiple chromosomal rearrangements. *Frontiers in Plant Science* 11: 205. https://doi.org/10.3389/fpls.2020.00205

Bai, Q., Ma, Z., Zhang, Y., Su, S., Leng, P. 2019. The sex expression and sex determining mechanism in *Pistacia* species. *Breeding Science* 69(2): 205-214. https://doi.org/10.1270/jsbbs.18167

Baránková, S., Pascual-Díaz, J.P., Sultana, N., Alonso-Lifante, M.P., Balant, M., Barros, K., … Garcia, S. 2020. Sex-chrom, a database on plant sex chromosomes. *New Phytologist* 227(6): 1594-1604. https://doi.org/10.1111/nph.16635

Beaudry, F.E.G., Barrett, S.C.H., Wright, S.I. 2020. Ancestral and neo-sex chromosomes contribute to population divergence in a dioecious plant. *Evolution* 74(2): 256-269. https://doi.org/10.1111/evo.13892

Beaudry, F.E.G., Rifkin, J.L., Peake, A.L., Kim, D., Jarvis-Cross, M., Barrett, S.C.H., Wright, S.I. 2022. Effects of the neo-X chromosome on genomic signatures of hybridization in *Rumex hastatulus*. *Molecular Ecology* 31(13): 3708-3721. https://doi.org/10.1111/mec.16496

Bergero, R., Forrest, A., Kamau, E., Charlesworth, D. 2007. Evolutionary strata on the X chromosomes of the dioecious plant *Silene latifolia*: evidence from new sex-linked genes. *Genetics* 175(4): 1945-1954. https://doi.org/10.1534/genetics.106.070110

Blaser, O., Grossen, C., Neuenschwander, S., Perrin, N. 2013. Sex-chromosome turnovers induced by deleterious mutation load. *Evolution* 67(3): 635-645. https://doi.org/10.1111/j.1558-5646.2012.01810.x

Blaser, O., Neuenschwander, S., Perrin, N. 2014. Sex-chromosome turnovers: the hot-potato model. *The American Naturalist* 183(1): 140-146. https://doi.org/10.1086/674026

Branco, C., Roxo, G., Chapoix, I., Rego, R.M.C., Tessarotto, H., Santoni, S., Moura, M., Marais, G.A.B. 2025. An XY chromosome system in *Laurus azorica*, an endemic dioecious laurel from the Azores. *Journal of Evolutionary Biology* 38(7): 1008-1015. https://doi.org/10.1093/jeb/voaf032

Brazier, T., Glémin, S. 2022. Diversity and determinants of recombination landscapes in flowering plants. *PLoS Genetics* 18(8): e1010141. https://doi.org/10.1371/journal.pgen.1010141

Brothers, A.N., Delph, L.F. 2010. Haldane's rule is extended to plants with sex chromosomes. *Evolution* 64(12): 3643-3648. https://doi.org/10.1111/j.1558-5646.2010.01095.x

Bull, J.J. 1983. Evolution of sex determining mechanisms. Menlo Park, CA: Benjamin Cummings.

Bull, J.J., Charnov, E.L. Changes in the heterogametic mechanism of sex determination. *Heredity* 39: 1-14. https://doi.org/10.1038/hdy.1977.38

Carey, S.B., Aközbek, L., Lovell, J.T., Jenkins, J., Healey, A.L., Shu, S., … Harkess, A. 2024. ZW sex chromosome structure in *Amborella trichopoda*. *Nature Plants* 10: 1944-1954. https://doi.org/10.1038/s41477-024-01858-x

Carey, S.B., Jenkins, J., Lovell, J.T., Maumus, F., Sreedasyam, A., Payton, A.C., … McDaniel, S.F. 2021. Gene-rich UV sex chromosomes harbor conserved regulators of sexual development. *Science Advances* 7(27): eabh2488. https://doi.org/10.1126/sciadv.abh2488

Cauret, C.M.S., Mortimer, S.M.E., Roberti, M.C., Ashman, T.L., Liston, A. 2022. Chromosome-scale assembly with a phased sex-determining region resolves features of early Z and W chromosome differentiation in a wild octoploid strawberry. *G3 Genes|Genomes|Genetics* 12(8): jkac139. https://doi.org/10.1093/g3journal/jkac139

Charlesworth, B. 1978. Model for evolution of Y chromosomes and dosage compensation. *Proceedings of the National Academy of Sciences* 75(11): 5618-5622. https://doi.org/10.1073/pnas.75.11.5618

Charlesworth, B. 1996. The evolution of chromosomal sex determination and dosage compensation. *Current Biology* 6: 149-162. https://doi.org/10.1016/S0960-9822(02)00448-7

Charlesworth, B., Campos, J.L., Jackson, B.C. 2018. Faster-X evolution: theory and evidence from *Drosophila*. *Molecular Ecology* 27(19): 3753-3771. https://doi.org/10.1111/mec.14534

Charlesworth, B., Charlesworth, D. 1978*a*. A model for the evolution of dioecy and gynodioecy. *The American Naturalist* 112(988): 975-997. https://doi.org/10.1086/283342

Charlesworth, B., Charlesworth, D. 1978*b*. Population genetics of partial male-sterility and the evolution of monoecy and dioecy. *Heredity* 41: 137-153. https://doi.org/10.1038/hdy.1978.83

Charlesworth, B., Charlesworth, D. 2000. The degeneration of Y chromosomes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 355(1403): 1563-1572. https://doi.org/10.1098/rstb.2000.0717

Charlesworth, B., Olito, C. 2024. Making sense of recent models of the "sheltering" hypothesis for recombination arrest between sex chromosomes. *Evolution* 78(12): 1891-1899. https://doi.org/10.1093/evolut/qpae119

Charlesworth, B., Wall, J.D. 1999. Inbreeding, heterozygote advantage and the evolution of neo-X and neo-Y sex chromosomes. *Proceedings of the Royal Society B: Biological Sciences* 266(1414): 51-56. https://doi.org/10.1098/rspb.1999.0603

Charlesworth, D. 2002. Plant sex determination and sex chromosomes. *Heredity* 88: 94-101. https://doi.org/10.1038/sj.hdy.6800016

Charlesworth, D. 2012. Plant sex chromosome evolution. *Journal of Experimental Botany* 64(2): 405-420. https://doi.org/10.1093/jxb/ers322

Charlesworth, D. 2015. Plant contributions to our understanding of sex chromosome evolution. *New Phytologist* 208(1): 52-65. https://doi.org/10.1111/nph.13497

Charlesworth, D. 2016. Plant sex chromosomes. *Annual Review of Plant Biology* 67: 397-420. https://doi.org/10.1146/annurev-arplant-043015-111911

Charlesworth, D. 2019. Young sex chromosomes in plants and animals. *New Phytologist* 224(3): 1095-1107. https://doi.org/10.1111/nph.16002

Charlesworth, D. 2022. The mysterious sex chromosomes of haploid plants. *Heredity* 129: 17-21. https://doi.org/10.1038/s41437-022-00524-2

