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REVIEW

The role of repetitive DNA in structure and evolution of sex chromosomes in plants

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Eukaryotic genomes contain a large proportion of repetitive DNA sequences, mostly transposable elements (TEs) and tandem repeats. These repetitive sequences often colonize specific chromosomal (Y or W chromosomes, B chromosomes) or subchromosomal (telomeres, centromeres) niches. Sex chromosomes, especially non-recombining regions of the Y chromosome, are subject to different evolutionary forces compared with autosomes. In non-recombining regions of the Y chromosome repetitive DNA sequences are accumulated, representing a dominant and early process forming the Y chromosome, probably before genes start to degenerate. Here we review the occurrence and role of repetitive DNA in Y chromosome evolution in various species with a focus on dioecious plants. We also discuss the potential link between recombination and transposition in shaping genomes.
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Introduction

Transposable elements (TEs), both retrotransposons and DNA transposons, considered earlier as 'junk DNA,' are now viewed as major players in genome evolution (Kidwell and Lisch, 2001; Biemont and Vieira, 2006). Their distribution in genomes is variable: some are widespread, while others colonize specific chromosomal niches. Repeated sequence elements can be viewed as members of a community inhabiting the genome ecosystem (Leonardo and Nuzhdin, 2002; Brookfield, 2005).

The chromosomal distribution of TEs is often governed by the status of chromatin compaction and rates of recombination of particular genomic regions. In general, regions with suppressed or no recombination tend to accumulate repetitive DNA sequences (for review see Charlesworth *et al*., 1994; Gvozdev *et al*., 2005). Non-recombining parts of the Y chromosome have accumulated repetitive DNA, particularly in the mammalian (Erlandsson *et al*., 2000; Skaletsky *et al*., 2003) and *Drosophila melanogaster* (Pimpinelli *et al*., 1995) Y chromosomes, which are evolutionarily ancient, originating before 165 and 60 mya, respectively (Graves, 2005; Veyrunes *et al*., 2008). However, the process of accumulation of repetitive sequences is apparent even in evolutionarily young sex chromosomes, such as in *Drosophila miranda* (Steinemann and Steinemann, 1992), *Silene latifolia* (Hobza *et al*., 2006; Kejnovsky *et al*., 2006a) or *Carica papaya* (Liu *et al*., 2004). Repeat accumulation thus potentially represents an early process shaping the Y chromosome, even before the genes start to degenerate (Steinemann and Steinemann, 2005).

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Sex chromosomes: special parts of genomes

The definition of a sex chromosome is not always clear-cut. It is generally applied to a pair of chromosomes on which the sex determination locus resides regardless of whether they are morphologically distinguishable (heteromorphic) and mostly non-recombining, or conversely, morphologically indistinguishable (homomorphic) and recombining along much of their length. In most species the males are the heterogametic (XY) sex, whereas the females are homogametic (XX). In some groups such as birds and lepidopterans, the reverse is true: females are heterogametic (ZW) and males are homogametic (ZZ). Here we will focus on the XY/XX system, but the same processes were observed in ZW/ZZ system as well (Traut and Marec, 1997; Ezaz *et al*., 2006; Tsuda *et al*., 2007).

The origin and evolution of sex chromosomes have interested evolutionary biologists for a long time. Although sex chromosomes evolve from a pair of autosomes (Ohno, 1967), over time they become different, both from each other and the autosomes, in gene content and structure. While sex chromosomes in most mammals are ancient, sex chromosomes in some fish, platypus, some insects and dioecious plants are evolutionarily young (for review see Vyskot and Hobza, 2004; Charlesworth *et al*., 2005). Despite the different ages of sex chromosomes in different taxonomic groups, they probably follow similar evolutionary trajectories with discrete identifiable stages.

