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Genomic and phenotypic consequences of allopolyploidization in *Capsella*

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Abstract

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Allopolyploidization, the combination of whole-genome duplication (WGD) and interspecific hybridization, is a frequent and influential event in plant evolution. Allopolyploidization potentially affects both adaptation and diversification, yet the understanding of the consequences of allopolyploidy has been obscured by several issues. First, a broadly defined phenomenon, “genomic shock”, is assumed to be a general instant outcome of allopolyploidization, but this assumption has been challenged by recent studies. Second, effects of WGD and interspecific hybridization are confounded in allopolyploidization, which hinders the understanding of the specific effects of either component. Third, in natural allopolyploid species, instant and long-term effects of allopolyploidization are mixed, masking the evolution trajectory of allopolyploid genomes.

To address these issues, we studied the outcome of allopolyploidization in *Capsella bursa-pastoris*, a 100,000-year-old natural allotetraploid species. *C. bursa-pastoris* is a self-fertilizing weed with a worldwide distribution that originated through the hybridization between two diploid *Capsella* species with distinct mating systems. First, we investigated gene expression pattern in natural *C. bursa-pastoris* accessions with DNA- and RNA-sequencing data. Next, we resynthesized *C. bursa-pastoris*-like allotetraploids, along with diploid hybrids and autotetraploids. Phenotype and gene expression patterns were compared among those synthetic *Capsella* plants and natural *C. bursa-pastoris* to (i) distinguish the instant effects of hybridization from WGD and (ii) tell apart instant effects from long-term ones.

In general, non-additive gene expression was limited in both natural and resynthesized *C. bursa-pastoris*. We found the original TE-mediated genomic shock hypothesis did not fit the consequences of allopolyploidization in *Capsella*. Instead, homoeolog expression bias and the limited non-additive gene expression in resynthesized can be better explained by homoeologous exchanges and the intergenomic interaction of regulatory elements.

The relative gene expression pattern in resynthesized *C. bursa-pastoris* was mainly determined by hybridization, not WGD, but WGD still significantly affected phenotypes, likely through altering cell-size-related physical attributes. Both WGD and hybridization decrease the quality of pollen and seeds, but the two events were less deleterious when combined. In addition, the breakdown of self-incompatibility in *Capsella* could not be induced by pure WGD but was caused by the dominant interactions between S-alleles in hybrids.

Both gene expression patterns and phenotypes of *C. bursa-pastoris* were largely reshaped by long-term evolution. Almost all the transgressive gene expressions were unique to natural *C. bursa-pastoris*. Similarly, selfing syndrome and improvement of pollen and seed quality were likely acquired through long-term evolution. Compared to resynthesized allotetraploids, natural *C. bursa-pastoris* had more expression-level dominance toward the self-fertilizing parent, especially in flowers, mirroring a pronounced selfing syndrome. Nonetheless, the instant effect of allopolyploidization did contribute to gene expression patterns, as about 40% of expression level dominance in natural *C. bursa-pastoris* can already be found in resynthesized allotetraploids.

Keywords: Allopolyploidy, Polyploidy, Hybridization, Neopolyploid lines, Gene expression, Self-incompatibility, *Capsella bursa-pastoris*

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List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I. Kryvokhyzha D, Milesi P, Duan T, Orsucci M, Wright SI, Glémin S, Lascoux M (2019). Towards the new normal: Transcriptomic convergence and genomic legacy of the two subgenomes of an allopolyploid weed (*Capsella bursa-pastoris*). *PLOS Genetics* 15: e1008131.
- II. Duan T, Sicard A, Glémin S, Lascoux M (2022). Expression pattern of resynthesized allotetraploid *Capsella* is determined by hybridization, not whole genome duplication. *New Phytologist* (in press)
- III. Duan T, Sicard A, Glémin S, Lascoux M (2022). The evolution of an allotetraploid species and the development of the selfing syndrome: From resynthesized to established *Capsella bursa-pastoris*. (Manuscript)
- IV. Duan T, Zhang Z, Genete M, Poux C, Sicard A, Lascoux M, Castic V, Vekemans X (2022). The relative dominance of self-incompatibility alleles inherited from the parental species is a key determinant of the mating system of nascent *Capsella* allopolyploids. (Manuscript)

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Orsucci M, Yang X, Vanikiotis T, Guerrina M, **Duan T**, Lascoux M, Glémin S (2022). Competitive ability depends on mating system and ploidy level across *Capsella* species. *Annals of Botany* 129: 697–708.

Contents

Introduction.....	11
Allopolyploidization, the combination of interspecific hybridization and whole-genome duplication	12
Effects from interspecific hybridization.....	13
Effects from WGD	16
The confounded effects of hybridization and WGD	18
The myth of “genomic shock”	18
Mating system transition.....	19
Do hybridization and WGD interact?.....	22
The genus <i>Capsella</i> as a model system of studying allopolyploidization	24
Aims of the thesis.....	27
The present thesis.....	28
Paper I: Detailed gene expression pattern and the distribution of deleterious mutations in natural <i>C. bursa-pastoris</i>	28
Paper II: Dissecting the instant effects of hybridization and WGD in allopolyploidization.....	31
Paper III: Assessing the short- and long-term outcomes of allopolyploidization.....	35
Paper IV: The molecular basis of the breakdown of self-incompatibility in allopolyploids.....	40
Conclusions and future perspectives.....	43
Instant genomic and transcriptomic changes may come with allopolyploidization in <i>Capsella</i> , but do not constitute a genomic shock	43
WGD and hybridization played distinct roles in allopolyploidization.....	44
Svensk sammanfattning	46
Acknowledgements.....	50
References.....	52

Abbreviations

ELD	Expression-level dominance
HE	Homoeologous exchange
MEG	Maternally expressed gene
PEG	Paternally expressed gene
SC	Self-compatibility/Self-compatible
SI	Self-incompatibility/Self-incompatible
TE	Transposable element
TRE	Transgressive gene expression
WGD	Whole-genome duplication

Introduction

Diploidy, possessing two sets of homologous chromosomes, seems to be one paradigm of eukaryotes. The common ancestor of eukaryotes may have experienced the fusion or endomitosis of haploid (possessing one set of homologous chromosomes or plasmids) prokaryotic cells, leading to a significant increase in genome size (Goodenough & Heitman, 2014; Markov & Kaznacheev, 2016). Now most eukaryotes reproduce sexually with an alternation of diploid and haploid phases (Mable & Otto, 1998). Many groups of eukaryotes, including animals and vascular plants, spend most of their life cycle in the diploid phase (Otto & Gerstein, 2008), making diploidy the most familiar cytotype to people. However, the whole-genome duplication (WGD) that led to diploidy is not the only WGD event. WGD has recurrently occurred along the evolutionary history of most groups of eukaryotes (Aury *et al.*, 2006; Albertin & Marullo, 2012; Van De Peer *et al.*, 2017; Schwager *et al.*, 2017; Simakov *et al.*, 2020), generating organisms with more than two sets of homologous chromosomes (polyploids). WGD has a series of genetic and ecological consequences and has long been hypothesized to be the basis of the emergence of complex traits (Crow & Wagner, 2006; Freeling & Thomas, 2006), hence is likely a critical mechanism for the evolution of eukaryotes.

Apart from diploidy, another paradigm of eukaryotes was the “Tree of life” (Darwin, 1859; Doolittle & Baptiste, 2007; Burki *et al.*, 2020). The evolutionary history of eukaryotes has generally been depicted by a bifurcating tree, in which species split into new species but do not exchange genetic materials once formed. In other words, under this paradigm, interspecific hybridization has been overlooked. Nowadays hybridization among split species is known to be more common than previously thought and may prominently affect the process of adaptation and diversification (Mallet, 2005; Svoldal *et al.*, 2020; Edelman & Mallet, 2021; Steensels *et al.*, 2021).

WGD and interspecific hybridization, the two seemingly exceptional processes often come in pairs, giving rise to a unique process, allopolyploidization. Allopolyploidization is not only the sum of WGD and interspecific hybridization but may have its own attributes, and the main aim of the present thesis is to understand those attributes and how they evolved.