Charlesworth, D., Charlesworth, B. 1980. Sex differences in fitness and selection for centric fusions between sex-chromosomes and autosomes. *Genetics Research* 35(2): 205-214. https://doi.org/10.1017/S0016672300014051

Charlesworth, D., Charlesworth, B., Marais, G. 2005. Steps in the evolution of heteromorphic sex chromosomes. *Heredity* 95(2): 118-128. https://doi.org/10.1038/sj.hdy.6800697

Charnov, E., Bull, J., Maynard Smith, J. 1976. Why be an hermaphrodite? *Nature* 263: 125-126. https://doi.org/10.1038/263125a0

Chen, M., Yang, X., Xun, L., Qu, Z., Yang, S., Yang, Y., Yang, Y. 2025. The genome of *Hippophae salicifolia* provides new insights into the sexual differentiation of sea buckthorn. *GigaScience* 14: giaf046. https://doi.org/10.1093/gigascience/giaf046

Cherif, E., Zehdi-Azouzi, S., Crabos, A., Castillo, K., Chabrillange, N., Pintaud, J.C., … Aberlenc-Bertossi, F. 2016. Evolution of the sex chromosomes prior to speciation in the dioecious *Phoenix* species. *Journal of Evolutionary Biology* 29(8): 1513-1522. https://doi.org/10.1111/jeb.12887

Choi, K., Zhao, X., Tock, A.J., Lambing, C., Underwood, C.J., Hardcastle, T.J., … Henderson, I.R. 2018. Nucleosomes and DNA methylation shape meiotic DSB frequency in *Arabidopsis thaliana* transposons and gene regulatory regions. *Genome Research* 28(4): 532-546. https://doi.org/10.1101/gr.225599.117

Coelho, S.M., Gueno, J., Lipinska, A.P., Cock, J.M., Umen, J.G. 2018. UV chromosomes and haploid sexual systems. *Trends in Plant Science* 23(9): 794-807. https://doi.org/10.1016/j.tplants.2018.06.005

Cormier, F., Lawac, F., Maledon, E., Gravillon, M.C., Nudol, E., Mournet, P., … Arnau, G. 2019. A reference high-density genetic map of greater yam (*Dioscorea alata* L.). *Theoretical and Applied Genetics* 132: 1733-1744. https://doi.org/10.1007/s00122-019-03311-6

Coster, W.D., Weissensteiner, M.H., Sedlazeck, F.J. 2021. Towards population-scale long-read sequencing. *Nature Reviews Genetics* 22: 572-587. https://doi.org/10.1038/s41576-021-00367-3

Cowell, F. 2023. 100 years of Haldane's rule. *Journal of Evolutionary Biology* 36(2): 337-346. https://doi.org/10.1111/jeb.14112

Coyne, J.A., 1992. Genetics and speciation. *Nature* 355(6360): 511-515. https://doi.org/10.1038/355511a0

Coyne, J.A., Orr, H.A. 1989. Two rules of speciation. In: Otte, D., Endler, J., editors. Speciation and its consequences. Sunderland (Massachusetts): Sinauer Associates. pp. 180-207.

Crowson, D., Barrett, S.C.H., Wright, S.I. 2017. Purifying and positive selection influence patterns of gene loss and gene expression in the evolution of a plant sex chromosome system. *Molecular Biology and Evolution* 34(5): 1140-1154. https://doi.org/10.1093/molbev/msx064

Cuñado, N., Navajas-Pérez, R., de la Herrán, R., Rejón, C.R., Santos, J.L., Garrido-Ramos, M.A. 2007. The evolution of sex chromosomes in the genus *Rumex* (Polygonaceae): identification of a new species with heteromorphic sex chromosomes. *Chromosome Research* 15: 825-833. https://doi.org/10.1007/s10577-007-1166-6

Dagilis, A.J., Sardell, J.M., Josephson, M.P., Su, Y., Kirkpatrick, M., Peichel, C.L. Searching for signatures of sexually antagonistic selection on stickleback sex chromosomes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 377(1856): 20210205. https://doi.org/10.1098/rstb.2021.0205

De Waal Malefijt, M., Charlesworth, B. 1979. A model for the evolution of translocation heterozygosity. *Heredity* 43: 315-331. https://doi.org/10.1038/hdy.1979.85

Dufay, M., Champelovier, P., Käfer, J., Henry, J.P., Mousset, S., Marais, G.A.B. 2014. An angiosperm-wide analysis of the gynodioecy-dioecy pathway. *Annals of Botany* 114(3): 539-548.

van Doorn, G.S., Kirkpatrick, M. 2007. Turnover of sex chromosomes induced by sexual conflict. *Nature* 449(7164): 909-912. https://doi.org/10.1038/nature06178

van Doorn, G.S., Kirkpatrick, M. 2010. Transitions between male and female heterogamety caused by sex-antagonistic selection. *Genetics* 186(2): 629-645. https://doi.org/10.1534/genetics.110.118596

Ferris, P., Olson, B.J.S.C., de Hoff, P.L., Douglass, S., Casero, D., Prochnik, S., … Umen, J.G. 2010. Evolution of an expanded sex-determining locus in *Volvox*. *Science* 328(5976): 351-354. https://doi.org/10.1126/science.1186222

Fruchard, C., Badouin, H., Latrasse, D., Devani, R.S., Muyle, A., Rhoné, B., … Marais, G.A.B. 2020. Evidence for dosage compensation in *Coccinia grandis,* a plant with a highly heteromorphic XY system. *Genes* 11(7): 787. https://doi.org/10.3390/genes11070787

Fu, Y., Zhang, X., Zhang, T., Sun, W., Yang, W., Shi, Y., … Xu, B. 2025. Evidence for evolution of a new sex chromosome within the haploid-dominant Marchantiales plant lineage. *Journal of Integrative Plant Biology*. https://doi.org/10.1111/jipb.13867

Fujito, S., Takahata, S., Suzuki, R., Hoshino, Y., Ohmido, N., Onodera, Y. 2015. Evidence for a common origin of homomorphic and heteromorphic sex chromosomes in distinct *Spinacia* species. *G3 Genes|Genomes|Genetics* 5(8): 1663-1673. https://doi.org/10.1534/g3.115.018671

Geraldes, A., Hefer, C.A., Capron, A., Kolosova, N., Martinez-Nuñez, F., Soolanayakanahally, R.Y., … Cronk, Q.C.B. 2015. Recent Y chromosome divergence despite ancient origin of dioecy in poplars (*Populus*). *Molecular Ecology* 24(13): 3243-3256. https://doi.org/10.1111/mec.13126

Gerchen, J.F., Veltsos, P., Pannell, J.R. 2022. Recurrent allopolyploidization, Y-chromosome introgression and the evolution of sexual systems in the plant genus *Mercurialis*. *Philosophical Transactions of the Royal Society B: Biological Sciences* 377: 20210224. https://doi.org/10.1098/rstb.2021.0224