The trajectory from autosomes to sex chromosomes may start with the emergence of a sex-determining gene with one allele that determines male individuals and the other female individuals. A two-loci model was

suggested by Charlesworth *et al*. (2005) in which mutation in one gene on the proto-X chromosome results in male sterility and mutation in another gene on the proto-Y chromosome results in female sterility. Acquisition of a sex-determining gene(s) may be followed by the suppression of recombination in the vicinity of the gene(s). Later, other sex-determining genes that influence the development of a particular sex, or are antagonistic to the opposing sex, may accumulate around the sex-determining gene. Such sex-determining regions can, in some instances, translocate between chromosomes and create new sex chromosomes (Traut and Willhoeft, 1990; Willhoeft and Traut, 1990; Traut and Wollert, 1998). The initiating mechanisms of recombination suppression are not yet clear, though some models based on epigenetic silencing (Jablonka, 2004) or inversions (Lahn and Page, 1999) have been proposed. Zluvova *et al*. (2005) suggested that the inversion on the Y chromosome of *Silene latifolia* is a consequence of recombination arrest as opposed to its cause. In addition, non-recombining regions may expand through the accumulation of repetitive DNA sequences (Charlesworth, 1991), which often form heterochromatin. Ultimately the processes, because of a lack of recombination in meiosis, may lead to a lower expression of the Y-linked genes and eventually to their degeneration into pseudogenes (Bachtrog, 2006; Marais *et al*., 2008). Once the Y chromosome has become a genetic desert, the balance between mechanisms that expand the chromosome (for example, transposition) and those that cause it to contract (for example, deletions), will govern the long-term fate of the chromosome. At this stage, large regions of the Y chromosome without genes are dispensable and can be lost. It is not clear yet whether the processes of gene degeneration, TEs accumulation and expansions on one hand and contractions on the other hand are stepwise or are occurring simultaneously.

However, the lifetime of an old Y chromosome is often prolonged by the addition of segments transferred from autosomes (Graves, 2005). Acquisition of new genes from autosomes mediated by retrotransposition has been shown in humans (Lahn and Page, 1999), and a similar duplicative transfer has also been shown in the young Y chromosomes of *Silene latifolia* (Matsunaga *et al*., 2003). A final possibility is that sex is determined not by the specific Y-linked gene, but only by the ratio of X chromosome to autosomes (X/A ratio). Then the Y chromosome either remains as a genetic entity or could be lost entirely. A new autosomal pair can then be chosen to become a new pair of sex chromosomes and the cyclic process can continue. The persistence of the Y chromosome indicates that it can repeatedly arise *de novo*, for example, by the fusion between an autosome and an X chromosome followed by the fixation of the neo-X and the neo-Y chromosomes as was shown in grasshopper *Podisma pedestris* (Westerman and Hewitt, 1985; Veltsos *et al*., 2008).

Forces different from those working on the Y chromosome or autosomes form the X chromosome. The X chromosome accumulates both recessive genes advantageous for males (masculinizing the X) and dominant genes advantageous for females (feminizing the X). In mammals, for example, genes primarily expressed in the brain and muscle or involved in sperm production, are enriched on the X chromosome (Hurst, 2001). These genes are often transferred onto the X chromosome by retrotransposition. In mammals, it was shown that retrotransposition both on and off the X chromosome is more frequent than between autosomes (Emerson *et al*., 2004; Khil *et al*., 2005) in which gene movement from the X chromosome is probably caused by meiotic sex chromosome inactivation (MSCI), during which sex chromosomes are condensed and transcription is repressed. Gene movement from the X chromosome then results in copies of the originally X-linked genes on autosomes.

It is not yet clear whether the accumulation of retrotransposing sequences on the X chromosome is a result of more efficient selection against this process in autosomes or preferential targeting to the X chromosome. Retrotranspositions to the X chromosome may also be a consequence of LINE element activity (Myers *et al*., 2002). However, the presence of recent elements ($\sim$2 mya) on the X chromosome supports the latter argument (Myers *et al*., 2002). L1 elements show a two-fold higher enrichment on the human X chromosome and are clustered at the X inactivation centre. Perhaps the L1 elements serve as a DNA signal to propagate and stabilize X chromosome inactivation (Bailey *et al*., 2000; Lyon, 2000).

Processes acting in regions of reduced recombination

There are three models describing the population genetics of TEs in regions of reduced recombination (for review see Nuzhdin, 1999; Hua-Van *et al*., 2005). First, the 'deleterious insertion model' is based on the higher elimination of TEs from high-gene density regions (Charlesworth, 1991). Second, the 'ectopic recombination model' explains the higher abundance of TEs in low recombining regions by the reduced frequency of their removal by ectopic recombination (Langley *et al*., 1988). Third, the 'deleterious transposition model' is based on the deleterious effects of transposition, for example, the formation of chromosome breaks (Brookfield, 1991).

