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Centromere diversity and its evolutionary impacts on plant karyotypes and plant reproduction

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Contents

Summary	1879	V. When centromeres are everywhere: the holocentric case scenario	1883
I. What karyotype changes occur, and how do they impact plant reproduction?	1879	VI. Conclusions	1884
II. When placing matters: the centromere repositioning case scenario	1880	Acknowledgements	1885
III. When two is too much: the dicentric case scenario	1880	References	1885
IV. When lacking something important: the 'weak' centromere/acentric case scenario	1883		

Summary

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Karyotype changes are a formidable evolutionary force by directly impacting cross-incompatibility, gene dosage, genetic linkage, chromosome segregation, and meiotic recombination landscape. These changes often arise spontaneously and are commonly detected within plant lineages, even between closely related accessions. One element that can influence drastic karyotype changes after only one (or few) plant generations is the alteration of the centromere position, number, distribution, or even its strength. Here, we briefly explore how these different centromere configurations can directly result in karyotype rearrangements, impacting plant reproduction and meiotic recombination.

I. What karyotype changes occur, and how do they impact plant reproduction?

The so-called 'primary' chromosome rearrangement consists of changes in the sequence order of a chromosome, usually caused by two or more simultaneous double-strand breaks (DSBs), which can result in deletions, inversions, translocations, or duplications

(Schubert, 2024). Their impact on plant reproduction usually depends on the degree of modification. For instance, primary rearrangements deflect meiotic recombination, effectively impacting genetic linkage without necessarily disturbing meiotic progression or plant viability (Heng & Heng, 2023). Illustrative examples are seen when CRISPR/Cas9 is employed for reverting natural chromosome inversions in *Arabidopsis*, maize, and rice, effectively

restoring meiotic recombination in chromosome loci deprived of meiotic CO formation (Schmidt *et al.*, 2020; Rönspies *et al.*, 2022).

By contrast, multiple or 'abundant' rearrangements often result in defective meiotic chromosome segregation and aneuploid gametes, compromising plant viability (Heng, 2019). Numerous karyotype rearrangements can result in a reproductive barrier between closely related accessions, leading to the early steps of speciation (Lucek *et al.*, 2023). These 'abundant' chromosome rearrangements often consist of complex combinations of primary rearrangements involving dozens (or even hundreds) of breakpoints affecting one or more chromosomes, resulting in structural and/or numerical karyotype changes (Schubert, 2024). Multiple simultaneous rearrangements arise during 'chromoanagenesis' events, resulting from 'catastrophic' phenomena like stress during DNA replication, defective DNA repair, exposure to genotoxic agents (Guo *et al.*, 2023) or abnormal centromere behaviour (the focus of the present review), among many other causes. Most organisms or cells affected by many rearrangements will likely perish. However, a small fraction with a viable novel karyotype could persist, resulting in a gene flow barrier and potentially triggering speciation (Lucek *et al.*, 2023). The observation that closely related species can drastically differ in their karyotype arrangement supports this assumption. Chromoanagenesis in plants has been reviewed by Guo *et al.* (2023), with some putative examples seen in Hoang *et al.* (2022) and Tan *et al.* (2023). The influence of karyotype changes in speciation has been recently reviewed in Lucek *et al.* (2023) with some recent putative examples in plants seen in Ferguson *et al.* (2024) and Martin *et al.* (2020).