Allopolyploidization, the combination of interspecific hybridization and whole-genome duplication

Allopolyploidization is a compound process of interspecific hybridization and WGD. Genomes that have independently evolved in separate species merge again, resulting in organisms with doubled and highly heterozygous genomes. This peculiar process is widespread in eukaryotes. Allopolyploid species have been found in fungi (Albertin & Marullo, 2012), animals (Betto-Colliard *et al.*, 2018; Conant, 2020; Simakov *et al.*, 2020; Kuhl *et al.*, 2022), algae (Neiva *et al.*, 2017; Nomaguchi *et al.*, 2018; Sousa *et al.*, 2019), and land plants (Karlin *et al.*, 2009; Wu *et al.*, 2016; Sigel, 2016; Barbulescu *et al.*, 2017). In particular, allopolyploidization is pervasive in vascular plants, among which about 11% are allopolyploid species (Barker *et al.*, 2016).

Organisms with only WGD but no interspecific hybridization are called autopolyploids. Both allopolyploids and autopolyploids are referred to as polyploids. The conceptual distinction between them is interspecific hybridization (Parisod *et al.*, 2010b; Spoelhof *et al.*, 2017). In practice, allopolyploids are distinguished from autopolyploids by phylogenetic analysis (e.g., Wang *et al.*, 2021), disomic inheritance (chromosomes segregate from their homologous partner but not from the homoeologous partners during the first meiotic division, Hurka *et al.*, 1989), fixed heterozygosity between subgenomes (Cornille *et al.*, 2016), or biased retention of subgenomes (Garsmeur *et al.*, 2014; Simakov *et al.*, 2020). However, reminiscent of the vast grey zone in delimitating a species (De Queiroz, 2007; Roux *et al.*, 2016), a conceptual grey zone lies between autopolyploids and allopolyploids. Autopolyploids which arise from the intraspecific crosses between distant populations could have subgenomes with some degree of differentiation, while the parental species of allopolyploids could have various levels of molecular divergence. Besides, disomic inheritance may not always be established at once in allopolyploids. As a result, the segregation and recombination of homoeologous chromosomes would create “segmental allopolyploids” (Gaut & Doebley, 1997; Mason & Wendel, 2020) with both autopolyploid and allopolyploid genomic regions. Backcross with diploid or polyploid parental species is another possible source of segmental allopolyploids (Winterfeld *et al.*, 2012). In addition, empirically distinguishing ancient autopolyploidization and allopolyploidization can be challenging, especially when the close living relatives of parental species are not available for sampling. Many criteria (except phylogeny) for identifying allopolyploids are more about testing the divergence between subgenomes and do not necessarily match the mode of origin of polyploids (Le Comber *et al.*, 2010; Glover *et al.*, 2016; Spoelhof *et al.*, 2017). For all the reasons above, autopolyploidy and allopolyploidy are often regarded as the two ends of a continuum of different levels of parental divergence, rather than binary categories (Stebbins, 1971; Buggs *et al.*, 2009b; Tayalé & Parisod, 2013; Doyle & Sherman-Broyles, 2017).

Organismal-level WGD most likely arises through unreduced gametes, given the prevalence of unreduced gametes among plant taxa (Ramsey & Schemske, 1998; Kreiner *et al.*, 2017). But the most common pathway of allopolyploidization is still unknown. One hypothesis is that allopolyploids arise from the unreduced gametes of interspecific homoploid hybrids (Ramsey & Schemske, 1998), which means WGD follows hybridization. This hypothesis is mainly based on the fact that unreduced gametes are widespread, and that the rate of unreduced gametes can be greatly enhanced by interspecific hybridization reaching a considerable magnitude (Ramsey & Schemske, 1998; Sora *et al.*, 2016). On the other hand, the alternative order, in which WGD is followed by hybridization, is still possible. First, WGD in one or both parental species may largely reduce the barriers to interspecific hybridization and facilitate gene flow (Mooring, 2001; Eriksson *et al.*, 2017; Lafon-Placette *et al.*, 2018; Marburger *et al.*, 2019). Second, intraspecies ploidy level variation is common in angiosperms (Kim *et al.*, 2012; Zhang *et al.*, 2019a; Ebersbach *et al.*, 2020) but has been historically underestimated (Soltis *et al.*, 2007; Spoelhof *et al.*, 2017). In some cases, the extant allopolyploid species have both diploid and tetraploid parental populations (Novikova *et al.*, 2017; Ebersbach *et al.*, 2020), making the “WGD-first” hypothesis a plausible pathway. The paths of allopolyploid species formation may be diverse, and empirical studies still need to support the common belief in the predominance of the “hybridization-first” model.

Two key features of allopolyploidy are the reunion of divergent genomes (hybridization) and the sharply increased genome size (WGD). Both factors are influential and give unique features to the evolution of allopolyploid species. As hybridization and WGD often co-occur, the two elements become confounding variables to each other. The confounding effects are potentially the cause of the many long debates on the outcome and evolutionary significance of hybridization and WGD (Folk *et al.*, 2018). Another confusion about allopolyploidization can also arise from the outcomes of allopolyploidization over different timescales. The immediate effects of genome doubling and hybridization during allopolyploidization can be confused with the results of long-term evolution. Below, I first summarize the separate effect of hybridization and WGD at different time scales. Then I discuss several topics that are prone to the confounding effects of hybridization and WGD. Finally, possible interactions between hybridization and WGD are introduced.

Effects from interspecific hybridization

Instead of perturbing noises in the bifurcating evolutionary history, interspecific hybridization has been recognized as a critical source of genetic variation and may facilitate adaptation or diversification (Folk *et al.*, 2018; Taylor & Larson, 2019; Svardal *et al.*, 2020; Edelman & Mallet, 2021; Steensels *et al.*,

2021). Interspecific hybridization is especially prevalent in plants, both among extant species and among ancient lineages (Mallet, 2005; Whitney *et al.*, 2010; Yang *et al.*, 2018).

Despite the prevalence and potential evolutionary significance of interspecific hybridization, on average, newly formed interspecific hybrids have lower fitness than their parental species (hybrid incompatibility, Maheshwari & Barbash, 2011). Hybrid incompatibility reflects the divergence between parental genomes. The molecular divergence between parental genomes is not only determined by the time after divergence, but also accelerated by adaptation (Bombliès *et al.*, 2007; Chae *et al.*, 2014; McGirr & Martin, 2020), parental conflict (Vaid & Laitinen, 2019) and the activity of selfish elements, such as transposable elements (TEs, Hollister *et al.*, 2011), meiotic drivers (Fishman & Willis, 2005; Courret *et al.*, 2019), and competing regulatory elements (e.g., "enhancer run-away", Landry *et al.*, 2005; Fyon *et al.*, 2015).

Corresponding to these evolutionary drivers of divergence, various interactions between divergent genomes can immediately cause drastic genomic or transcriptomic changes in hybrids. The majority of the genetic interactions fit the Bateson–Dobzhansky–Muller model (BDM, Bateson, 1909; Dobzhansky, 1937; Müller, 1942), in which incompatibilities are caused by the negative epistatic effects between two or more loci that have independently evolved in separate species (Fishman & Sweigart, 2018). First, the divergence between regulatory networks is a common source of transcriptomic changes (McManus *et al.*, 2010; Maheshwari & Barbash, 2012; Combes *et al.*, 2015). The new intergenomic interactions of divergent cis- and trans-regulatory elements may cause diverse gene expression changes in hybrids, in particular, deviation from the mid-parent gene expression levels, i.e., non-additive gene expression, or in the extreme, transgressive gene expression (TRE) where the hybrid expression is larger or lower than in both parental species. Second, when parental species differ in TE loads and their epigenetic control, the mismatch between TE load and TE silencing mechanisms may reactivate TEs in hybrids, increasing TE expression or proliferation (Parisod *et al.*, 2010a; Romero-Soriano *et al.*, 2017; Mhiri *et al.*, 2019). A large-scale TE re-activation could further induce chromosomal structural changes (Parisod *et al.*, 2009; Chen *et al.*, 2020) and gene expression changes (Kashkush *et al.*, 2002; Butelli *et al.*, 2012). Third, parental conflict results in co-evolved epigenetic regulations on paternally expressed genes (PEGs) and maternally expressed genes (MEGs) in endosperms. Species with different mating systems (e.g., outcrossing and self-fertilization) are expected to have distinct strengths of parental conflicts and, therefore, to diverge in parental epigenetic control of gene expression (i.e., imprinting). The mismatch of imprinting control would cause a parental dosage imbalance in hybrids failing the development of the seed nutritive tissue, the endosperm, which is a common form of hybrid incompatibility in plants (Wolff *et al.*, 2015; Lafon-Placette *et al.*, 2018; Roth *et al.*, 2019; Coughlan *et al.*, 2020).