Gibson, J.R., Chippindale, A.K., Rice, W.R. 2002. The X chromosome is a hot spot for sexually antagonistic fitness variation. *Proceedings of the Royal Society B: Biological Sciences* 269(1490): 499-505. https://doi.org/10.1098/rspb.2001.1863

Gong, W., Filatov, D.A. 2022. Evolution of the sex-determining region in *Gingko biloba*. *Philosophical Transactions of the Royal Society B: Biological Sciences* 377(1850): 20210229. https://doi.org/10.1098/rstb.2021.0229

Grant, K.D., Koenemann, D., Mansaray, J., Ahmed, A., Khamar, H., Oualidi, J.E., Burke, J.M. 2022. A new phylogeny of *Rumex* (*Polygonaceae*) adds evolutionary context to the diversity of reproductive systems present in the genus. *PhytoKeys* 204: 57-72. https://doi.org/10.3897/phytokeys.204.85256

Graves, J.A.M. 2016. Evolution of vertebrate sex chromosomes and dosage compensation. *Nature Reviews Genetics* 17: 33-46. https://doi.org/10.1038/nrg.2015.2

Guo, L., Bloom, J.S., Dols-Serrate, D., Boocock, J., Ben-David, E., Schubert, O.T., … Kruglyak, L. 2022. Island-specific evolution of a sex-primed autosome in a sexual planarian. *Nature* 606: 329-334. https://doi.org/10.1038/s41586-022-04757-3

Haenel, Q., Laurentino, T.G., Roesti, M., Berner, D. 2018. Meta-analysis of chromosome-scale crossover rate variation in eukaryotes and its significance to evolutionary genomics. *Molecular Ecology* 27(11): 2477-2497. https://doi.org/10.1111/mec.14699

Haldane, J.B.S. 1922. Sex-ratio and unisexual sterility in hybrid animals. *Journal of Genetics* 12(2): 101-109. https://doi.org/10.1007/bf02983075

Hall, D.W. 2004. Meiotic drive and sex chromosome cycling. *Evolution* 58(5): 925-931. https://doi.org/10.1111/j.0014-3820.2004.tb00426.x

Handley, L.J.L., Ceplitis, H., Ellegren H. 2004. Evolutionary strata on the chicken Z chromosome: implications for sex chromosome evolution. *Genetics* 167(1): 367-376. https://doi.org/10.1534/genetics.167.1.367

Harkess, A., Huang, K., der Hulst, R.V., Tissen, B., Caplan, J.L., Koppula, A., … Leebens-Mack, J. 2020. Sex determination by two Y-linked genes in garden asparagus. *The Plant Cell* 32(6): 1790-1796. https://doi.org/10.1105/tpc.19.00859

Harkess, A., Zhou, J., Xu, C., Bowers, J.E., der Hulst, R.V., Ayyampalayam, S., … Chen, G. 2017. The asparagus genome sheds light on the origin and evolution of a young Y chromosome. *Nature Communications* 8: 1279. https://doi.org/10.1038/s41467-017-01064-8

He, L., Guo, F.Y., Cai, X.J., Chen, H.P., Lian, C.L., Wang, Y., … Wang, X.R. 2023. Evolutionary origin and establishment of a dioecious diploid-tetraploid complex. *Molecular Ecology* 32(11): 2732-2749. https://doi.org/10.1111/mec.16902

He, L., Hörandl, E. 2022. Does polyploidy inhibit sex chromosome evolution in angiosperms? *Frontiers in Plant Science* 13: 976765. https://doi.org/10.3389/fpls.2022.976765

He, Y., Wang, M., Dukowic-Schulze, S., Zhou, A., Tiang, C.L., Shilo, S., … Pawlowski, W.P. 2017. Genomic features shaping the landscape of meiotic double-strand-break hotspots in maize. *Proceedings of the National Academy of Sciences* 114(46): 12231-12236. https://doi.org/10.1073/pnas.1713225114

He, L., Wang, Y., Wang, Y., Zhang, R.G., Wang, Y., Hörandl, E., … Ming, R. 2024. Allopolyplodization from two dioecious ancestors leads to recurrent evolution of sex chromosomes. *Nature Communications* 15: 6893. https://doi.org/10.1038/s41467-024-51158-3

Healey, A.L., Piatkowski, B., Lovell, J.T., Sreedasyam, A., Carey, S.B., Mamidi, S., … Shaw, A.J. 2023. Newly identified sex chromosomes in the *Sphagnum* (peat moss) genome alter carbon sequestration and ecosystem dynamics. *Nature Plants* 9: 238-254. https://doi.org/10.1038/s41477-022-01333-5

Heilbuth, J.C. Lower species richness in dioecious clades. *The American Naturalist* 156(3): 221-241. https://doi.org/10.1086/303389

Hibbins, M.S., Rifkin, J.L., Choudhury, B.I., Voznesenka, O., Sacchi, B., Yuan, M., Gong, Y., Barrett, S.C.H., Wright, S.I. 2025a. Phylogenomics resolves key relationships in *Rumex* and uncovers a dynamic history of independently evolving sex chromosomes. *Evolution Letters* 9(2): 221-235. https://doi.org/10.1093/evlett/qrae060

Hibbins, M.S., Pyne, C., Sukmaniuk, M., Glasgow, E., Yuan, M., Gong, Y., Barrett, S.C.H., Wright, S.I. 2025b. Rapid evolution of synteny associated with multiple origins of dioecy and XY sex determination. *BioRxiv*. https://doi.org/10.64898/2025.12.21.695719

Horiuchi, A., Masuda, K., Shirasawa, K., Onoue, N., Fujita, N., Ushijima, K., Akagi, T. 2023. Ongoing rapid evolution of a post-Y region revealed by chromosome-scale genome assembly of a hexaploid monoecious persimmon (*Diospyros kaki*). *Molecular Biology and Evolution* 40(7): msad151. https://doi.org/10.1093/molbev/msad151

Hou, J., Ye., N., Zhang, D., Chen, Y., Fang, L., Dai, X., Yin, T. 2015. Different autosomes evolved into sex chromosomes in the sister genera of *Salix* and *Populus*. *Scientific Reports* 5: 9076. https://doi.org/10.1038/srep09076

Howell, E.C., Armstrong, S.J., Filatov, D.A. 2009. Evolution of neo-sex chromosomes in *Silene diclinis*. *Genetics* 182(4): 1109-1115. https://doi.org/10.1534/genetics.109.103580

Hu, X.S., Filatov, D.A. The large-X effect in plants: increased species divergence and reduced gene flow on the *Silene* X-chromosome. *Molecular Ecology* 25(11): 2609-2619. https://doi.org/10.1111/mec.13427

Hu, N., Sanderson, B.J., Guo, M., Feng, G., Gambhir, D., Hale, H., … Olson, M.S. 2023. Evolution of a ZW sex chromosome system in willows. *Nature Communications* 14: 7144. https://doi.org/10.1038/s41467-023-42880-5