II. When placing matters: the centromere repositioning case scenario

Centromeres correspond to chromosome loci that anchor the kinetochore assembly during cell division, ensuring balanced chromosome segregation (Naish & Henderson, 2024). In most plants, the centromere position is determined by centromeric histone 3 variant (CENH3) loading, often associated with methylated satellite DNA repeat sequences (Naish & Henderson, 2024). As a result, the centromere position remains relatively stable among lineages. However, centromere repositioning can occur spontaneously. For instance, inversions involving breakpoints within the centromeres of wheat chromosomes occurred during its evolution and domestication, resulting in centromere repositioning (Zhao *et al.*, 2023). Centromeres can also 'slide' to a different position by initially 'expanding' into nearby loci while later 'abandoning' their native position, as has been demonstrated in soybeans (Liu *et al.*, 2023). Remarkably, this 'sliding' can occur after only one (or few) generations (Liu *et al.*, 2023). Additionally, centromere repositioning also occurs by seeding/transposition of CENH3 to distant loci, which would require the inactivation of the original centromere, otherwise resulting in a dicentric case scenario (see the next section). An example can be seen in the *Arabideae* clade, where a high frequency of centromere repositioning while keeping the chromosome number and genome structure has been described (Mandakova *et al.*, 2020).

Centromere repositioning occurs in somatic tissues, although it would also have an impact when reaching the germline. Centromeric and pericentromeric loci typically suppress meiotic recombination in plants and other organisms, a phenomenon called the 'centromere effect' (Brazier & Glémin, 2022). Consequently, repositioning of the centromere could influence the meiotic recombination rate at loci near the new and old centromere positions (Fig. 1a,b), impacting genetic linkage (Brazier & Glémin, 2022). For instance, it has been proposed that the frequent transition from acrocentric to metacentric chromosomes observed in *Arabideae* may have modified the recombination landscape at the former shorter arms (Mandakova *et al.*, 2020). However, the impact of centromere repositioning at the meiotic recombination landscape remains to be explored.

Centromeres play a crucial role in shaping chromosome structure and behaviour, enabling chromosomes to be broadly classified into two main types: monocentric chromosomes, which have a single size-restricted centromere constriction; and holocentric chromosomes, where multiple centromere units are distributed along the entire chromosome (Naish & Henderson, 2024). In monocentric chromosomes, meiotic recombination tends to be 'biased' towards loci with high gene density and deflected in loci with an abundance of repetitive elements (e.g. centromeric/pericentromeric loci; Fig. 1a) (Brazier & Glémin, 2022). Recent studies on the holocentric plant *Rhynchospora breviuscula* have revealed that the distribution of meiotic recombination does not correlate with these genomic features associated with meiotic recombination in monocentric plants (Fig. 1e,f) (Castellani *et al.*, 2024). Likewise, *R. breviuscula* does not exhibit inhibition of meiotic recombination near centromeric units (no 'centromere effect') but only inside the core of centromeric units. Remarkably, this species exhibits a typical 'U-shaped' recombination landscape (Fig. 1e), probably caused by a telomere-led synapsis (Castellani *et al.*, 2024). However, this 'distal' recombination bias may not necessarily be a general rule among holocentric plants or other *Rhynchospora* species.

III. When two is too much: the dicentric case scenario

One remarkable feature of centromere position is that it can strongly influence the viability of dysploidy events involving one or two chromosomes (Schubert & Lysak, 2011). For instance, the generation of a stable reciprocal translocation mimicking an end-to-end 'fusion' (from now on referred to as *fusion*) of two metacentric chromosomes would require three steps: (1) formation of one terminal break in each chromosome; (2) reciprocal joint ligation; and (3) silencing/removal of one of the centromeres, otherwise resulting in complications discussed later in this section. By contrast, successful *fusion* of two acrocentric/telocentric chromosomes can occur after generating and ligating two breakpoints near the centromeric end. The resulting product would also be a dicentric chromosome. However, the adjacent centromeres would facilitate its behaviour as a functional (and longer) metacentric chromosome (Fig. 1c). After a *fusion* of two chromosomes, acentric fragments would also be generated, albeit lost in the subsequent cell division (see acentric case scenario)