Apart from genetic incompatibilities and genomic imbalance, general meiosis defects can also impair hybrid fitness and further induce genomic changes. Homoeologous chromosomes with a lower homology may have difficulties in meiotic synapsis, resulting in unreduced gametes or gametes with an abnormal number of chromosomes (Ramsey & Schemske, 1998; Zanders *et al.*, 2014). A distinct chromosome-level phenomenon is the recombination between homoeologous chromosomes (homoeologous exchange, HE). HE is a hybridization-specific phenomenon. Until recently, HE was thought to be rare in allopolyploids, but its prevalence and influence have been highlighted in different species (Lashermes *et al.*, 2014; Lloyd *et al.*, 2018; Hurgobin *et al.*, 2018; Mason & Wendel, 2020). HE generates great genotypic and phenotypic variation and is potentially a common target of selection. On the other hand, the segregation and recombination of homoeologous chromosomes will expose more recessive epistatic incompatibilities caused by other mechanisms (Li *et al.*, 2022), hence random segregation and frequent recombination of homoeologous chromosomes in hybrids may reduce fitness if recessive epistatic incompatibilities are prevalent (Moyle & Graham, 2006; Yamaguchi & Otto, 2020).

Although interspecific hybridization can immediately cause extensive genomic and transcriptomic changes and lead to genetic incompatibility, from the perspective of long-term evolution, hybridization also increases heterozygosity and generates genetic and phenotypic variation and novelties (e.g., chromosomal structural variation and TRE), hence provides abundant materials for selection and may fuel adaptation or diversification (Svardal *et al.*, 2020). Besides, hybridization may break evolutionary constraints (Seehausen *et al.*, 2014; Patton *et al.*, 2022). Through the view of the genotype-fitness landscape model (Wright, 1932; De Visser & Krug, 2014), adaptation can be seen as a population “walks” on a genotype-fitness landscape and “climbs” to positions with higher fitness by mutation and selection. A genotype-fitness landscape may have multiple fitness peaks, separated by low-fitness valleys, but not all fitness peaks are accessible by mutational paths due to epistasis. Hybridization and subsequent segregation and recombination generate various new combinations of divergent loci, which may enable hybrid populations to leap over low-fitness valleys and explore the regions that adaptive walks cannot reach with only point mutations. In addition, large-effect mutations could be favored when a population is far from the adaptive peak (Orr, 1998; Kopp & Hermisson, 2009). As an analog to the relationship between large-effect mutations and sudden environmental changes, a “leap” on the fitness landscape caused by hybridization may have a larger chance to be favored under extreme environmental changes or in novel ecological niches.

Effects from WGD

WGD is pervasive in the phylogenetic tree of land plants, from numerous deep branches to the tips of most major extant clades (Van De Peer *et al.*, 2017; Yang *et al.*, 2018; Ren *et al.*, 2018). Most plants and all angiosperms are paleopolyploids (descendants of ancient polyploids; Blanc & Wolfe, 2004; Jiao *et al.*, 2011; Li *et al.*, 2015), and about 24% of vascular plants are from recent WGD events (Barker *et al.*, 2016). WGD is not only a common large-effect mutation but perhaps also a major mechanism in plant evolution. The occurrence of WGD (or WGD+hybridization) in phylogenies seems to be associated with exceptional environmental changes (Fawcett *et al.*, 2009; Estep *et al.*, 2014; Vanneste *et al.*, 2014; Lohaus & Van de Peer, 2016), and polyploid species are overrepresented in arctic flora (Brochmann *et al.*, 2004), invasive plants (Pandit *et al.*, 2011; Moura *et al.*, 2021) and domesticated plants (Salman-Minkov *et al.*, 2016). These observations gave rise to the hypothesis that polyploid populations may have a larger potential in adapting to exceptional environmental changes or reaching new environmental niches (Eric Schranz *et al.*, 2012; Tank *et al.*, 2015; Baniaga *et al.*, 2020), but the evolutionary significance of WGD is still controversial (Mayrose *et al.*, 2011; Kellogg, 2016).

WGD is a tremendous change in the genome. The sharp increase in DNA content instantly alters a series of physical parameters. The core change in autopolyploids is the larger nuclear and cell size (Jovtchev *et al.*, 2006; Beaulieu *et al.*, 2008; Maciak *et al.*, 2011; Otero *et al.*, 2013), although this enlarging effect of WGD varies among different cell types (Katagiri *et al.*, 2016; Wilson *et al.*, 2021). The enlarged nuclear and cell size implies the simultaneous changes in the cell volume-surface ratio, the ratio of nuclear volume and cell volume (karyoplasmic ratio), the speed of cellular transport and signal transduction, and the time of DNA replication (Bennett, 1977; Maciak *et al.*, 2011; Drake *et al.*, 2013; Doyle & Coate, 2019; Bomblies, 2020). In particular, the absolute concentration of gene products can be different between ploidy levels (Mishra *et al.*, 2010; Visger *et al.*, 2019), which may in turn affect the expression and function of dosage-sensitive genes. Therefore, theoretically, both the absolute gene expression level (e.g., expression level per cell or per biomass) and the relative gene expression pattern could be changed by pure WGD, even without the participation of hybridization. These molecular-level changes in autopolyploids are reflected in typical polyploid phenotypes, such as larger pollen grains and stomata, larger organs, darker leaves, slower growth rate, and different flowering times (Osborn, 2004; Marhold & Lihová, 2006; Yao *et al.*, 2011; Miller *et al.*, 2012; Deng *et al.*, 2012; Dai *et al.*, 2015; Zhang *et al.*, 2019b; Hu *et al.*, 2021).

Another important instant effect of WGD is on meiotic chromosome synapsis. Autopolyploids contain more than two sets of homologous chromosomes with low differentiation. Newly generated autopolyploids often form a

large number of multivalents and complex DNA crossovers at the metaphase of meiosis I, and the missegregation of multivalents would result in chromosomal damage or aneuploid gametes (Ramsey & Schemske, 2002; Bomblies *et al.*, 2015; Morgan *et al.*, 2021). Consequently, the fertility of new autopolyploids can be largely reduced (Ramsey & Schemske, 2002; Yant *et al.*, 2013).