Ironside, J.E. 2010. No amicable divorce? Challenging the notion that sexual antagonism drives sex chromosome evolution. *BioEssays* 32(8): 718-726. https://doi.org/10.1002/bies.200900124

Iwasaki, M., Kajiwara, T., Yasiu, Y., Yoshitake, Y., Miyazaki, M., Kawamura, S., … Kohchi, T. 2021. Identification of the sex-determining factor in the liverwort *Marchantia polymorpha* reveals unique evolution of sex chromosomes in a haploid system. *Current Biology* 31(24): 5522-5532. https://doi.org/10.1016/j.cub.2021.10.023

Janousek, B., Gogela, R., Bacovsky, V., Renner, S.S. 2022. The evolution of huge Y chromosomes in *Coccinia grandis* and its sister, *Coccinia schimperi*. *Philosophical Transactions of the Royal Society B: Biological Sciences* 377(1850): 20210294. https://doi.org/10.1098/rstb.2021.0294

Jay, P., Véber, A., Giraud, T. 2025. Stepwise expansion of recombination suppression on sex chromosomes and other supergenes through lower load advantage and deleterious mutation sheltering. *BioRxiv*. https://doi.org/10.1101/2025.06.27.661902

Jeffries, D.L., Gerchen, J.F., Scharmann, M., Pannell, J.R. 2021. A neutral model for the loss of recombination on sex chromosomes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 376(1832): 20200096. https://doi.org/10.1098/rstb.2020.0096

Jia, H.M., Jia, H.J., Cai, Q.L., Wang, Y., Zhao, H.B., Yang, W.F., … Gao, Z.S. 2018. The red bayberry genome and genetic basis of sex determination. *Plant Biotechnology Journal* 17(2): 397-409. https://doi.org/10.1111/pbi.12985

Jung, H., Winefield, C., Bombarely, A., Prentis, P., Waterhouse, P. 2019. Tools and strategies for long-read sequencing and *de novo* assembly of plant genomes. *Trends in Plant Science* 24(8): 700-724. https://doi.org/10.1016/j.tplants.2019.05.003 \

Käfer, J. de Boer, H.J., Mousset, S., Kool, A., Dufay, M., Marais, G.A.B. 2014. Dioecy is associated with higher diversification rates in flowering plants. *Journal of Evolutionary Biology* 27(7): 1478-1490. https://doi.org/10.1111/jeb.12385

Käfer, J., Marais, G.A.B., Pannell, J.R. 2017. On the rarity of dioecy in flowering plants. *Molecular Ecology* 26(5): 1225-1241. https://doi.org/10.1111/mec.14020

Käfer, J., Bewick, A., Andres-Robin, A., Lapetoule, G., Harkess, A., Caïus, J., … Leebens-Mack, J. 2022. A derived ZW chromosome system in *Amborella trichopoda*, representing the sister lineage to all other extant flowering plants. *New Phytologist* 233(4): 1636-1624. https://doi.org/10.1111/nph.17662

Kafkas, S., Ma, X., Zhang, X., Topçu, H., Navajas-Pérez, R., Wai, C.M., … Ming, R. 2022. Pistachio gneomes provide insights into nut tree domestication and ZW sex chromosome evolution. *Plant Communications* 4(3): 100497. https://doi.org/10.1016/j.xplc.2022.100497

Kasjaniuk, M., Grabowska-Joachimiak, A., Joachimiak, A.J. 2019. Testing the translocation hypothesis and Haldane's rule in *Rumex hastatulus*. *Protoplasma* 256: 237-247. https://doi.org/10.1007/s00709-018-1295-0

Kent, T.V., Uzunović, J., Wright, S.I. 2017. Coevolution between transposable elements and recombination. *Philosophical Transcations of the Royal Society B: Biological Sciences* 372(1736): 20160458. https://doi.org/10.1098/rstb.2016.0458

Kim, B.Y., Huber, C.D., Lohmueller, K.E. 2018. Deleterious variation shapes the genomic landscape of introgression. *PLoS Genetics* 14(10): e1007741. https://doi.org/10.1371/journal.pgen.1007741

Kirkpatrick, M., Barton, N. 2006. Chromosome inversions, local adaptation and speciation. *Genetics* 173(1): 419-434. https://doi.org/10.1534/genetics.105.047985

Kozielska, M., Weissing, F.J., Beukeboom, L.W., Pen, I. 2010. Segregation distortion and the evolution of sex-determining mechanisms. *Heredity* 104: 100-112. https://doi.org/10.1038/hdy.2009.104

Krasovec, M., Chester, M., Ridout, K., Filatov, D.A. 2018. The mutation rate and the age of the sex chromosomes in *Silene latifolia*. *Current Biology* 28(11): 1832-1838. https://doi.org/10.1016/j.cub.2018.04.069

Krasovec, M., Kazama, Y., Ishii, K., Abe, T., Filatov, D.A. 2019. Immediate dosage compensation is triggered by the deletion of Y-linked genes in *Silena latifolia*. *Current Biology* 29(13): 2214-2221. https://doi.org/10.1016/j.cub.2019.05.060

Laenen, B., Machac, A., Gradstein, S.R., Shaw, B., Patiño, J., Désamoré, A., … Vanderpoorten, A. 2016. Increased diversification rates follow shifts to bisexuality in liverworts. *New Phytologist* 210(3): 1121-1129. https://doi.org/10.1111/nph.13835

Lahn, B.T., Page, D.C. 1999. Four evolutionary strata on the human X chromosome. *Science* 286(5441): 964-967. https://doi.org/10.1126/science.286.5441.964

Lenormand, T., Fyon, F., Sun, E., Roze, D. 2020. Sex chromosome degeneration by regulatory evolution. *Current Biology* 30(15): 3001-3006. https://doi.org/10.1016/j.cub.2020.05.052

Lenormand, T., Roze, D. 2022. Y recombination arrest and degeneration in the absence of sexual dimorphism. *Science* 375(6581): 663-666. https://doi.org/10.1126/science.abj1813

Lesaffre, T., Pannell, J.R., Mullon, C. 2024. An explanation for the prevalence of XY over ZW sex determination in species derived from hermaphroditism. *Proceedings of the National Academy of Sciences* 121(40): e2406305121. https://doi.org/10.1073/pnas.2406305121

Li, Y., Wang, D., Wang, W., Yang, W., Gao, J., Zhang, W., … Ma, T. 2023. A chromosome-level *Populus qiongdaeoensis* genome assembly provides insights into tropical adaptation and a cryptic turnover of sex determination. *Molecular Ecology* 32(6): 1366-1380. https://doi.org/10.1111/mec.16566

Liao, Q., Du, R., Gou, J., Guo, L., Shen, H., Liu, H., … Yan, J. 2020. The genomic architecture of the sex-determining region and sex-related metabolic variation in *Ginkgo biloba*. *The Plant Journal* 104(5): 1399-1409. https://doi.org/10.1111/tpj.15009