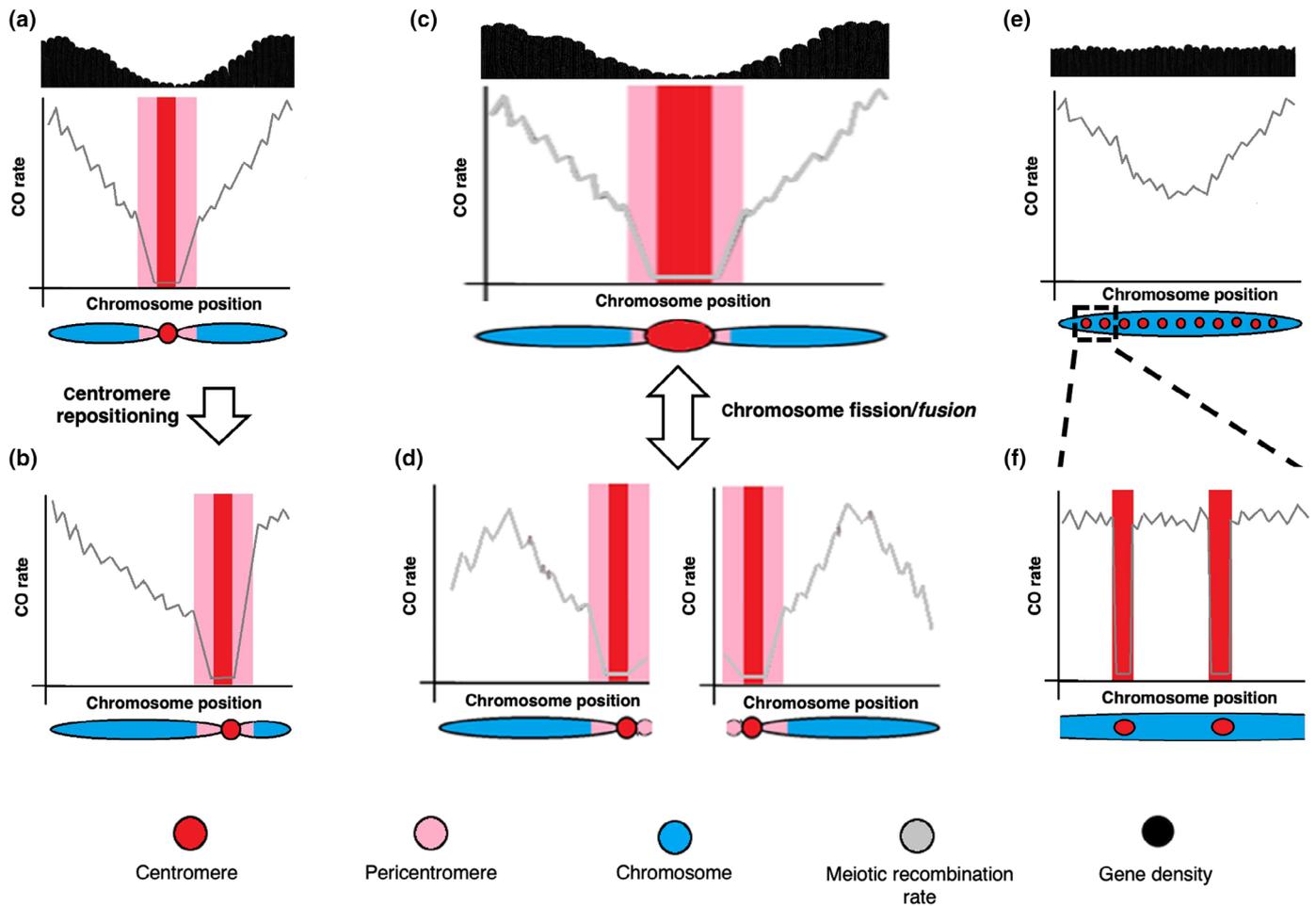


Fig. 1 Meiotic crossover (CO) rate in relation to centromere configuration. In monocentric plants (a–d), the centromeres (and pericentromeres) inhibit meiotic recombination. As a result, centromere repositioning (a to b) changes the CO landscape. Large chromosome size usually results in a U-shape CO landscape (a and c). Therefore, chromosome fissions and fusions (c to d and d to c) can change the CO landscape by impacting chromosome size. In contrast to monocentric chromosomes, holocentric plants (e to f) do not seem to exhibit pericentromeric inhibition of CO formation, although centromeres are also devoid of COs.

