



# Subgenome assignment in allopolyploids: challenges and future directions

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Whole genome duplications (WGDs), also known as polyploid events, have played a crucial role in the evolutionary success of angiosperms across recent and ancient timescales. A recurrent observation from the analysis of allopolyploids is that one of the parental subgenomes is generally more dominant, referred to as ‘subgenome dominance’, based on higher gene content and expression patterns. Subgenome dominance has far reaching implications to research areas ranging from crop improvement efforts to evolutionary and ecological studies. However, the analysis of subgenome dominance in more ancient polyploids is complicated by a long history of homoeologous exchanges among subgenomes. Here, we will discuss how resulting homoeolog rearrangements and replacements have been ignored in previous studies and urge future studies to integrate phylogenetic approaches to assign homoeologs to parental subgenomes.

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## Subgenome dominance in ancient allopolyploids

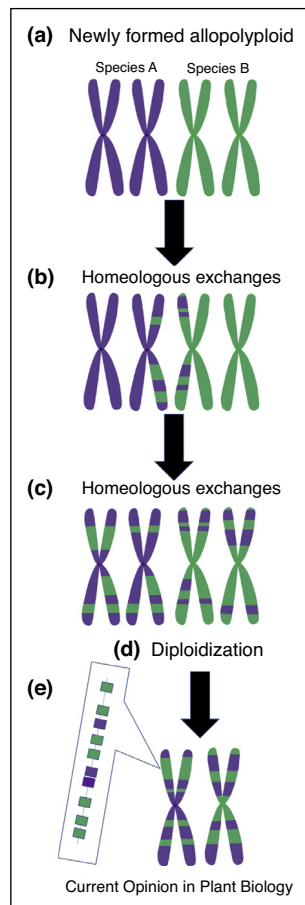
Previous studies of ancient polyploids revealed that not only is the retention of duplicate genes significantly biased towards certain functional gene categories [1<sup>••</sup>,2] but that one of the parental subgenomes often retains significantly more genes (i.e. dominant

subgenome) compared to the other recessive subgenome(s) (Figure 1) [3<sup>••</sup>,4]. Thomas *et al.* (2006) were the first to identify a dominant subgenome containing significantly more retained genes after the most recent ancient polyploid event in *Arabidopsis thaliana*. Subgenome dominance has since been documented in several other ancient polyploid genomes, including *Zea mays* (maize) [5], *Brassica rapa* (Chinese cabbage) [6], *Brassica oleracea* (European cabbage) [7] and *Gossypium hirsutum* (cotton) [8], among others. Furthermore, the dominant subgenome often exhibits significantly higher expression, stronger purifying selection, lower DNA methylation levels at CHH sites near genes, fewer siRNAs and contain significantly fewer transposable elements compared to the recessive subgenome(s) [5–10]. However, it is important to note that the dominant subgenome is not dominant in every homoeolog by homoeolog (i.e. gene level) comparison, but rather is more dominant based on subgenome-wide averages [9,11]. Thus, modern day ‘diploidized’ allopolyploids can be a mix of dominant homoeologs from multiple subgenomes (Figure 1d,e).

Subgenome dominance appears to be an emergent feature unique to allopolyploids and has not been observed in autopolyploids, likely because of genetic and epigenetic conflicts that arise between divergent subgenomes in allopolyploids [12–14]. The nucleus of autopolyploids contain three or more identical copies of a genome from only a single progenitor species [15–17]. Allopolyploidy, however, involves the hybridization of two or more diploid progenitor species, sometimes via polyploid intermediates for higher polyploids. Thus, allopolyploids face the unique challenge of organizing multiple distinct subgenomes, each with independent evolutionary histories and different (epi)genetic makeups, in a single nucleus [12,18]. The emergence of subgenome dominance, which was recently shown to become established in the first generation [9], resolves various genomic conflicts by preferentially silencing and gradually deleting the recessive subgenome(s) over evolutionary time. However, the mechanistic basis of subgenome dominance remains largely unknown, but is strongly correlated with subgenome differences in the density and regulation of transposable elements (TEs) [9,19<sup>••</sup>,20].