Centromeres are regions with lower recombination frequency (Beadle, 1932; Clarke and Carbon, 1980) and often exhibit interspersion of satellite sequences and TEs, as in cereals (Zhong *et al*., 2002), *Arabidopsis* (Copenhaver *et al*., 1999), insects (Sun *et al*., 2003) and fungi (Cambareri *et al*., 1998). There are indications of the evolutionary link between the centromere structure and TE's activity: centromeric satellite repeats may arise from DNA transposons (Kapitonov and Jurka, 1999). There are also similarities between the pogo-like superfamily of DNA transposons and the centromeric CENP-B protein (Smith and Riggs, 1996). CENP-B may have DNA nicking activity analogous to transposase, and it could promote the evolution of satellite arrays by stimulating homologous recombination (Kipling and Warburton, 1997). It is interesting that the CENP-B satellite is absent on the Y chromosome in a number of mammalian species from the only centromere in the genome that does not have a pairing partner in meiosis (Kipling and Warburton, 1997). Similarly, centromeric satellites STAR-C and STAR-Y are underrepresented only in centromeres of the Y chromosome in *Silene latifolia* (Hobza *et al*., 2007; Cermak *et al*., 2008).

The targeting of transposons can be achieved by the targeting domain of integrase, which interacts with

specific DNA–protein complexes such as telomeric heterochromatin (Xie *et al*., 2001). Transposons can also recognize specific DNA sequence (Jurka, 1997) or DNA secondary structure, such as kinked DNAs (Jurka *et al*., 1998). Integration is also influenced by the epigenetic state of the target region. Many studies have been done on yeast showing targeting of telomeric or subtelomeric repeats as well as rDNA loci (Xie *et al*., 2001; Zhu *et al*., 2003). Some TEs integrate into silent regions while others into actively transcribed regions (Kirchner *et al*., 1995).

DNA-based elements and retrotransposons differ in mechanisms of their amplification. Their dynamics and distribution in genomes are different but the reasons why are not clear (Hua-Van *et al*., 2005) but it could be influenced by recombination. In *Drosophila* there is a negative correlation between abundance of DNA transposons and recombination rate (Rizzon *et al*., 2002). In contrast, in *C. elegans*, DNA transposons but not retrotransposons are located preferentially in regions with a high recombination rate (Duret *et al*., 2000). The contrasting relationships between TEs and recombination in these two species can be explained by differences in meiotic pairing and recombination mechanisms (Rizzon *et al*., 2002). The genome might be more accessible for transposon insertions in regions of intense recombination. It remains unclear whether recombination promotes transposon insertions or, *vice versa* (Duret *et al*., 2000), although the latter explanation is supported by the finding that MuDR transposase increases the frequency of meiotic crossovers in the vicinity of Mu insertions (Yandeau–Nelson *et al*., 2005). The relationship between transposons and recombination (Downs and Jackson, 1999; Kapitonov and Jurka, 2005) is likely to have significant evolutionary implications, especially as many DNA transposons have an affinity to insert into genes (Bureau and Wessler, 1992; Bureau *et al*., 1996).

Together, recombination processes and the activity of TEs, lead to a high turnover of elements in eukaryotic genomes, particularly in plants (Gaut *et al*., 2007). Ectopic recombination (unequal recombination, that is, recombination between homologous elements located in non-homologous positions) and TEs can cause large rearrangements. Ectopic recombination has been suggested to be the most important mechanism of genome size reduction and may provide a partial 'return ticket from genomic obesity' (Vicient *et al*., 1999; Petrov *et al*., 2003). The evidence that deletions are mediated by recombination is the presence of 'solo long terminal repeats (LTRs)' that remain in the genome after recombination between two LTRs deletes the internal regions (Vitte and Panaud, 2003). It is possible that this reduction took place on the small mammalian Y chromosome during its evolution. If ectopic recombination between retrotransposons played an important role in size reduction, we can predict a higher frequency of 'solo LTRs' on the human Y chromosome compared with other chromosomes.