Liu, J., Han, J., Sharma, A., Wai, C.M., Ming, R., Yu, Q. 2021. Transcriptional regulation of dosage compensation in *Carica papaya*. *Scientific Reports* 11: 5854. https://doi.org/10.1038/s41598-021-85480-3

Liu, Z., Moore, P.H., Ma, H., Ackerman, C.M., Ragiba, M., Yu, Q., … Ming, R. 2004. A primitive Y chromosome in papaya marks incipient sex chromosome evolution. *Nature* 427: 348-352. https://doi.org/10.1038/nature02228

Liu, Y., Wang, S., Li, L., Yang, T., Dong, S., Wei, T., … Zhang, S. 2022. The *Cycas* genome and the early evolution of seed plants. *Nature Plants* 8: 389-401. https://doi.org/10.1038/s41477-022-01129-7

Lloyd, D.G. 1980. The distributions of gender in four angiosperm species illustrating two evolutionary pathways to dioecy. *Evolution* 34(11): 123-134. https://doi.org/10.2307/2408321

Lu, X.M., Yu, X.F., Li, G.Q., Qu, M.H., Wang, H., Liu, C., … Wang, Y.C. 2024. Genome assembly of autotetraploid *Actinidia arguta* highlights adaptive evolution and enables dissection of important economic traits. *Plant Communications* 5(6): 100856. https://doi.org/10.1016/j.xplc.2024.100856

Lund-Hansen, K.K., Olito, C., Morrow, E.H., Abbott, J.K. 2021. Sexually antagonistic coevolution between the sex chromosomes of *Drosophila melanogaster*. *Proceedings of*

the National Academy of Sciences 118(8): e2003359118. https://doi.org/10.1073/pnas.2003359118

Luthringer, R., Lipinska, A.P., Roze, D., Cormier, A., Macaisne, N., Peters, A.F., Cock, J.M., Coelho, S.M. 2015. The pseudoautosomal regions of the U/V sex chromosomes of the brown alga *Ectocarpus* exhibit unusual features. *Molecular Biology and Evolution* 32(11): 2973-2985. https://doi.org/10.1093/molbev/msv173

Ma, X., Yu, L., Fatima, M., Wadlington, W.H., Hulse-Kemp, A.M., Zhang, X., … Ming, R. 2022. The spinach YY genome reveals sex chromosome evolution, domestication, and introgression history of the species. *Genome Biology* 23: 75. https://doi.org/10.1186/s13059-022-02633-x

Mank, J.E., Vicoso, B., Berlin, S., Charlesworth, B. 2010. Effective population size and the faster-X effect: empirical results and their interpretation. *Evolution* 64(3): 663-647. https://doi.org/10.1111/j.1558-5646.2009.00853.x

Mao, X., Rafati, N., Tellgren-Roth, C., Ingvarsson, P.K., Karrenberg, S. 2026. Sex chromosome evolution mediated by a large inversion and a possible switch of the sex determination gene. *Genome Biology* 27:120. https://doi.org/10.1186/s13059-026-04038-6

Marín, I., Siegal, M.L., Baker, B.S. 2000. The evolution of dosage-compensation mechanisms. *BioEssays* 22(12): 1106-1114. https://doi.org/10.1002/1521-1878(200012)22:12<1106::AID-BIES8>3.0.CO;2-W

Martin, H., Carpentier, F., Gallina, S., Godé, C., Schmitt, E., Muyle, A., Marais, G.A.B., Touzet, P. 2019. Evolution of young sex chromosomes in two dioecious sister plant species with distinct sex determination systems. *Genome Biology and Evolution* 11(2): 350-361. https://doi.org/10.1093/gbe/evz001

Martin, S.H., Davey, J.W., Salazar, C., Jiggins, C.D. 2019. Recombination rate variation shapes barriers to introgression across butterfly genomes. *PLoS Biology* 17(2): e2006288. https://doi.org/10.1371/journal.pbio.2006288

Massonenet, M., Cochetel, N., Ricciardi, V., Minio, A., Figueroa-Balderas, R., Londo, J.P., Cantu, D. 2025. Evolutionary conservation of the grape sex-determining region in angiosperms and emergence of dioecy in Vitaceae. *Nature Communications* 16: 6047. https://doi.org/10.1038/s41467-025-61387-9

McDaniel, S.F., Atwood, J., Burleigh, J.G. 2012. Recurrent evolution of dioecy in bryophytes. *Evolution* 67(2): 567-572. https://doi.org/10.1111/j.1558-5646.2012.01808.x

Meisel, R.P., Connallon, T. 2013. The faster-X effect: integrating theory and data. *Trends in Genetics* 29(9): 537-544. https://doi.org/10.1016/j.tig.2013.05.009

Meyer, E.M., Rosenberg, M.S., Boyd, B.M., Eckert, A.J. 2026. Traits and hidden states; is self-fertilization associated with rates of diversification across mating and sexual systems? *BioRxiv*. https://doi.org/10.64898/2026.06.18.733044

Michael, T.P., VanBuren, R. 2020. Building near-complete plant genomes. *Current Opinion in Plant Biology* 54: 26-33. https://doi.org/10.1016/j.pbi.2019.12.009

Ming, R., Bendahmane, A., Renner, S.S. 2011. Sex chromosomes in land plants. *Annual Review of Plant Biology* 62: 485-514. https://doi.org/10.1146/annurev-arplant-042110-103914

Ming, R., Wang, J., Moore, P.H., Paterson, A.H. 2007. Sex chromosomes in flowering plants. *American Journal of Botany* 94(2): 141-150. https://doi.org/10.3732/ajb.94.2.141

Montgomery, J.S., Giacomini, D.A., Weigel, D., Tranel, P.J. 2020. Male-specific Y-chromosomal regions in waterhemp (*Amaranthus tuberculatus*) and Palmer amaranth (*Amaranthus palmeri*). *New Phytologist* 229(6): 3522-3533. https://doi.org/10.1111/nph.17108

Moraga, C., Branco, C., Rougemont, Q., Jedlička, P., Mendoza-Galindo, E., Veltsos, P., … Marais, G.A.B. 2025. The *Silene latifolia* genome and its giant Y chromosome. *Science* 387(6734): 630-636. https://doi.org/10.1126/science.adj7430

Muller, H.J. 1925. Why polyploidy is rarer in animals than in plants. *The American Naturalist* 59(663): 346-353. https://doi.org/10.1086/280047

Muralidhar, P. 2026. Chromosome-specific drift under stabilizing selection generates polygenic barriers to sex chromosome turnover. *Proceedings of the National Academy of Sciences* 123(15): e2528925123. https://doi.org/10.1073/pnas.2528925123

Muyle, A., Marais, G.A.B., Bačovský, V., Hobza, R., Lenormand, T. 2022. Dosage compensation evolution in plants: theories, controversies, and mechanisms. *Philosophical Transactions of the Royal Society B: Biological Sciences* 377(1850): 20210222. https://doi.org/10.1098/rstb.2021.0222

Muyle, A., Shearn, R., Marais, G.A.B. 2017. The evolution of sex chromosomes and dosage compensation in plants. *Genome Biology and Evolution* 9(3): 627-645. https://doi.org/10.1093/gbe/evw282