Apart from the instant organism-level effects, WGD also has far-reaching influences on the evolution of polyploid populations. First, the newly formed polyploid is a minority cytotype surrounded by its diploid relatives. As inter-ploidy crosses usually result in nonviable offspring (“triploid block”; Köhler *et al.*, 2010), newly formed polyploids suffer from the lack of appropriate mating partners. This fertility bottleneck of new polyploids is termed “minority cytotype exclusion” (Levin, 1975) and is a major challenge for the establishment of polyploid populations (Husband, 2000). Second, possessing an extra copy of the genome masks the effect of recessive mutations and may lead to a period of relaxed selection. Relaxed purifying selection accelerates the accumulation of deleterious mutations in polyploids (“polysomic masking”, Douglas *et al.*, 2015; Paape *et al.*, 2018; Baduel *et al.*, 2019), which speeds up the degeneration of duplicated gene copies, but may also allow gene copies to partition the original function (subfunctionalization) or gain new functions (neofunctionalization; Conant & Wolfe, 2008; Flagel & Wendel, 2009). Therefore, the WGD-caused genomic redundancy is often thought to be an important mechanism of the evolution of genomic complexity, such as gene families with diversified functions and complex gene networks (Crow & Wagner, 2006; Freeling & Thomas, 2006; Glasauer & Neuhaus, 2014). Third, the long-term evolution of polyploid genomes may be driven by the adaptation to the short-term effects of WGD (Hollister, 2015; Bomblies, 2020). The cell-size-related WGD effects change the requirement and allocation of nutrition and energy (Šmarda *et al.*, 2013; Eliášová & Münzbergová, 2017; Anneberg & Segraves, 2020), and affect the efficiency of physiological processes (Maciak *et al.*, 2011; Roddy *et al.*, 2020; Bomblies, 2020), hence may push newly formed polyploids away from the original fitness optima. Meiotic problems are another serious challenge posed by WGD. In this shifted “genomic environment”, variants that restore a new stoichiometric balance of gene products or improve chromosome behaviors in meiotic synapsis are expected to be under positive selection. The long-term evolution of polyploid species may be confused with the instant mechanical effect of WGD (Baduel *et al.*, 2019), but can be distinguished by comparing natural and resynthesized polyploids (Yant *et al.*, 2013; Van Drunen & Husband, 2018; Domínguez-Delgado *et al.*, 2021).

As the joint result of random chromosome rearrangements, relaxed purifying selection, and selection on WGD-adapted alleles, polyploid species will gradually lose their polyploid status, although this process can be slowed down by purifying selection on the stoichiometric balance of dosage-sensitive genes (Bekaert *et al.*, 2011; Birchler & Veitia, 2012; Teufel *et al.*, 2016).

Eventually, paleopolyploids become more similar to diploids in terms of genome size, the number of functional homoeologous genes, and the mode of inheritance (“diploidization”, (Dodsworth *et al.*, 2016; Qiao *et al.*, 2019; Shi *et al.*, 2020). But the experience of once being a polyploid is not in vain. Many gene families are long-lived traces of WGD and are still supporting complex traits in paleopolyploids (Meng *et al.*, 2019; Hong *et al.*, 2021). And the recurrent WGD and re-diploidization processes in plants can aptly be described as “wondrous cycles of polyploidy” (Wendel, 2015).

The confounded effects of hybridization and WGD

The myth of “genomic shock”

A commonly tested hypothesis is that newly formed allopolyploids would undergo a “genomic shock” as a result of hybridization or WGD (Edger *et al.*, 2017; Baduel *et al.*, 2019; Burns *et al.*, 2021). Initially, the idea of genomic shock (genome shock) was introduced by Barbara McClintock (1984) to describe an instant stress-induced global reactivation of TEs, which further causes *stochastic* genomic restructuring. Hybridization was suggested to be one form of genomic stress that may trigger genomic shock. Over the past decades, the concept of genomic shock has been largely extended regarding its cause, mechanisms, and consequences. As the genomic shock hypothesis was often tested in allopolyploids, in which the effects of hybridization and WGD were mixed, sometimes WGD was assumed to be a cause of genomic shock (Baduel *et al.*, 2018). Other forms of genomic changes are also considered the manifestation of genomic shock, such as changes in methylation levels (Wang *et al.*, 2014; Edger *et al.*, 2017), gene expression changes (Hegarty *et al.*, 2006; Ha *et al.*, 2009; Buggs *et al.*, 2011; Dion-Côté *et al.*, 2014; Xu *et al.*, 2014; Wu *et al.*, 2018), and homoeologous gene loss (Wang *et al.*, 2014), although the changes may not necessarily result from a stress-induced global reactivation of TEs.

If we keep the narrow definition of the original “genomic shock” (genomic shock *s.s.*), which emphasized that genomic shock results from an instant stress-induced global reactivation of TEs, it is still not clear whether hybridization or WGD would trigger a genomic shock *s.s.* in newly formed allopolyploids. Studies on TE activity showed mixed results. Some studies revealed elevated TE activities in hybrids, autopolyploids, or allopolyploids (Ungerer *et al.*, 2006; Romero-Soriano *et al.*, 2017; Mhiri *et al.*, 2019), although the elevation of TE transcription or proliferation is usually moderate or restricted to several TE families. In contrast, many other studies found no evidence of TE reactivation after hybridization or WGD (Ågren *et al.*, 2016; Göbel *et al.*, 2018; Burns *et al.*, 2021). In general, genomic shock *s.s.* does not seem to be

a general outcome of allopolyploidization, and the magnitude of the shock is often limited.

On the other hand, if we adopt the broader and casual concept of “genomic shock” (genomic shock *s.l.*) and include all the instant genomic/transcriptomic changes that deviate from the expectation of *in silico* “hybrids” (simulated parental mixtures with no intergenomic interaction), regardless of the mechanisms, the remaining questions are: 1) For allopolyploids, is hybridization or WGD the main contributor of each form of the rapid genomic/transcriptomic changes? 2) To what extent would the initial “shock” reshape the genome and phenotypes of allopolyploids, compared to later long-term evolution? Is it a reshuffling of the genome, as indicated by its name, or mainly minor changes? Studies that compared allopolyploids with corresponding diploid hybrids or autopolyploids have provided insights for the first question. Hybridization, rather than WGD, seems to be responsible for several forms of instant changes in allopolyploids. In *Spartina* (Parisod et al., 2009; Salmon et al., 2005) and *Gossypium* (Song et al., 2017), the majority of the methylation changes in the resynthesized allopolyploids can already be found in diploid hybrids. Regarding gene expression changes, hybridization usually causes more non-additive gene expression than WGD (Wang et al., 2006; Chaudhary et al., 2009; Riddle et al., 2010). The second question is still open. Studies that compared natural and resynthesized allopolyploids revealed the significant influence of both instant effects and long-term evolution (Chaudhary et al., 2009; Buggs et al., 2009a; Flagel & Wendel, 2010; Zhang et al., 2016b).

Mating system transition

The transition from outcrossing to self-fertilization is often assumed to be one outcome of WGD (Barringer, 2007; Robertson et al., 2011), although the association between SI and polyploidy is not overwhelming (Mable, 2004). However, the causal relationships among WGD, hybridization, and the shifting of mating system may be hidden by the co-occurrence of hybridization and polyploidization. When allopolyploids and autopolyploids were not distinguished, polyploidy seemed to be associated with self-fertilization (Barringer, 2007). But some studies suggested that only allopolyploids are predominantly self-fertilizing, while autopolyploid species usually have an outcrossing or mixed mating system (Galloway et al., 2003; Husband et al., 2008). This distinction suggests that hybridization also plays a part in the association between WGD and self-fertilization in some cases. Several non-exclusive possible causal relationships are summarized below to explain the association between allopolyploidization and the shift to self-fertilization (**Figure 1**).

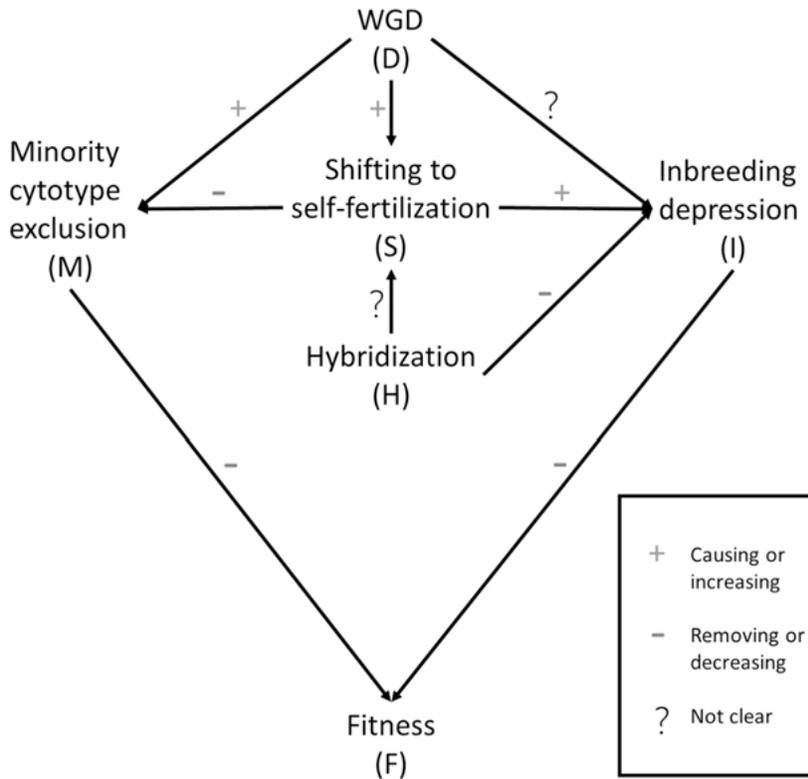


Figure 1. Plausible causal paths explaining the association between allopolyploidy and self-fertilization.