Another recombination-related process is gene conversion, which can homogenize elements of a repeat family resulting in concerted evolution (Liao, 2003). Gene conversion most frequently occurs within, rather than between, chromosomes as indicated by the higher intrachromosomal similarity of TEs and tandem repeats (Hood *et al*., 2005; Krzywinski *et al*., 2005). Similarly, in white campion (*Silene latifolia*), TEs are more homogenous on the Y chromosome than on the X chromosome and autosomes (Kejnovsky *et al*., 2007).

The other important process acting in non-recombining regions is gene degeneration (Charlesworth, 1991; Charlesworth and Charlesworth, 2000). Degeneration could be a consequence of TE accumulation (Steinemann and Steinemann, 2005; Marais *et al*., 2008). The random inactivation model (Bachtrog, 2006) suggests that the process of gene inactivation is triggered by the disruption of promoter regions by TE insertion. TE insertions can lead to an epigenetic phenomenon, or global changes in chromatin status (heterochromatization). In *D. miranda* the random inactivation model best explains neo-Y chromosome inactivation. Recent results by Zhang *et al*. (2008) on the papaya show that in MSY (male-specific region of the Y chromosome), but not in corresponding X chromosomal region, there are multiple knob-like heterochromatin structures. Such knobs are usually composed of satellite DNA and transposons. Moreover, in the papaya they show that the knob regions are extensively methylated. Heterochromatinization of the region, which may have originally served as a defense against TEs, probably started, or at least accelerated, the degeneration of the MSY in the papaya (Zhang *et al*., 2008).

Bachtrog *et al*. (2008) showed that in the neo-Y chromosome of *D. miranda* there are 20 times as many TE insertions compared with the neo-X chromosome. They also show that the fraction of TE insertions is similar in functional and non-functional genes. These data suggest the role of TE insertions adjacent to the genes in gene inactivation on the neo-Y. It is still not clear whether TEs affect the vicinity of genes in terms of epigenetic status by chromatin modification in the vicinity of TE insertion or by producing antisense transcripts of adjacent genes and subsequent inactivation by RNAi (Slotkin and Martienssen, 2007).

Accumulation of repetitive DNA in plant sex chromosomes

The main stages of the sex chromosome evolution: the establishment of the sex-determining region, local suppression of recombination, accumulation of repeats, degeneration of genes, and shrinkage by deletions: have been shown in several plant species. In contrast to mammals, most dioecious plants do not possess heteromorphic sex chromosomes (Gorelick, 2005). However about one-tenth of angiosperm species have separate sexes (Yampolsky and Yampolsky, 1922), and of these only a few species are known to have heteromorphic sex chromosomes (Vyskot and Hobza, 2004). In plants with heteromorphic sex chromosomes, the Y chromosome is usually larger than the X chromosome: the reverse of the situation in mammals. Perhaps the larger Y in plants is caused by the accumulation of repeats; indeed, plant genomes in general show high levels of genome plasticity compared with mammals. There are several plant model species that enable the study of different stages of sex chromosome evolution.

The sex in the squirting cucumber (*Ecballium elaterium*) is determined by one locus localized on a structurally and functionally undifferentiated pair of autosomes. The Y chromosome of the asparagus (*Asparagus officinalis*) is probably evolutionarily young, as the YY genotype is

viable and only a small amount of the Y chromosome contains constitutive heterochromatin (Loptien, 1979). Sex chromosomes of the kiwi fruit (*Actinidia chinensis*) are at a similar stage (Harvey *et al*., 1997). In the papaya (*Carica papaya*), the MSY is short: about 8–9 Mbp (Yu *et al*., 2008), covering about 20% of the Y chromosome. The MSY region has lost many genes, and the YY genotype is lethal. Despite the short period of time for the divergence of the X and Y, the MSY region of the Y chromosome is already enriched for local segmental duplications, TEs and plastid DNA insertions compared with its X partner (Liu *et al*., 2004; Yu *et al*., 2007).