Muyle, A., Zemp, N., Deschamps, C., Mousset, S., Widmer, A., Marais, G.A.B. 2012. Rapid de novo evolution of X chromosome dosage compensation in *Silene latifolia*, a plant with young sex chromosomes. *PLoS Biology* 10(4): e1001308. https://doi.org/10.1371/journal.pbio.1001308

Muyle, A., Zemp, N., Fruchard, C., Cegan, R., Vrana, J., Deschamps, C., … Marais, G.A.B. 2018. Genomic imprinting mediates dosage compensation in a young plant XY system. *Nature Plants* 4: 677-680. https://doi.org/10.1038/s41477-018-0221-y

Neves, C.J., Matzrafi, M., Thiele, M., Lorant, A., Mesgaran, M.B., Stetter, M.G. 2020. Male linked genomic region determines sex in dioecious *Amaranthus palmeri. Journal of Heredity* 111(7): 606-612. https://doi.org/10.1093/jhered/esaa047

Ngwe, F.N., Siljak-Yakovlev, S. 2023. Sex determination in *Dioscorea dumetorum*: evidence of heteromorphic sex chromosomes and sex-linked NORs. *Plants* 12(2): 228. https://doi.org/10.3390/plants12020228

Njuguna, W., Liston, A., Cronn, R., Ashman, T.L., Bassil, N. 2013. Insights into phylogeny, sex function and age of *Fragaria* based on whole chloroplast genome sequencing. *Molecular Phylogenetics and Evolution* 66(1): 17-29. https://doi.org/10.1016/j.ympev.2012.08.026

Obbard, D.J., Harris, S.A., Buggs, R.J.A., Pannell, J.R. 2006. Hybridization, polyploidy, and the evolution of sexual systems in *Mercurialis* (Euphorbiaceae). *Evolution* 60(9): 1801-1815. https://doi.org/10.1554/06-104.1

Orr, H.A. 1990. "Why polyploidy is rarer in animals than in plants" revisited. *The American Naturalist* 136(6): 759-770. https://doi.org/10.1086/285130

Otto, S.P. 2019. Evolutionary potential for genomic islands of sexual divergence on recombining sex chromosomes. *New Phytologist* 224(3): 1241-1251. https://doi.org/10.1111/nph.16083

Palmer, D.H., Rogers, T.F., Dean, R., Wright, A.E. 2019. How to identify sex chromosomes and their turnover. *Molecular Ecology* 28(21): 4709-4724. https://doi.org/10.1111/mec.15245

Papadopulos, A.S.T., Chester, M., Ridout, K., Filatov, D.A. 2015. Rapid Y degeneration and dosage compensation in plant sex chromosomes. *Proceedings of the National Academy of Sciences* 112(42): 13021-13026. https://doi.org/10.1073/pnas.1508454112

Picq, S., Santoni, S., Lacombe, T., Latrielle, M., Weber, A., Ardisson, M., … Bacilieri, R. 2014. A small XY chromosomal region explains sex determination in wild dioecious *V. vinifera* and the reversal to hermaphroditism in domesticated grapevines. *BMC Plant Biology* 14: 229. https://doi.org/10.1186/s12870-014-0229-z

Plath, S., Klocke, E., Nothnagel, T. 2022. Karyological and nuclear DNA content variation of the genus *Asparagus*. *PLOS One* 17(3): e0265405. https://doi.org/10.1371/journal.pone.0265405

Pokorná, M., Kratochvíl, L. 2009. Phylogeny of sex-determining mechanisms in squamate reptiles: are sex chromosomes an evolutionary trap? *Zoological Journal of the Linnean Society* 156(1): 168-183. https://doi.org/10.1111/j.1096-3642.2008.00481.x.

Ponnikas, S., Sigeman, H., Abbott, J.K., Hansson, B. 2018. Why do sex chromosomes stop recombining? *Trends in Genetics* 34(7): 492-503. https://doi.org/10.1016/j.tig.2018.04.001

Prentout, D., Razumova, O., Rhoné, B., Badouin, H., Henri, H., Feng, C, … Marais, G.A.B. 2020. An efficient RNA-seq-based segregation analysis identifies the sex chromosomes of *Cannabis sativa*. *Genome Research* 30: 164-172. https://doi.org/10.1101/gr.251207.119

Prentout, D., Stajner, N., Cerenak, A., Tricou, T., Brochier-Armanet, C., Jakse, J., Käfer, J., Marais, G.A.B. 2021. Plant genera *Cannabis* and *Humulus* share the same pair of well-differentiated sex chromosomes. *New Phytologist* 231(4): 1599-1611. https://doi.org/10.1111/nph.17456

Presgraves, D.C. 2018. Evaluating genomic signatures of "the large-X effect" during complex speciation. *Molecular Ecology* 27(19): 3822-3830. https://doi.org/10.1111/mec.14777

Pucker, B., Irisarri, I., de Vries, J., Xu, B. 2022. Plant genome sequence assembly in the era of long reads: progress, challenges, and future directions. *Quantitative Plant Biology* 3: e5. https://doi.org/10.1017/qpb.2021.18

Raiyemo, D.A., Montgomery, J.S., Cutti, L., Abdollahi, F., Llaca, V., Fengler, K., … Tranel, P.J. 2025. Chromosome-level assemblies of *Amaranthus palmeri*, *Amaranthus retroflexus*, and *Amaranthus hybridus* allow for genomic comparisons and identification of a sex-determining region. *The Plant Journal* 121(4): e70027. https://doi.org/10.1111/tpj.70027

Renner, S.S. 2014. The relative and absolute frequencies of angiosperm sexual systems: dioecy, monoecy, gynodioecy, and an updated online database. *American Journal of Botany* 101(10): 1588-1596. https://doi.org/10.3732/ajb.1400196

Renner, S.S., Müller, N.A. 2021. Plant sex chromosomes defy evolutionary models of expanding recombination suppression and genetic degeneration. *Nature Plants* 7: 392-402. https://doi.org/10.1038/s41477-021-00884-3

Rice, W.R. 1987. The accumulation of sexually antagonistic genes as a selective agent promoting the evolution of reduced recombination between primitive sex chromosomes. *Evolution* 41(4): 911-914. https://doi.org/10.1111/j.1558-5646.1987.tb05864.x

Rice, W.R., 1992. Sexually antagonistic genes: experimental evidence. *Science* 256(5062): 1436-1439. https://doi.org/10.1126/science.1604317

Rice, W.R. 1994. Degeneration of a nonrecombining chromosome. *Science* 263(5144): 230-232. https://doi.org/10.1126/science.8284674.