(Schubert & Lysak, 2011). Regarding chromosome fissions, the generation of a break in a chromosome arm would require neocentromere formation in the split section, otherwise also generating an acentric fragment (Yin *et al.*, 2021; Dawe *et al.*, 2023). However, a break within the centromere of a metacentric chromosome could result in two smaller telocentric chromosomes if both fragments can retain a functional centromere while generating new telomeres at the breakpoint (Fig. 1d) (Heng, 2019).

The presence of two or more centromeres on the same chromosome usually results in complications during chromosome segregation, with some notable exceptions (see the holocentric case scenario below). This has been demonstrated in *Arabidopsis* and maize, where artificial neocentromere formation has been established by a tethering approach involving the recruitment of CENH3 constructs to specific repeats (Yin *et al.*, 2021; Dawe *et al.*, 2023). The dicentric chromosome generates anaphase bridges, ultimately leading to chromosome fission (Fig. 2c) (Dawe *et al.*, 2023; Li *et al.*, 2023). However,

broken dicentric chromosomes may re-join during DNA repair. In that case, the bridge formation process would re-occur during the subsequent mitosis, potentially leading to anaphase bridge–breakage–fusion cycles, which can ultimately result in complex chromosomal rearrangements (Li *et al.*, 2023). The appearance of anaphase bridge–breakage–fusion cycles has long been described in plants like maize, with a recent example seen in Dawe *et al.* (2023).

In humans, fusions between the acrocentric chromosomes 14 and 13 or 21 frequently arise during female meiosis due to ectopic recombination between pseudo-homologous loci located at their respective short chromosome arms (de Lima *et al.*, 2024). The resulting metacentric chromosomes can be monocentric or dicentric (de Lima *et al.*, 2024). In the dicentric case, the two centromeres are located *c.* 5 Mb apart and are faithfully transmitted during cell division (de Lima *et al.*, 2024). Remarkably, the fused chromosomes are inherited more often than Mendelian ratios, indicating meiotic drive (de Lima *et al.*, 2024). Whether the dicentric nature of these fusions or the centromere size facilitates