The subgenomes of some ancient polyploids, including *Glycine max* (soybean), which have been hypothesized to be autopolyploid [13,21], do not exhibit characteristics of

Figure 1



Homeologous exchanges shuffle homeologs among parental subgenomes. **(a)** Homeologous exchanges (HEs) between parental chromosomes (parental species A shown in purple, parental species B shown in green) begin to occur during meiosis immediately following allopolyploid formation and continue over successive generations [24]. **(b)** HEs lead to chromosomal regions from one parental species to be swapped with chromosomal regions from the other parental species. **(c)** Multiple HEs become fixed leading to varied homeolog ratios (e.g. 4:0, 3:1, 1:3, and 0:4) and swapping among parental chromosomes during subsequent generations. **(d)** Over deep evolutionary time, this leads to complete diploidization (i.e. base chromosome number reduction) with remnant duplicate blocks from the ancient polyploid event [32,33]. **(e)** A close-up view of one subgenome block consisting of a mix of homeologs from both parental species.

a dominant and recessive subgenome [10,22]. Zhao *et al.* (2017) recently showed that the two subgenomes in soybean were far more similar to one another compared to the two subgenomes in maize based on several criteria including gene content and expression, DNA methylation patterns, and overall transposable element content. However, this and previous studies were unable to further elucidate if soybean was an autotetraploid or an allotetraploid between two very closely related species with similar TE content. The magnitude of subgenome dominance is expected to be positively correlated with the

degree of genomic differences of the diploid progenitor species [13]. Thus, it is possible that the genomes of some ancient allopolyploids do not exhibit a strong signal for subgenome dominance simply because of the relative similarity of their parental genomes.

### Homeologous exchanges may obscure autopolyploidy versus allopolyploidy

Zhao *et al.* (2017) also reported that the soybean genome had undergone a greater number of chromosomal rearrangements compared to the maize genome. This is an important observation that may support an alternative explanation for the observed lack of subgenome dominance in soybean. Homeologous chromosomes have long been known to recombine, yielding homeologous exchanges (HEs) often resulting in complete replacement of chromosomal regions of one diploid progenitor species with that of another (Figures 1 and 2b) [23–25]. For example, an analysis of natural cultivars and resynthesized lines of allopolyploid *Brassica napus* (rapeseed) revealed that HEs are highly abundant, ongoing and biased towards one of the subgenomes [26\*]. The subgenome bias and high frequency of HE was also observed in other allopolyploids including cotton, *Tragopogon* (salsify), wheat, and *Brassica juncea* (brown mustard) [27–29]. For example, in cotton, the frequency of HEs was found to be approximately 8-fold greater than random mutations over the past 1–2 million years since polyploid formation [28]. Furthermore, a 5-fold subgenome bias for HEs was observed in cotton [28]. Thus, it is possible that the most recent whole genome duplication shared by soybean was an allopolyploid event, in which the recessive subgenome was largely replaced with the dominant subgenome over the past ~10 million years [22,30\*\*]. Extensive, subgenome biased HEs may also explain subgenome patterns reported in other currently assumed ancient autopolyploids [13].

It is essential that we as a community more critically evaluate how subgenomes are defined in ancient polyploids or acknowledge the limitations of the analyses of imperfectly phased subgenomes. In the remainder of this review, we will argue that future studies investigating the evolution of polyploid genomes should, if possible, incorporate phylogenetic approaches to more accurately assign homeologs to each parental subgenome. A phylogenetic approach could assist in resolving major outstanding issues in the field of polyploid genomics ranging from accurately differentiating polyploid classes [13] to identifying homeologs that are no longer in their original parental subgenomic blocks (Figure 1e). Furthermore, we anticipate that more accurately partitioned subgenomes will provide novel insights into subgenome dominance and the emergence of subgenome (parent) specific traits in allopolyploids [31]. However we acknowledge that homeologs in many ancient polyploid genomes will not be able to be completely partitioned to parental

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