First, WGD or hybridization may directly cause the breakdown of self-incompatibility (SI) in some plants (**Figure 1**, paths D->S and H-> S). The transition to self-compatibility (SC) can be a byproduct of WGD or hybridization, without any fitness benefit. For plants with a gametophytic SI system, SI depends on the recognition between gene products of parental plant and haploid male gametocytes, therefore, WGD may instantly break the SI system by generating heterozygous diploid gametes (Zenil-Ferguson *et al.*, 2019). On the other hand, for plants with a sporophytic SI system, pollen rejection depends on the recognition between pollen coat protein and receptors on stigma, both of which were encoded by the self-incompatibility (S)-locus of the parental plant (2n). For these plants, WGD is not expected to cause an instant change to SC, but the hybridization between SC and SI parental species (population) often gave rise to SC allopolyploid species (Novikova *et al.*, 2017; Bachmann *et al.*,

2021; Kolesnikova *et al.*, 2022). When allopolyploid *Capsella* plants were resynthesized with the extant SC and SI parental species, all the resynthesized allopolyploids are SC, possibly due to the dominance relationship of alleles at the S-locus (Bachmann *et al.*, 2021). Hybridization could directly increase the prevalence of self-fertilization among allopolyploid species, if the hybridization between SC and SI species gives rise to more than 50% of SC offspring. Alternatively, hybridization may indirectly facilitate the change to self-fertilization by introducing variation of SC into polyploid populations and providing essential substrates for selection on mating system.

Second, the most widely accepted hypothesis is that self-fertilization is under positive selection among newly formed polyploids as one way to bypass the minority cytotype exclusion (Levin, 1975; **Figure 1**, paths D->M->F and S->M->F). Minority cytotype exclusion is a major challenge for new polyploid populations. The probability of the establishment of polyploid populations can be largely increased by adopting self-fertilization (Ramsey & Schemske, 1998; Rausch & Morgan, 2005; Fowler & Levin, 2016).

Finally, while self-fertilization helps polyploids to overcome minority cytotype exclusion, it comes with a cost, inbreeding depression. Inbreeding depression is the decrease in fitness due to higher homozygosity associated with inbreeding, possibly caused by exposing recessive deleterious alleles in homozygotes or reducing beneficial heterozygous loci (Charlesworth & Willis, 2009). The effect of WGD on inbreeding depression is still controversial and may depend on the genetic basis of inbreeding depression (Spoelhof *et al.*, 2017). Both higher and lower inbreeding depression has been observed in polyploids (Galloway *et al.*, 2003; Husband *et al.*, 2008; Barringer & Geber, 2008; Siopa *et al.*, 2020; Yao *et al.*, 2020). But at least inbreeding depression still exists in polyploid species and may increase over time (Husband *et al.*, 2008; Ozimec & Husband, 2011). Apart from that, highly homozygous chromosomes may aggravate the meiotic synapsis problems in autopolyploids, hence recurrent self-fertilization may be particularly harmful to autopolyploids. Hybridization may rescue autopolyploids from these self-fertilizing-related problems. In allopolyploids, the difficulties associated with self-fertilization are likely less severe due to their fixed heterozygosity, allowing the triple association among WGD, hybridization, and self-fertilization (**Figure 1**, paths S->I->F and H->I->F).

The transition from outcrossing to self-fertilization is generally accompanied by a series of morphological and physiological changes that together make a selfing syndrome (Sicard & Lenhard, 2011). These changes include a decrease in flower size, pollen-to-ovule ratio, scent and nectar production. They are believed to evolve in response to the relieve of the requirement of pollinators for reproduction, leading to the reallocation of the resources invested in building large and showy flowers to other fitness functions. While this syndrome has been well documented after the transition to selfing in diploid species, it remains unclear whether resource limitations similarly drive

flower evolution in outcrosser x selfer allopolyploids. For instance, if the incipient allopolyploidy is self-compatible, a dominance of the selfer alleles could be sufficient to readily generate a flower phenotype best suited for a selfing strategy. If, however, outcrosser alleles have some level of dominance, resource limitations may trigger the evolution of selfing syndrome traits. A question in the later scenario would then be whether the preferred evolutionary path could be to “repress” dominant outcrosser alleles at loci underlying the selfing syndrome in the selfer parent. Comparing genome expression and flower phenotypes of newly synthesized and established allopolyploids may answer these questions.

Do hybridization and WGD interact?

A naive yet complicated question is: why are allopolyploid species disproportionately common? If there is no association between interspecific hybridization and WGD, we may expect the ratio of autopolyploids and allopolyploids to be similar to the ratio of non-hybrid diploids and hybrid diploids. While the allopolyploid plant species are as common as autopolyploid species (Barker *et al.*, 2016), diploid hybrids do not seem to be as common as non-hybrid diploid species. The disproportional prevalence of allopolyploids could be an observation bias, as the raw rate of interspecific hybridization (Taylor & Larson, 2019; Suvorov *et al.*, 2020) or WGD (Soltis *et al.*, 2007) may be largely underestimated. In other words, allopolyploids may be common simply because WGD is a common mutation, and hybridization is a pervasive process. However, the alternative hypothesis that hybridization and WGD have beneficial interactions is also plausible. The interaction between hybridization and WGD can happen at several stages: the incidence of the two processes, individual fitness, and the possibility of speciation.

First, the incidence of WGD may be increased by interspecific hybridization. As mentioned earlier in this introduction, meiotic missegregation in interspecific hybrids can lead to unreduced gametes, which is hypothesized to be a major mechanism of WGD (Mason & Pires, 2015). In some cases, the rate of unreduced gametes was increased 50 times by hybridization (Ramsey & Schemske, 1998).

Second, once an allopolyploid organism is formed, the second possibility is that the combination of hybridization and WGD confer allopolyploids larger fitness than the corresponding homoploid hybrids and autopolyploids. Organismal-level beneficial interactions occur by at least two mechanisms:

- i) Hybridization and WGD may improve meiotic stability for each other. Meiotic synapsis in homoploid hybrids is impeded by the low homology between homoeologous chromosomes, while in autopolyploids meiotic synapsis is disrupted by the existence of multiple homologous chromosomes with low differentiation. The latter problem is expected

to be particularly challenging when WGD occurs in the species with a self-fertilizing history and extremely high homozygosity. In both cases, meiotic abnormality can largely decrease the viability of gametes (Kamstra *et al.*, 1999; Yant *et al.*, 2013). By combining hybridization and WGD, allopolyploids have both homologous chromosomes as proper synapsis partners and differentiation between homoeologous chromosomes, which is one prerequisite of regular preferential synapsis. Theoretically, the combination of hybridization and WGD can mitigate meiotic problems in both directions, but the strength of this interaction is unclear, as newly formed allopolyploids usually still have meiotic problems to some level (Szadkowski *et al.*, 2010; Henry *et al.*, 2014).