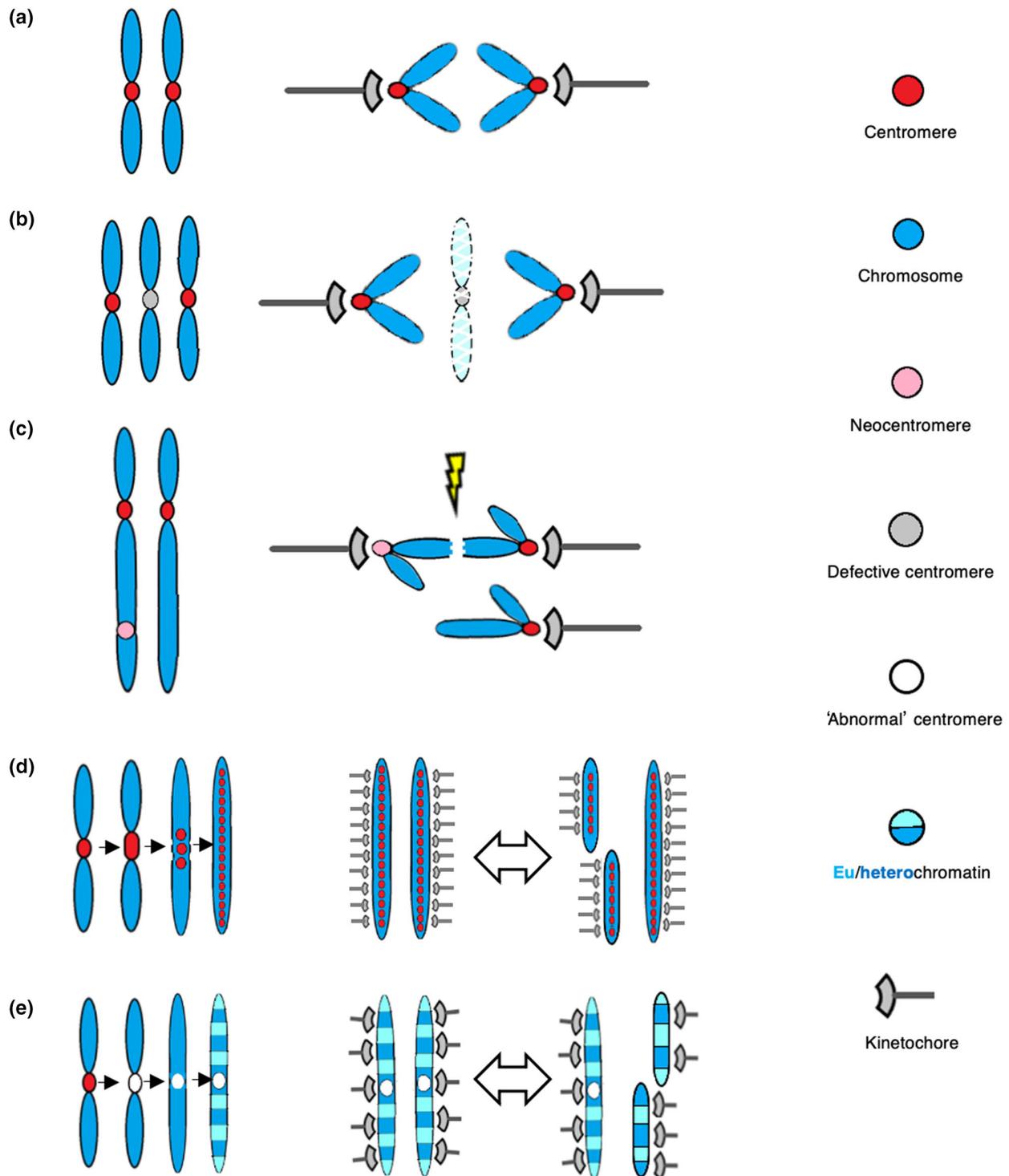


Fig. 2 Centromere configuration impacts chromosome dynamics during cell division. In monocentric plants (a), one centromere results in one anchor for the kinetochore. In acentric chromosomes (b), absence of a functional centromere prevents anchoring of the kinetochore, resulting in chromosome loss during cell division. Dicentric chromosomes (c) can result in chromosome breaks during chromosome segregation. Centromere expansion (d) may have resulted in holocentric chromosomes with many kinetochore anchors along the chromosome. (e) Alternatively, abnormal kinetochore components may have resulted in a different kind of holocentric chromosome by using heterochromatin-dense loci as anchors. Holocentric chromosomes are more tolerant to chromosome fissions or *fusions* (d, e, middle panels) when contrasted to monocentric chromosomes precisely because of the multiple kinetochore anchors.

drive or whether similar scenarios can arise during plant meiosis remains to be explored.

When reaching the germline, the dysploidy arising from chromosome fission/fusions can affect the genome-wide recombination landscape, considering that at least one recombination event per chromosome pair is necessary for correct segregation during meiosis in most organisms (Brazier & Glémin, 2022). Similarly, the increase/reduction in chromosome length would also impact gene linkage when considering that, in many plant species, larger chromosome sizes correlate with the distal location of meiotic recombination events (Fig. 1c,d) (Brazier & Glémin, 2022).