Rifkin, J.L., Hnatovska, S., Yuan, H., Sacchi, B.M., Choudhury, B.I., Gong, Y., … Wright, S.I. 2022. Recombination landscape dimorphism and sex chromosome evolution in the dioecious plant *Rumex hastatulus*. *Philosophical Transactions of the Royal Society B*: *Biological Sciences* 377(1850): 20210226. https://doi.org/10.1098/rstb.2021.0226

Russell, J.R.W., Pannell, J.R. 2015. Sex determination in dioecious *Mercurialis annua* and its close diploid and polyploid relatives. *Heredity* 114: 262-271. https://doi.org/10.1038/hdy.2014.95

Sabath, N., Goldberg, E.E., Glick, L., Einhorn, M., Ashman, T.L., Ming, R., … Mayrose, I. 2015. Dioecy does not consistently accelerate or slow lineage diversification across multiple genera of angiosperms. *New Phytologist* 209(3): 1290-1300. https://doi.org/10.1111/nph.13696

Sacchi, B., Humphries, Z., Kružlicová, J., Bodláková, M., Pyne, C., Choudhury, B.I., … Wright, S.I. 2024. Phased assembly of neo-sex chromosomes reveals extensive Y degeneration and rapid genome evolution in *Rumex hastatulus*. *Molecular Biology and Evolution* 41(4): msae074. https://doi.org/10.1093/molbev/msae074

Sacchi, B.M., Yuan, M., Pyne, C., Choudhury, B., Gong, Y., Barrett, S.C.H., Wright, S.I. 2025. Widespread loss of Y expression in the absence of transcriptional dosage compensation in *Rumex hastatulus*. *BioRxiv.* https://doi.org/10.1101/2025.11.20.689509

Sardell, J.M., Kirkpatrick, M. 2020. Sex differences in the recombination landscape. *The American Naturalist* 195(2): 361-379. https://doi.org/10.1086/704943

Saul, F., Scharmann, M., Wakatake, T, Rajaraman, S., Marques, A., Freund, M., … Fukushima, K. 2023. Subgenome dominance shapes novel gene evolution in the decaploid pitcher plant *Nepenthes gracilis*. *Nature Plants* 9: 2000-2015. https://doi.org/10.1038/s41477-023-01562-2

Saunders, P.A., Neuenschwander, S., Perrin, N. 2018. Sex chromosome turnovers and genetic drift: a simulation study. *Journal of Evolutionary Biology* 31(9): 1413-1419. https://doi.org/10.1111/jeb.13336

Saunders, P.A., Neuenschwander, S, Perrin, N. 2019. Impact of deleterious mutations, sexually antagonistic selection, and mode of recombination suppression on transitions between male and female heterogamety. *Heredity* 123: 419-428. https://doi.org/10.1038/s41437-019-0225-z

Scharmann, M., Grafe, T.U., Metali, F., Widmer, A. 2019. Sex is determined by XY chromosomes across the radiation of dioecious *Nepenthes* pitcher plants. *Evolution Letters* 3(6): 586-597. https://doi.org/10.1002/evl3.142

She, H., Liu, Z., Li, S., Xu, Z., Zhang, H., Cheng, F., … Qian, W. 2023. Evolution of the spinach sex-linked region within a rarely recombining pericentromeric region. *Plant Physiology* 193(2): 1263-1280. https://doi.org/10.1093/plphys/kiad389

She, H., Liu, Z., Xu, Z., Zhang, H., Wu, J., Cheng, F., Wang, X., Qian, W. 2025. A complete telomere-to-telomere assembly of the *Spinacia oleracea* genome reveals Y chromosome evolution and centromere landscape. *Plant Communications* 6(9): 101410. https://doi.org/10.1016/j.xplc.2025.101410

Siljak-Yakovlev, S., Cerbah, M., Sarr, A., Benmalek, S., Bounaga, N., Coba de la Pena, T., Brown, S.C. 1996. Chromosomal sex determination and heterochromatin structure in date palm. *Sexual Plant Reproduction* 9: 127-132. https://doi.org/10.1007/BF02221391

Singh, S., Davies, K.M., Chagné, D., Bowman, J.L. 2023. The fate of sex chromosomes during the evolution of monoicy from dioicy in liverworts. *Current Biology* 33(17): 3597-3609. https://doi.org/10.1016/j.cub.2023.07.023

Slancarova, V., Zdanska, J., Janousek, B., Talianova, M., Zschach, C., Zluvova, J., … Vyskot, B. 2013. Evolution of sex determination systems with heterogametic males and females in *Silene*. *Evolution* 67(12): 3669-3677. https://doi.org/10.1111/evo.12223

Šmarda, P., Horová, L., Knápek, O., Dieck, H., Ražná, K., Hrubík, P., … Bureš, P. 2018. Multiple haploids, triploids, and tetraploids found in modern-day "living fossil" *Ginkgo biloba*. *Horticulture Research* 5(55). https://doi.org/10.1038/s41438-018-0055-9

Sousa, A., Fuchs, J., Renner, S.S. 2017. Cytogenic comparison of heteromorphic and homomorphic sex chromosomes in *Coccinia* (Cucurbitaceae) points to sex chromosome turnover. *Chromosome Research* 25: 191-200. https://doi.org/10.1007/s10577-017-9555-y

Spigler, R.B., Lewers, K.S., Main, D.S., Ashman, T.L. 2008. Genetic mapping of sex determination in a wild strawberry, *Fragaria virginiana*, reveals earliest form of sex chromosome. *Heredity* 101: 507-517. https://doi.org/10.1038/hdy.2008.100

Stapley, J., Feulner, P.G.D., Johnston, S.E., Santure, A.W., Smadja, C.M. 2017. Variation in recombination frequency and distribution across eukaryotes: patterns and processes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372(1736): 20160455. https://doi.org/10.1098/rstb.2016.0455

Tennessen, J.A., Wei, N., Straub, S.C.K., Govindarajulu, R., Liston, A., Ashman, T.L. 2018. Repeated translocation of a gene cassette drives sex-chromosome turnover in strawberries. *PLoS Biology* 16(8): e2006062. https://doi.org/10.1371/journal.pbio.2006062

Tessarotto, H., Beulé, T., Cherif, E., Orjuela, J., Lindstrom, A., Lemansour, A., … Aberlenc, F. 2024. Convergent evolution of sex chromosomes in palms. *Hal.science*: hal-04794248. https://dx.doi.org/10.1101/2024.06.27.600560

Tiley, G.P., Burleigh, J.G. 2015. The relationship of recombination rate, genome structure, and patterns of molecular evolution across angiosperms. *BMC Evolutionary Biology* 15: 194. https://doi.org/10.1186/s12862-015-0473-3

Torres, M.F., Mathew, L.S., Ahmed, I., Al-Azwani, I.K., Krueger, R., Rivera-Nuñez, D., … Malek, J.A. 2018. Genus-wide sequencing supports a two-locus model for sex-determination in *Phoenix*. *Nature Communications* 9: 3969. https://doi.org/10.1038/s41467-018-06375-y

Úbeda, F., Patten, M.M., Wild, G. 2015. On the origin of sex chromosomes from meiotic drive. *Proceedings of the Royal Society B: Biological Sciences* 282(1798): 20141932. https://doi.org/10.1098/rspb.2014.1932