- ii) Fixed heterozygosity is a unique feature of allopolyploids. Once disomic inheritance has been established in allopolyploids, the divergent subgenomes would be maintained in the genome for a long time. Fixed heterozygosity would enable polyploids to benefit from the reproductive assurance of self-fertilization without the cost of inbreeding depression. For hybrids, fixed heterozygosity may also be beneficial. The recessive epistasis (interactions between homozygous loci) and dominant-recessive epistasis (interactions between a heterozygous and a homozygous locus) seem to be more influential forms of hybrid incompatibility, compared to the dominant epistasis (interactions between heterozygous loci, Turelli & Orr, 2000). A straightforward phenomenon that relates to this hypothesis is “hybrid breakdown”, that hybrid fitness largely decreases in F2 or backcrosses compared to F1 (Oka *et al.*, 2004). Without WGD, the segregation and recombination of homoeologous chromosomes in diploid hybrids would quickly expose a large amount of recessive deleterious epistasis within a few generations. The effect of genetic incompatibility may be too strong and devastating for the establishment of hybrid populations. In comparison, a WGD right after hybridization would hide the most severe type of genetic incompatibility, the interactions between homozygous loci or between a heterozygous and a homozygous locus.

Finally, after the establishment of an allopolyploid population, the combination of hybridization and WGD may give allopolyploids a larger advantage in speciation. WGD provided the “triploid block” (Köhler *et al.*, 2010) as instant reproductive isolation, largely reducing the backcross with parental species, while interspecific hybridization may result in transgressive phenotypes (Rieseberg *et al.*, 1999) and facilitate niche differentiation between hybrids and parental species (Arrigo *et al.*, 2016). The double effects of isolation may give allopolyploid population a higher chance of speciation.

Although the above mechanisms are listed side by side, their contributions to the prevalence of allopolyploid species may vary widely. Interpreting the evolutionary significance of allopolyploidization still requires assessing the magnitude of each level of potential interactions.

The genus *Capsella* as a model system of studying allopolyploidization

The genus *Capsella* is an excellent model system for studying allopolyploidization. It is a small genus in Brassicaceae, currently having four well accepted species (Hurka *et al.*, 2012): three diploid species, *Capsella orientalis* Klokov, *Capsella rubella* Reuter, and *Capsella grandiflora* (Fauché & Chaub.) Boiss, and one allotetraploid species, *Capsella bursa-pastoris* (L.) Medik. *C. bursa-pastoris* originated from the hybridization of the ancestral population of *C. orientalis* and the (*C. grandiflora* + *C. rubella*) lineage around 100,000 years ago (**Figure 2**, modified from Douglas *et al.*, 2015), in which *C. grandiflora* served as the pollen donor (Hurka *et al.*, 2012). Whereas *C. orientalis* split from the (*C. grandiflora* + *C. rubella*) lineage around 900,000 years ago (Douglas *et al.*, 2015). The four species strongly differ in their distribution range (POWO, 2022). *C. orientalis* grows in the steppes between Eastern Europe and Central Asia, while *C. grandiflora* and *C. rubella* are restricted to Mediterranean region. In contrast to these diploid species, the allotetraploid *C. bursa-pastoris* currently has a worldwide distribution. Nowadays there are reproductive barriers among the three diploid species, mainly caused by the dosage imbalance of imprinted genes in endosperm (Lafon-Placette *et al.*, 2018), but signals of gene flow from *C. orientalis* and *C. grandiflora* are found in different populations of *C. bursa-pastoris* (Han *et al.*, 2015; Kryvokhyzha *et al.*, 2019).

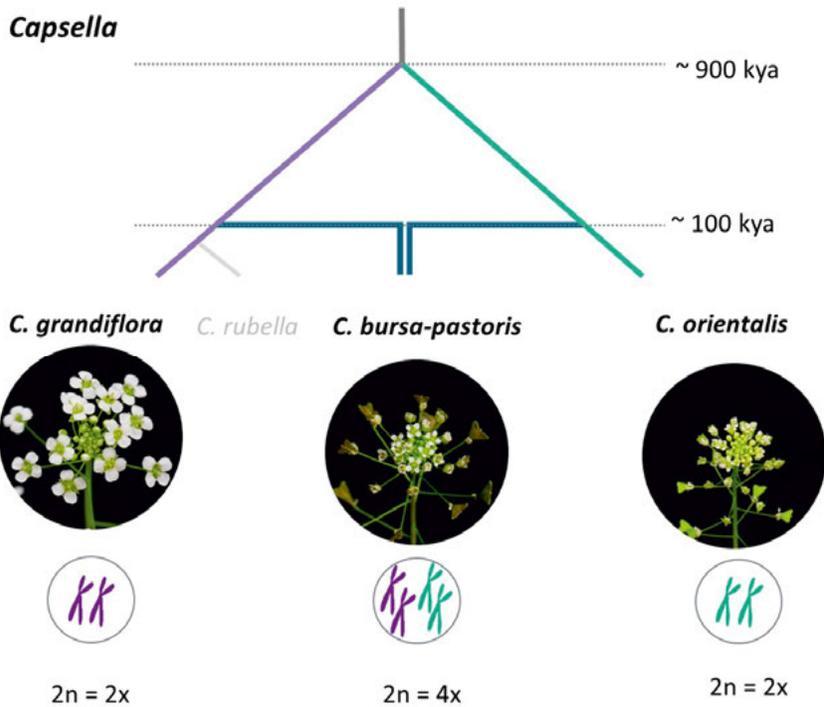


Figure 2. The *Capsella* genus. Plant material from *Capsella grandiflora*, *Capsella rubella*, *Capsella bursa-pastoris* were used in the present thesis. The published reference genome of *Capsella rubella* (Slotte *et al.*, 2013) was also used in analyses. The phylogenetic relationship and the time of divergence and allopolyploidization are from Douglas *et al.* (2015).

Among the four *Capsella* species, *C. grandiflora* is an outcrossing species, and the other three are self-fertilizing species. *C. grandiflora* has a sporophytic self-incompatibility system, in which pollen rejection is determined by self-recognition. The self-recognition is based on the interaction between a pollen coat ligand protein (encoded by the *SCR* gene) and a transmembrane receptor kinase on the surface of stigma (encoded by the *SRK* gene, Shiba *et al.*, 2001; Takayama *et al.*, 2001; Bachmann *et al.*, 2019). The two genes are tightly linked and are located in a small genomic region called S-locus. The transition to self-fertilization occurred at least twice in the *Capsella* genus. In *C. orientalis*, the transition from outcrossing to self-fertilization most likely achieved before the formation of *C. bursa-pastoris*, as *C. orientalis* and *C. bursa-pastoris* share the same frameshift deletion in the nonfunctional *SCR* allele (Bachmann *et al.*, 2019). In accordance with their mating systems, the three self-fertilizing species show typical selfing syndromes. Compared to the outcrossing *C. grandiflora*, the self-fertilizing *Capsella* species have smaller

flower size, a lower pollen-to-ovule ratio, and reduced emission of floral scent (Sicard *et al.*, 2011; Neuffer & Paetsch, 2013; Jantzen *et al.*, 2019; Woźniak *et al.*, 2020). Some of these changes in *C. orientalis* and *C. rubella* were shown to be due to convergent evolution (Woźniak *et al.*, 2020) and to encompass a broad array of traits even if changes tend to be stronger in reproductive traits (Zhang *et al.*, 2022). Self-fertilizing history also shapes the pattern of genetic variation. The self-fertilizing *C. orientalis* has extremely low nucleotide diversity and a larger proportion of deleterious mutations, compared to the outcrossing *C. grandiflora* (Kryvokhyzha *et al.*, 2019). Finally, different mating systems may affect the activity of selfish elements. Self-fertilizing species are expected to have a lower level of parental conflict and lower TE activity (Brandvain & Haig, 2005; Wright *et al.*, 2008). In congruence with these expectations, the genome of *C. grandiflora* contains more imprinted genes with higher expression levels, and a larger copy number of TEs than that of *C. orientalis* (Ågren *et al.*, 2014; Lafon-Placette *et al.*, 2018). The mating-system related divergence is expected to intensify genomic incompatibilities in the hybridization between self-fertilizing and outcrossing *Capsella* species.