Diversification of sex chromosomes can lead to heteromorphic sex chromosomes that are found in mammals, *Drosophila*, and some dioecious plants: liverwort (*Marchantia polymorpha*), white campion (*Silene latifolia*), sorrel (*Rumex acetosa*), hop (*Humulus lupulus*) and hemp (*Cannabis sativa*). In hop, the Y chromosome is the smallest chromosome in the genome (Winge, 1929); however, there are no data concerning the specific structure of sex chromosomes in this species. Hemp shows male-specific accumulation of LINE-like retrotransposons (Sakamoto *et al*., 2000), as well as a high abundance of MADC3 and MADC4 (male-associated DNA sequences in *C. sativa*), encoding gag/pol polyproteins of *copia*-like retrotransposons (Sakamoto *et al*., 2005). The Y chromosome of liverwort has specific repeat sequences that contain multiplicated genes. These data suggest that the Y chromosome-amplified protein-coding genes evolved in concert with specific repeat sequences (Okada *et al*., 2001; Ishizaki *et al*., 2002).

In the white campion, the Y chromosome is the largest chromosome in the karyotype and is mostly non-recombining with the X chromosome. The homologous genes characterized on the X and Y chromosomes of *S. latifolia* have not diverged much, yet the YY genotype is not viable, indicating a significant erosion of crucial genes on the Y chromosome. It is interesting that the Y chromosome of *S. latifolia* is euchromatic except at subtelomeric regions, which contain clusters of tandem repeats (reviewed below).

Sorrel is unique among plants because it has XY_1Y_2 males and XX females (Kihara and Ono, 1923). Sex is determined by the ratio of X chromosomes to autosomes. It is also the only example of a plant possessing largely heterochromatic Y chromosomes (Pazourkova, 1964) condensed at interphase (Ruiz Rejon *et al*., 1994; Lengerova and Vyskot, 2001). Sorrel Y chromosomes contain two types of satellite DNA called RAE180 and RAYS (Shibata *et al*., 1999, 2000). RAYSI and RAYSIII are specific for both Y chromosomes whereas RAYSII is specific for the Y1 chromosome (Mariotti *et al*., 2009). RAE180 is a major component of the Y1 chromosome, but is also located on the Y2 and at a single autosomal locus. RAYSI is restricted only to the Y chromosomes in *R. acetosa* and also occurs in several related species with multiple sex chromosome systems (Shibata *et al*., 1999, 2000; Navajas–Perez *et al*., 2005; Cunado *et al*., 2007).

Silene latifolia: a model dioecious plant with heteromorphic sex chromosomes

Silene latifolia ($2n = 24$ white campion) has the most studied heteromorphic sex chromosomes in plants. The first indirect evidence that X and Y chromosomes differed in *S. latifolia*, not only in size but also in DNA composition, was differential labeling of X and Y chromosomes by fluorescent *in situ* hybridization (FISH) using microdissected sex chromosome-derived probes. The hybridization conditions of the experiments (low amount of probe and short hybridization time) showed that chromosomes probably differ in their repetitive DNA structure (Hobza *et al*., 2004). In later experiments, several bacterial artificial chromosome (BAC) clones that originally served as anonymous cytogenetic markers (Lengerova *et al*., 2004) were sequenced and new repetitive DNA sequences from the Y chromosomes were characterized. It was also shown that chloroplast DNA accumulates preferentially on Y chromosome (Kejnovsky *et al*., 2006a).

Tandem repeats in *S. latifolia* were described by Buzek *et al*. (1997), Matsunaga *et al*. (1999), Garrido-Ramos *et al*. (1999), Sykorova *et al*. (2001), Kazama *et al*. (2003, 2006) and Kazama and Matsunaga (2008). The subtelomeric tandem repeat X-43.1 (Buzek *et al*., 1997) similarly as Ssp15 (Sykorova *et al*., 2001) are located not only on the sex chromosomes but also on the autosomes. The role of tandem repeat amplification in Y chromosome evolution was shown by the characterization of the TRAYC element (tandem repeat accumulated on the Y chromosome) (Hobza *et al*., 2006) and STAR-Y (*Silene* tandem repeat amplified on the Y chromosome) (Hobza *et al*., 2007). Both sequences are located in the centromeric regions of some autosomes and are highly abundant on the Y chromosome. The data suggest a centromeric origin of TRAYC and STAR-Y sequences, which then accumulated on the Y chromosome in *S. latifolia*. Sequence analysis also showed that microsatellites are overrepresented on the Y chromosome (Kubat *et al*., 2008). Comparisons of microsatellite distributions between *R. acetosa* and *S. latifolia* chromosomes show that some motifs (for example, CAA or TAA) are strongly accumulated in non-recombining regions of the Y chromosome in both species (Figure 1), whereas other motifs have different patterns: $(GC)_{15}$ is abundant on the Y chromosomes in *S. latifolia* and absent in *R. acetosa*. Perhaps some simple DNA repeats regularly expand on Y chromosomes as speculated Kubat *et al*. (2008). This may be because of their DNA conformational properties or dependent on other circumstances (for example, the stage of evolution of the sex chromosomes, co-transposition with some retroelements).