IV. When lacking something important: the 'weak' centromere/acentric case scenario

Chromosomes completely lacking a functional centromere or with a partially functional centromere can arise during chromosome fission, translocation, deletion, centromere silencing, and due to defective CENH3 loading. These acentric/weak chromosomes usually lag during mitosis, after which they conform to a 'micronucleus', where they are endonucleolytically degraded (Fig. 2b). However, fragmented chromosomes can be tethered back to the nucleus, potentially resulting in the incorporation of fragments of the 'eliminated' chromosomes into the surviving ones (Trivedi *et al.*, 2023). Examples can be observed during chromosome fissions generated by telomere seeding (telomere-mediated chromosome truncation, TMCT), resulting in acentric fragments in plants (Yin *et al.*, 2021). These TMCT-generated 'mini-chromosomes' present a limited transmission efficiency during cell division, resulting in the loss of genetic material, limiting plant viability (Yin *et al.*, 2021). Additionally, CRISPR-Cas has been employed for editing centromere repeats, eliminating chromosomes in specific plant organs (Schindele *et al.*, 2022). By contrast, CRISPR-Cas editing of centromere repeats resulted in drastic chromosomal rearrangements in the fungus *Cryptococcus neoformans*, leading to reproductive incompatibility with the original strain (Yadav *et al.*, 2020).

'Weak' centromeres can also affect the plant germline, as seen in the so-called 'haploid-inducer' lines: in *Arabidopsis*, alterations in CENH3 protein result in its removal from chromosomes during egg and zygote development (Marimuthu *et al.*, 2021). These CENH3-depleted centromeres fail to recruit the kinetochore, resulting in chromosome elimination (Marimuthu *et al.*, 2021). Similarly, mutating the inner kinetochore component KNL2 also produces a haploid-inducer line (Ahmadli *et al.*, 2023). The *knl2* haploid-inducer capacity increases when exposed to high temperatures (Ahmadli *et al.*, 2023). This heat-stress enhancement of haploid induction is also observed in plants expressing recombinant CENH3-GFP-tailswap and CENH3^{G83E} (Jin *et al.*, 2023). All haploid-inducer lines share a common feature: the haploid offspring often comes together with some aneuploid individuals, as well as with translocations of fragments of the eliminated chromosomes into surviving chromosomes (Tan *et al.*, 2015; Guo *et al.*, 2023).

V. When centromeres are everywhere: the holocentric case scenario

In some holocentric plants, like *Rhynchospora*, *Luzula* or *Chionographis japonica*, satellite repeat arrays are occupied by CENH3, establishing centromeric units with an epigenetic regulation comparable to that of their monocentric counterparts (Hofstatter *et al.*, 2022; Kuo *et al.*, 2023; Mata-Sucre *et al.*, 2024). This also occurs in some species of legumes with an 'expanded centromere' composed by multiple CENH3-enriched domains covering up to one-third of each chromosome (Macas *et al.*, 2023). This configuration (metapolycentric chromosome) may represent a 'transition' state between monocentric and holocentric chromosomes with repeat-based centromeres (Fig. 2d) (Macas *et al.*, 2023). However, some holocentric plants, such as *Luzula elegans*, lack a clear association between satellite repeats and centromere position (Heckmann *et al.*, 2013). CENH3 enrichment does not coincide with centromere function in others, like *Cuscuta*. Instead, it accumulates at heterochromatin loci, resulting in a 'defective' kinetochore assembly and spindle attachment along the entire chromosome length (Fig. 2e) (Neumann *et al.*, 2023). All these differences highlight the many evolutionary paths that can lead to the transition from mono- to holocentric chromosomes (Kuo *et al.*, 2024).