Early allozymic studies on several loci suggested that natural *C. bursa-pastoris* have disomic inheritance (Hurka *et al.*, 1989), and a more recent simulation with an approximate Bayesian computation (ABC) method and high-throughput sequencing data confirmed that disomic inheritance is the most likely model for *C. bursa-pastoris* (Roux & Pannell, 2015). Compared to some newly formed allopolyploids with dramatic genomic changes (Szadkowski *et al.*, 2010; Chester *et al.*, 2012; Zhang *et al.*, 2016a; Lloyd *et al.*, 2018) or older paleopolyploids with severe genomic fractionation (Woodhouse *et al.*, 2010, 2014; Tang *et al.*, 2012; Renny-Byfield *et al.*, 2015), genomic changes in the allotetraploid *C. bursa-pastoris* seem surprisingly limited, deviating from the expectations of an initial “genomic shock”. In the genome of *C. bursa-pastoris*, there is no large-scale homoeologous gene loss, and no sign of large-scale chromosomal deletion or homoeologous exchanges (Douglas *et al.*, 2015). On average there is no large expression bias between the two subgenomes either (Kryvokhyzha *et al.*, 2019). Nonetheless purifying selection has been less efficient in *C. bursa-pastoris*, as a result of polysomic masking, demographic bottleneck and the change of mating system (Douglas *et al.*, 2015).

Today, the well-studied phylogenetic relationship (Douglas *et al.*, 2015), demographic history (Han *et al.*, 2015; Cornille *et al.*, 2016; Kryvokhyzha *et al.*, 2019), mechanisms of reproductive isolation (Lafon-Placette *et al.*, 2018) and self-incompatibility system (Bachmann *et al.*, 2019, 2021), together with the availability of a good reference genome (Slotte *et al.*, 2013) make the *Capsella* genus an excellent model to study the evolution of allopolyploidy.

Aims of the thesis

This thesis aims to investigate the outcomes of allopolyploidization in the genus *Capsella*. In particular, I asked:

1. What is the effect of allopolyploidization on gene expression in the natural *C. bursa-pastoris*? (Paper I)
2. Is there likely a genomic shock upon the formation of *C. bursa-pastoris*? If so, how severe is it? (Paper I, and II)
3. What are the separate instant effects of WGD and hybridization in allopolyploids, on gene expression and phenotypes? Which of these phenomena plays a larger role? Do the two processes interact? (Paper II)
4. How much of the gene expression pattern and other phenotypic changes in *C. bursa-pastoris* can be attributed to the instant effects of allopolyploidization and long-term evolution, respectively? (Paper III)
5. Does WGD or hybridization directly cause the breakdown of self-incompatibility in *Capsella* allopolyploids? If so, what is the underlying molecular mechanism? (Paper II and IV)

The present thesis

The four articles in the present thesis are part of a series of studies to understand the evolution of the shepherd's purse, *Capsella bursa-pastoris*, an allotetraploid species with a worldwide distribution. In the present thesis, Paper I, as previous studies, was based on natural accessions. In Paper I, we focused on changes in genomic and gene expression in three tissues, flowers, leaves, and roots. The three following papers mark a departure from Paper I and previous studies as they are all based on the newly created series of resynthesized hybrids and polyploids. In Paper II, we used the resynthesized polyploids to ask which of WGD and hybridization cause the strongest perturbations in relative gene expression patterns and phenotypes. In Paper III, we went one step further and asked to which extent the changes observed between the natural *C. bursa-pastoris* and its parental species could reflect the instant effect of allopolyploidization or long-term evolution. Finally, Paper IV builds on our series of resynthesized hybrids and polyploids but also on the knowledge accumulated over the last decades on the Brassicaceae self-incompatibility system. It demonstrates that the dominance relationship among S-alleles inherited from the self-compatible and self-incompatible parental species could cause the breakdown of self-compatibility in *Capsella* allotetraploids.

Paper I: Detailed gene expression pattern and the distribution of deleterious mutations in natural *C. bursa-pastoris*

Paper I was conceived as an extension of an earlier article on the genomics and transcriptomics of *Capsella bursa-pastoris* (Kryvokhyzha *et al.*, 2019). Both studies were our first attempt to leverage whole genome and transcriptomic data to assess the relative importance of parental legacy (Gottlieb, 2003) and genomic and regulatory changes in shaping a new allotetraploid species.

Natural *C. bursa-pastoris* is still at the onset of diploidization, but compared to some younger allopolyploid species with dramatic genomic and transcriptomic changes (Szadkowski *et al.*, 2010; Chester *et al.*, 2012; Zhang *et al.*, 2016a; Lloyd *et al.*, 2018), it seems to be exempt or have recovered from

the presumed “genomic shock” as there is no sign of massive genomic rearrangements or large scale gene loss (Douglas *et al.*, 2015; Kryvokhyzha *et al.*, 2019). How are homoeologous genes expressed in natural *C. bursa-pastoris*? Are their expression levels still largely determined by the inherited cis-regulatory variants (parental legacy) or reshaped by the presumed “genomic shock” and the 100,000-year evolution? Besides, the two diploid parental species of *C. bursa-pastoris* have different mating systems, which give rise to their distinct genetic features. Compared to the outcrossing species *C. grandiflora*, the self-fertilizing species *C. orientalis* has much lower genetic diversity and a higher proportion of deleterious mutations (Kryvokhyzha *et al.*, 2019). How did the divergent homoeologs evolve in natural *C. bursa-pastoris*? Did inherited deleterious mutations lead to further degeneration of homoeologs and affect gene expression? Finally, both *C. orientalis* and *C. bursa-pastoris* are self-fertilizing species with typical selfing syndromes such as flower size (Neuffer & Paetsch, 2013; Woźniak *et al.*, 2020). Would this similarity be reflected by expression patterns in *C. bursa-pastoris*? One possibility is that the global expression pattern of the *C. grandiflora*-derived subgenome has gradually converged towards the global pattern of expression of the *C. orientalis*-derived subgenome in flower tissues, but probably not in leaves and roots. To measure this relative change in gene expression in the different tissues we defined new convergence indices.

To characterize the transcriptomes and genome of the natural *C. bursa-pastoris*, we investigated detailed gene expression patterns and the distribution of deleterious mutations in this young allotetraploid species. Short-read (Illumina) whole-genome sequencing and RNA-sequencing of three tissues (flowers, leaves and roots) were conducted simultaneously on 16 accessions of natural *C. bursa-pastoris*, along with 4 accessions each of *C. grandiflora* and *C. orientalis*. The 16 accessions of *C. bursa-pastoris* were from three well-characterized major phylogenetic clusters (ASI, EUR, ME; Kryvokhyzha *et al.*, 2019) and a less studied unknown population (CASI), representing the natural variation of *C. bursa-pastoris* (**Figure 3**). The two subgenomes of *C. bursa-pastoris* and their expression levels were phased by the fixed variation between the *C. grandiflora* and *C. orientalis*. Putative deleterious mutations were identified from both subgenomes of *C. bursa-pastoris* and the parental species, based on the degree of conservation of protein sequences.

In general, the gene expression pattern in *C. bursa-pastoris* was conserved without drastic changes. The expression level of most genes in *C. bursa-pastoris* was still similar to one or both of the parental species, or has an intermediate value between parental species. Transgressive gene expression was rare. Meanwhile, the expression ratio of homoeologous genes can be well predicted by the expression ratio of the same gene in the two diploid parental species, showing a strong parental legacy.