Matsunaga *et al*. (2002) and Obara *et al*. (2002) studied the retrotransposons in *S. latifolia*. Later, Pritham *et al*. (2003) isolated a transcriptionally active DNA transposon residing on the Y chromosome. The first active MITE elements in *S. latifolia* were described by Bergero *et al*. (2008). A comprehensive systematic study of repetitive DNA in *S. latifolia* showed that *Copia* retroelements are the most abundant DNA element on the Y chromosome (Cermak *et al*., 2008). Cermak *et al*. (2008) also showed the enigmatic distribution of the *Ogre*-like retroelement, which colonizes only recombining parts of the genome of *S. latifolia* (is absent in non-recombining parts of the Y chromosome). This distribution of *Ogre*-like elements could be explained either by their spreading in connection with the recombination machinery or by their activity only in females, for example, because of some inhibition mechanisms (for example, RNAi) present only

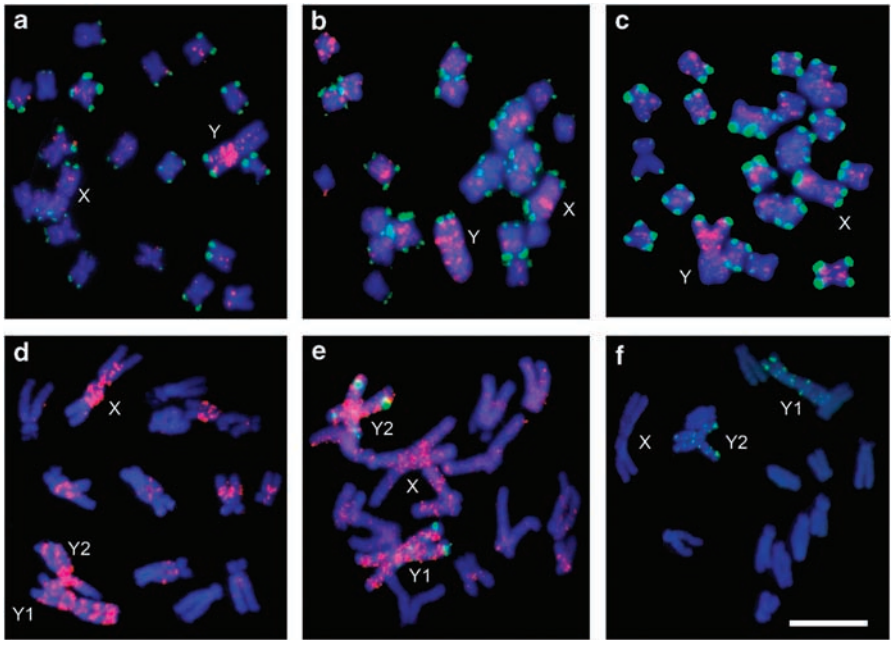

Figure 1 Chromosomal distribution of labeled microsatellites—containing oligonucleotides $(CAA)_{10}$ in *Silene latifolia* (**a**) and *Rumex acetosa* (**d**), microsatellites $(TAA)_{10}$ in *S. latifolia* (**b**) and *R. acetosa* (**e**), and microsatellites $(GC)_{15}$ in *S. latifolia* (**c**) and *R. acetosa* (**f**). Chromosomes were counterstained with DAPI (blue). Microsatellite probes were directly labeled with Cy3 during synthesis (red signals). The tandem repeat X-43.1, which is present at most subtelomeres of *S. latifolia* but on the Y chromosome only on its q-arm, was labeled with SpectrumGreen-conjugated nucleotides (green signals in **a**–**c**). In *R. acetosa*, Y1 and Y2 chromosomes were specifically labeled by *RAYS1* probe (green in **e**, **f**). The X and Y chromosomes are indicated. Bar = 10 μm.