Due to their multiple centromeres, holocentric chromosomes are expected to tolerate higher rates of both chromosome fissions and fusions (Fig. 2d,e). This flexibility allows holocentric chromosomes to maintain stability through cell division despite these rearrangements, unlike monocentric chromosomes, thereby potentially promoting the fixation of chromosomal changes (Hofstatter *et al.*, 2022; Escudero *et al.*, 2023; Mata-Sucre *et al.*, 2024). Regarding chromosome fissions, a nonplant example can be seen in the butterfly *Leptidea sinapis*, with extreme intraspecific variation in chromosome numbers ranging from $2n = 56$ to 110, due to at least 27 fissions events (Näsvalld *et al.*, 2023). Regarding fusions, a plant example is seen when contrasting the karyotypes of *Rhynchosporas* (Hofstatter *et al.*, 2022). Their predicted five-chromosome ancestral karyotype conserves high synteny with other clade members (Fig. 3a). The main differences arise from whole-genome duplications followed by consecutive fusions resulting in five (larger) chromosomes (Fig. 3a; *R. pubera*) or by chromosome fusions leading to a reduction from five to two chromosomes (Fig. 3a; *R. tenuis*). These fusions are probably facilitated by recombining repeat enriched loci close to the chromosome ends (Hofstatter *et al.*, 2022).

Holocentric chromosomes may present issues due to meiotic-specific regulation of centromere cohesion required for chromosome segregation (Cabral *et al.*, 2014). Therefore, holocentric organisms evolved particular meiotic adaptations like inverted meiosis or achiasmatic meiosis (Cabral *et al.*, 2014; Heckmann *et al.*, 2014; Näsvalld *et al.*, 2023). Incidentally, these adaptations may facilitate balanced meiotic chromosome segregation despite dysploidy caused by fissions/fusions. During a typical meiosis, each homologous chromosome pair is physically linked by meiotic crossover (CO), an essential step for chromosome segregation. During fission/fusions, CO formation could result in the linkage of