Veller, C., Muralidhar, P., Constable, G.W.A., Nowak, M.A. 2017. Drift-induced selection between male and female heterogamety. *Genetics* 207(2): 711-727. https://doi.org/10.1534/genetics.117.300151

Veltsos, P., Cossard, G., Beaudoing, E., Beydong, G., Bianchi, D.S., Roux, C., González-Martínez, S.C., Pannell, J.R. 2018. Size and content of the sex-determining region of the Y chromosome in dioecious *Mercurialis annua*, a plant with homomorphic sex chromosomes. *Genes* 9(6): 277. https://doi.org/10.3390/genes9060277

Veltsos, P., Ridout, K.E., Toups, M.A., González-Martínez, S.C., Muyle, A., Emery, O., … Pannell, J.R. 2019. Early sex-chromosome evolution in the diploid dioecious plant *Mercurialis annua*. *Genetics* 212(3): 815-835. https://doi.org/10.1534/genetics.119.302045

Vicoso, B. 2019. Molecular and evolutionary dynamics of animal sex-chromosome turnover. *Nature Ecology and Evolution* 3: 1632-1641. https://doi.org/10.1038/s41559-019-1050-8

Vicoso, B., Bachtrog, D. 2009. Progress and prospects toward our understanding of the evolution of dosage compensation. *Chromosome Research* 17: 585-602. https://doi.org/10.1007/s10577-009-9053-y

Villarreal, J.C., Renner, S.S. 2013. Correlates of monoicy and dioicy in hornworts, the apparent sister group to vascular plants. *BMC Ecology and Evolution* 13: 239. https://doi.org/10.1186/1471-2148-13-239

Walas, L., Mandryk, W., Thomas, P.A., Tyrata-Wierucka, Z., Iszkuto, G. 2018. Sexual systems in gymnosperms: a review. *Basic and Applied Ecology* 31: 1-9. https://doi.org/10.1016/j.baae.2018.05.009

Wang, Y., Gong, G.N., Wang, Y., Zhang, R.G., Hörandl, E., Zhang, Z.X., Charlesworth, D., He, L. 2024. Gap-free X and Y chromosome assemblies of *Salix arbutifolia* reveal an evolutionary change from male to female heterogamety in willows, without a change in the position of the sex-determining locus. *New Phytologist* 242(6): 2872-2887. https://doi.org/10.1111/nph.19744

Wang, D., Li, Y., Li, M., Yang, W., Ma, X., Zhang, L., … Ma, T. 2022. Repeated turnovers keep sex chromosomes young in willows. *Genome Biology* 23: 200. https://doi.org/10.1186/s13059-022-02769-w

Wang, J., Na, J.K., Yu, Q., Gschwend, A.R., Han, J., Zeng, F., … Ming, R. 2012. Sequencing papaya X and Y^h chromosomes reveals molecular basis of incipient sex chromosome evolution. *Proceedings of the National Academy of Sciences* 109(34): 13710-13715. https://doi.org/10.1073/pnas.1207833109

Wang, Y., Zhang, R.G., Hörandl, E., Zhang, Z.X., Charlesworth, D., He, L. 2024. Evolution of sex-linked genes and the role of pericentromeric regions in sex chromosomes: insights from diploid willows. *Molecular Biology and Evolution* 41(11): msae235. https://doi.org/10.1093/molbev/msae235

Warmke, H.E., Blakeslee, A.F. 1939. Sex mechanism of polyploids of *Melandrium*. *Science* 89(2313): 391-392. https://doi.org/10.1126/science.89.2313.391

Wong, E.L.Y., Filatov, D.A. 2023. Pericentromeric recombination suppression and the 'large X effect' in plants. *Scientific Reports* 13: 21682. https://doi.org/10.1038/s41598-023-48870-3

Wu, M., Haak, D.C., Anderson, G.J., Hahn, M.W., Moyle, L.C., Guerrero, R.F. 2021. Inferring the genetic basis of sex determination from the genome of a dioecious nightshade. *Molecular Biology and Evolution* 38(7): 2946-2957. https://doi.org/10.1093/molbev/msab089

Wu, X., Wang, J., Na, J.K., Yu, Q., Moore, R.C., Zee, F., Huber, S.C., Ming, R. 2010. The origin of the non-recombining region of sex chromosomes in *Carica* and *Vasconcellea*. *The Plant Journal* 63(5): 801-810. https://doi.org/10.1111/j.1365-313X.2010.04284.x

Xia, Z., Dai, X., Fan, W., Liu, C., Zhang, M., Bian, P., … Zhao, A. 2022. Chromosome-level genomes reveal the genetic basis of descending dysploidy and sex determinatiuon in *Morus* plants. *Genomics, Proteomics & Bioinformatics* 20(6): 1119-1137. https://doi.org/10.1016/j.gpb.2022.08.005

Xue, Z.Q., Applequist, W.L., Hörandl, E., He, L. 2024. Sex chromosome turnover plays an important role in the maintenance of barriers to post-speciation introgression in willows. *Evolution Letters* 8(4): 467-477. https://doi.org/10.1093/evlett/qrae013

Yamamoto, K., Hamaji, T., Kawai-Toyooka, H., Matsuzaki, R., Takahashi, F., Nishimura, Y., … Nozaki, H. 2021. Three genomes in the algal genus *Volvox* reveal the fate of a haploid sex-determining region after a transition to homothallism. *Proceedings of the National Academy of Sciences* 118(21): e2100712118. https://doi.org/10.1073/pnas.2100712118

Yang, W., Wang, D., Li, Y., Zhang, Z., Tong, S., Li, M., … Ma, T. 2020. A general model to explain repeated turnovers of sex determination in the Salicaceae. *Molecular Biology and Evolution* 38(3): 968-980. https://doi.org/10.1093/molbev/msaa261

Yu, Q., Hou, S., Hobza, R., Feltus, A., Wang, X., Jin, W., … Ming, R. 2007. Chromosomal location and gene paucity of the male specific region on papaya Y chromosome. *Molecular Genetics and Genomics* 278: 177-185. https://doi.org/10.1007/s00438-007-0243-z

Zhang, H., Zhang, R., Yang, X., Gu, K.J., Chen, W., Chang, Y., … Xin, Z. 2019. Recent origin of an XX/XY sex-determination system in the ancient plant lineage *Ginkgo biloba*. *BioRxiv.* https://doi.org/10.1101/517946

Zhao, J., Wang, D., Chen, K., Xie, J., Li, Y., Wang, Y., … Ma, T. 2026. A new two-gene system of sex determination in a Salicaceae. *Current Biology* 36(2): 492-505. https://doi.org/10.1016/j.cub.2025.12.003

Zhou, S., Feng, C., Chen, X., Yang, T., Zhang, F., Kang, M. 2026. Phased chromosome-level genomes reveal young evolutionary origin of sex determination in *Magnolia kwangiensis*. *The Plant Journal* 126(1): e70830. https://doi.org/10.1111/tpj.70830