in males. The different evolutionary pressures acting on non-recombining regions influence TE distribution and affect sex chromosome evolution. We speculate that for some TEs recombination is an essential condition for transposition (Cermak *et al*., 2008). We can also speculate that different repetitive elements occupy the non-recombining part of the Y chromosome in different evolutionary steps of X–Y diversification.

Figure 2 represents a comprehensive summary of repetitive DNA distribution on sex chromosomes in *S. latifolia*. Most TEs are distributed uniformly along both the X and Y chromosomes. Two exceptions are *Retand* elements, which are localized at subtelomeres (Kejnovsky *et al*., 2006b) and *Ogre*-like elements, which are present on whole X chromosome but restricted to the PAR region of the Y chromosome (Cermak *et al*., 2008). Tandem repeats colonize the centromeres (STAR-C) and subtelomeres (X-43.1) of X chromosome, whereas in the Y chromosome STAR-C and STAR-Y are located in the middle of both arms and X-43.1 is at the subtelomere of the q-arm. Telomere-like sequences are present also in centromeres of the X and Y chromosomes (Uchida *et al*., 2002). It is evident that the Y chromosome has a different composition and localization of repetitive DNA compared with X chromosome and autosomes.

The presence of sex chromosomes and their tendency to accumulate repetitive DNA gives this dioecious species evolutionary potential different from what one might expect in the hermaphroditic species (Meagher and Costich, 2008). The content of repetitive DNA may have a role in phenotypic features (Meagher and Vassiliadis, 2005; Biemont, 2008). For example, a negative correlation between DNA content and flower and leaf size has been shown in four *Silene* species (Meagher and Costich, 2004).

Conclusions and prospects

Despite much theoretical and experimental progress, our understanding of sex chromosome evolution is more diagrammatic than dynamic. The contribution of many processes such as accumulation of repetitive DNA, degeneration of genes, additions of genes, small or large deletions, inversions, or heterochromatinization, is not clear. Neither is the sequence or timing of these events (for example, was accumulation followed by degeneration or vice versa, Steinemann and Steinemann, 2005) nor the interactions of these processes are well understood (for example, insertions of TE can cause degeneration of genes, Marais *et al*., 2008).

We are also far from understanding the dominant processes working on the Y chromosome such as the preferential accumulation of repetitive DNA in regions with suppressed recombination. Accumulation may be explained by reduced selective pressure against insertions. However, the targeted insertion of repeats onto the Y chromosome may also play a role. TE-rich regions on the Y chromosomes could be converted into heterochromatin and, as a result, can attract more TEs because of targeted insertion into heterochromatin regions (Zhu *et al*., 2003).

There are still not many data that show how, or even whether, non-recombining regions of plant sex chromosomes degenerate (Marais *et al*., 2008). Different effects of TE insertion (either genetic or epigenetic) on degeneration of the Y chromosome may play different roles in