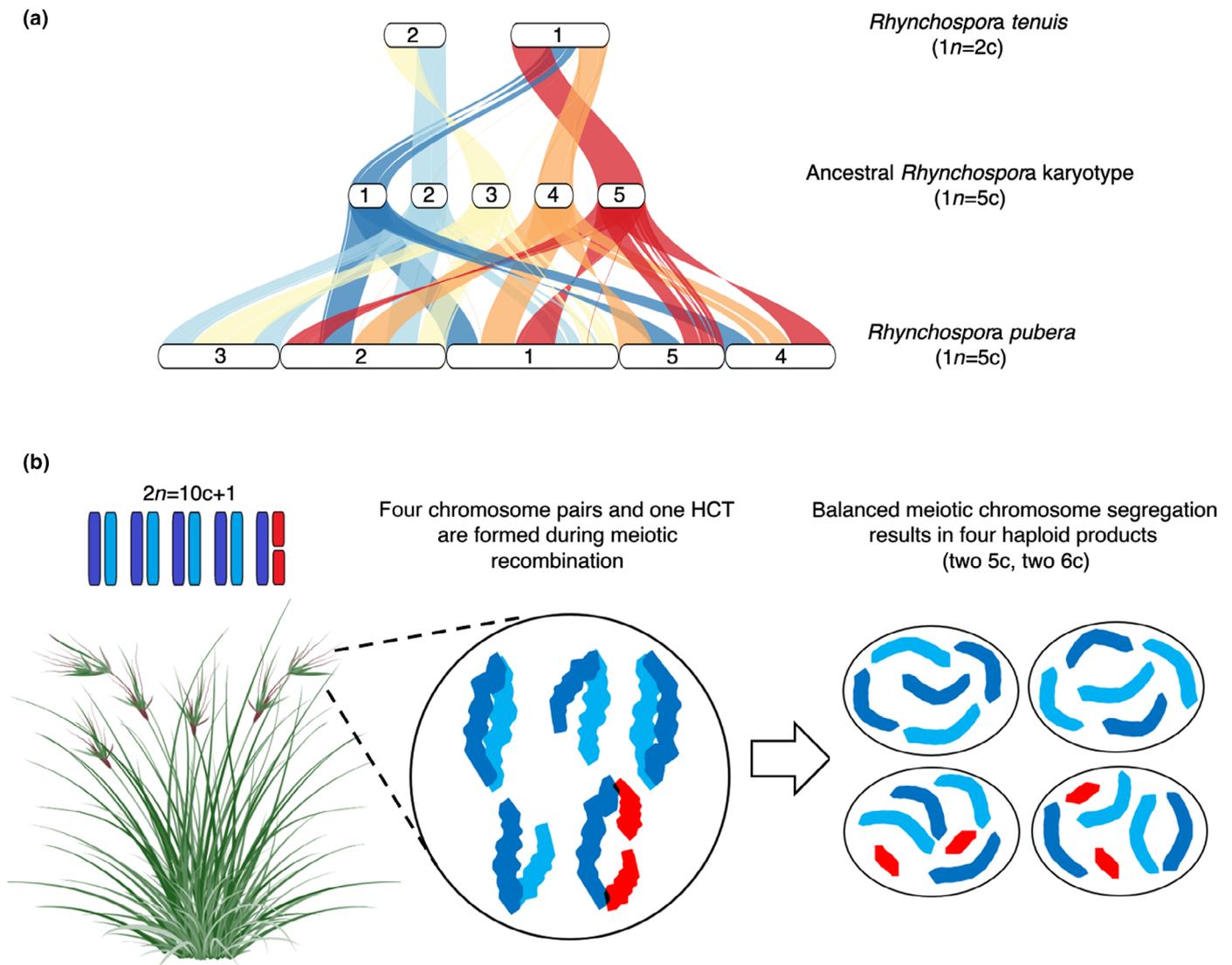


Fig. 3 Karyotype differences between *Rhynchosporas* and their impact on meiotic chromosome segregation. (a) Synteny plot between two *Rhynchospora* species and their predicted ancestral karyotype indicates how they evolved by chromosome fusions or a combination of whole-genome duplications followed by fusions. Chromosomes are scaled by physical position. (b) An accession of *R. pubera* with $2n = 11c$ due to chromosome fission results in four regular chromosome pairs (blue and light blue) and one heteromorphous chromosome trivalent (HCT/indicated in blue and red) during meiosis. However, holocentric-specific adaptations facilitate balanced segregation, generating four haploid nuclei with either 5c or 6c. This figure was partly created in BioRender (BioRender.com/k16f463).

three chromosomes, generating a ‘heteromorphous chromosome trivalent’ (HCT) (Fig. 3b), leading to chromosome missegregation. However, holocentric organisms navigate these dysploidy scenarios with ease: in *Leptidea sinapis*, hybrids of CAT ($2n = 56$) and SWE ($2n = 110$) exhibit balanced meiotic chromosome segregation despite numerous HCTs (Lukhtanov *et al.*, 2018). Likewise, in *Rhynchospora pubera* ($2n = 10$), an accession with 11 chromosomes arising from one fission ($2n = 10 + 1$) results in an HCT during meiosis, although balanced chromosome segregation is achieved, generating four haploid nuclei with either five or six chromosomes (Fig. 3b) (Cabral *et al.*, 2014). In a nutshell, holocentric chromosome adaptations involving somatic and meiotic cell divisions may facilitate the fixation of novel karyotypes,

highlighting the potential of holocentricity in driving rapid karyotype evolution.

VI. Conclusions

Significant progress has been made in understanding how centromeres change and induce chromosomes to change. Likewise, successful attempts to ‘harness’ centromere modifications with promising applicability for plant breeding programmes have been established. However, some approaches remain elusive, like targeted generation of stable chromosome fission/fusions. These limitations could be overcome by establishing ‘unconventional’ model organisms that are more ‘amicable’ to these chromosome

modifications. A monocentric candidate could be the fungus *Cryptococcus neoformans*, with a high tolerance to drastic chromosomal rearrangements. Other promising candidates could arise from the holocentric *Rhynchospora* clade, with some species having the correct attributes for becoming ideal laboratory plant models.

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Competing interests

None declared.

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