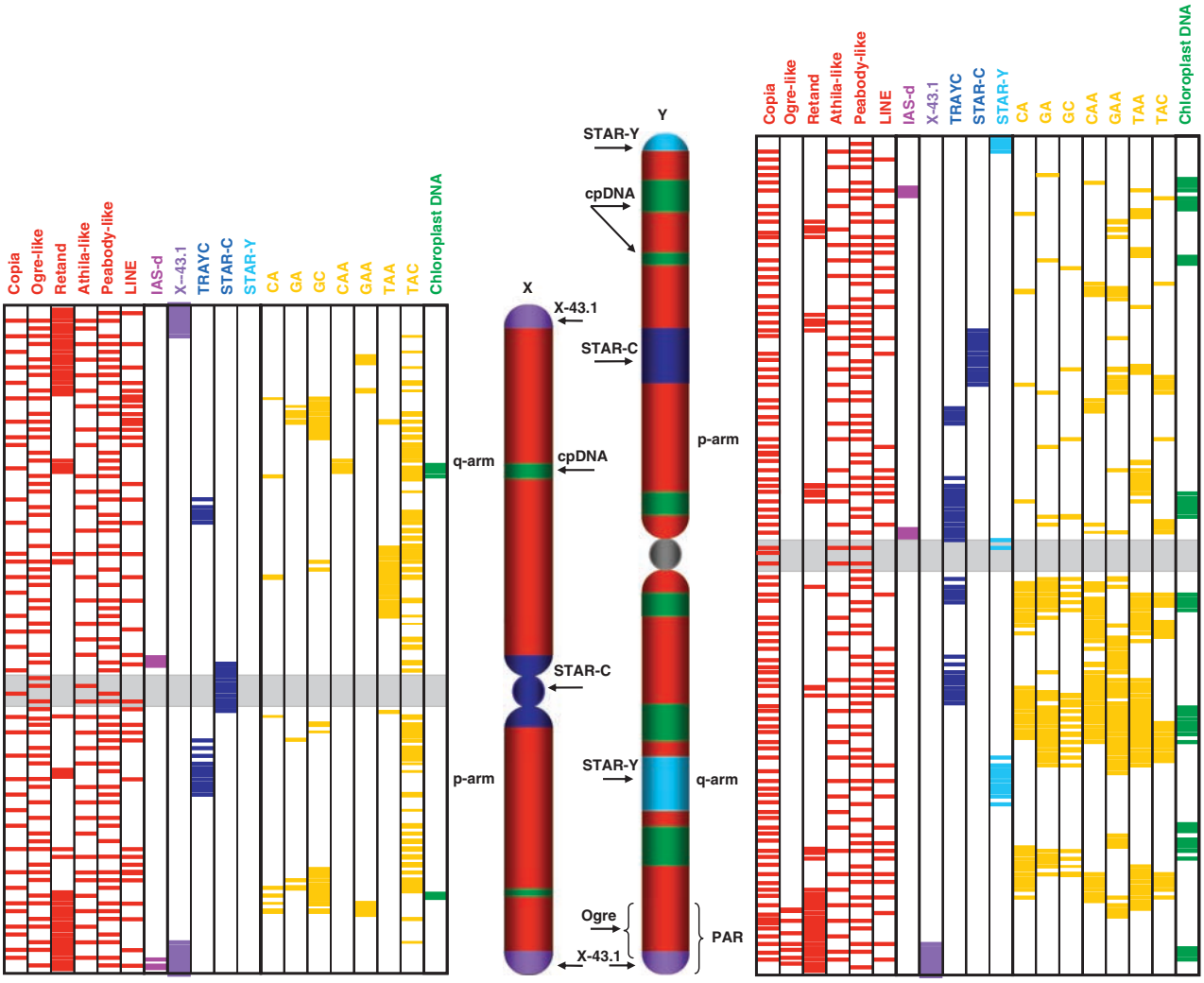

Figure 2 Schematic map of sex chromosomes of *Silene latifolia* with distribution of various types of repetitive DNA sequences—TEs (red), tandem repeats (blue), microsatellites (yellow) and chloroplast DNA (green). The patterns of elements distribution are derived from FISH data.

plants and animals. It could be that degeneration of the Y chromosome is as an evolutionary phenomenon restricted to animals, which, unlike plants, do not undergo strong selection in haploid gametophytes (Armstrong and Filatov, 2008). On the other hand, genes in plants are usually present in multiple copies or as large gene families, a consequence of duplications and polyploidization events. The loss of one allele of a specific gene, or a decrease in expression level as a result of degeneration should therefore not present a dramatic genetic imbalance for plant species that have other functional copies. Duplicity of genes could even accelerate the degeneration of Y chromosomes in plants. Another consequence of the back-up of genetic information in multiplicated plant genomes is different evolution of dosage compensation in plants. There are still no data that dosage compensation in plant sex chromosomes has evolved. Determining which evolutionary patterns after the evolution of sex chromosomes are common both in plants and animals and which ones are restricted to only one of these kingdoms will depend on an increasing amount of data from emerging plant models.

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