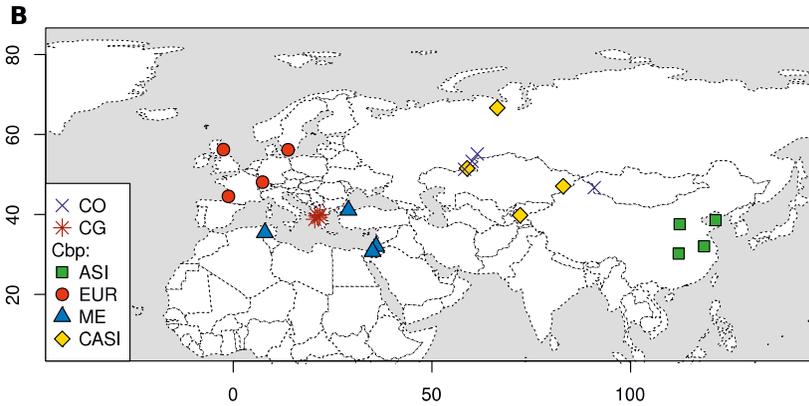


Figure 3. Sampling locations of the three *Capsella* species used in Paper I. CO, CG, ASI, EUR, ME, CASI correspond to *C. orientalis*, *C. grandiflora*, and four populations of *C. bursa-pastoris*, Cbp, (Asia, Europe, Middle East, and Central Asia), respectively. We shifted slightly population geographical coordinates when those overlapped to make all of them visible on the map.

Figure 4 summarizes one of the main findings of Paper I, namely that as expected, in flower tissues the global pattern of expression of the *C. grandiflora* subgenome shifted towards the global pattern of expression of the *C. orientalis* subgenome whereas in leaves and roots, the opposite, *i.e.* a shift of the *C. orientalis* pattern of expression towards that of *C. grandiflora*, is observed.

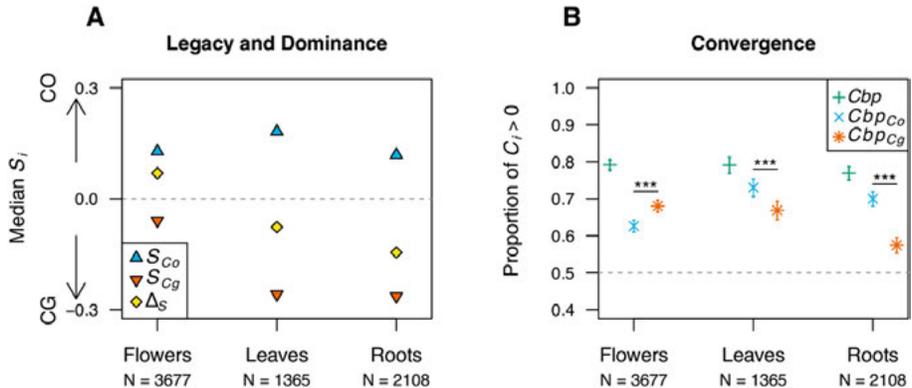


Figure 4. Similarity and convergence indices for differentially expressed genes between subgenomes of *C. bursa-pastoris*. A. For each tissue and each subgenome, the median of similarity indices for each subgenome (S_{Co} and S_{Cg}) are presented as well as the difference between the two indices (ΔS) that indicates the dominance of one parental genetic background. Grey dotted lines ($S = 0$) indicate level of no bias. B. The proportion of transcripts showing convergence ($C_i > 0$) is reported for the whole genome (green plus signs) or each subgenome (C_{bpCo} , C_{bpCg}). The significance of difference between the subgenome convergence indices is also depicted (binomial test, ***, $p < 0.001$). The number of differentially expressed genes considered for each tissue are indicated with N.

Paper I contains two other main findings on the evolution of an allopolyploid species. First, Paper I demonstrated the emergence of convergent homoeolog expression across the two subgenomes in *C. bursa-pastoris*. And secondly, the *C. orientalis* subgenome accumulated more deleterious mutations than the *C. grandiflora* genome, and this difference in the accumulation of deleterious mutations on the two subgenomes was associated with the level of gene expression.

Altogether, together with other recent genomewide studies of allopolyploid species (e.g., Griffiths *et al.*, 2019; Gordon *et al.*, 2020; Burns *et al.*, 2021) Paper I contributed to the ongoing re-evaluation of the evolution of allopolyploid species in the light of genomewide genomics and transcriptomics data, challenging a previous view that allopolyploidization would routinely lead to a drastic genomic shock. Paper I was still based on established allopolyploid species. In Papers II-IV we turn to resynthesized hybrids and polyploids to assess the importance of instant changes associated with the creation of a new allopolyploid species.

Paper II: Dissecting the instant effects of hybridization and WGD in allopolyploidization

To further dissect the different factors in allopolyploidization, we created a series of synthetic hybrids and polyploids with the diploid *C. orientalis* and *C. grandiflora* (**Figure 5**). These synthetic *Capsella* plants were later used in Paper II, III and IV.

In Paper II we focused on distinguishing and comparing the effects of interspecific hybridization and WGD in allopolyploidization. Both hybridization and WGD are often assumed to cause an instant genomic shock *s.s.*, dramatic genomic and transcriptomic changes induced by a global reactivation of transposable elements (McClintock, 1984; Bardil *et al.*, 2015; Fasano *et al.*, 2016; Baduel *et al.*, 2018). The relative contribution of hybridization and WGD to the initial gene expression patterns of allopolyploid organisms is unknown. Hybridization and WGD are also known for causing meiotic problems and decreasing the fertility of hybrids and autopolyploids (Szadkowski *et al.*, 2010; Mason *et al.*, 2011; Yant *et al.*, 2013; Bomblies *et al.*, 2016). It is not clear whether the two components have instant interactions on fitness. Theoretically the meiotic problems may be less severe in allopolyploids than that in diploid hybrids and autopolyploids.

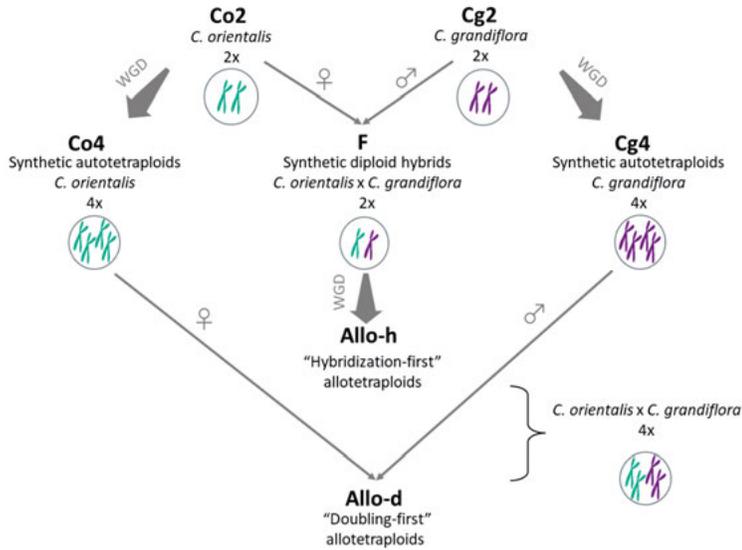


Figure 5. The seven groups of synthetic or natural *Capsella* plants used in this thesis. Synthetic diploid hybrids, autotetraploids and allotetraploids were generated with the diploid *Capsella orientalis* and *Capsella grandiflora*. Whole-genome duplication (WGD) was induced by colchicine treatments. *C. orientalis* served as maternal plant in all interspecific crosses, mimicking the formation of the natural *C. bursa-pastoris* (Hurka *et al.*, 2012). Group abbreviations are highlighted in bold. In paper III and IV, “Allo-h” and “Allo-d” were renamed as “Sh” and “Sd”, respectively.

We tackled these questions by comparing the RNA-sequencing data and other phenotypes among the seven groups of *Capsella* plants, i.e., two natural diploid species, diploid hybrids, two types of allotetraploids with different orders of hybridization and WGD, and two types of autotetraploids (**Figure 5**). The seven groups of *Capsella* plants were grown in a growth chamber under the same conditions. RNA from young inflorescence (flowers) and leaves was sequenced, and each of the seven groups was represented by six individuals. The relative expression of genes and TEs was quantified and compared among groups. For phenotypes, we recorded stem length, flowering time, pollen viability, the proportion of normal seeds, and the ability to produce seeds with only autonomous selfing, and each of the seven groups was represented by around 36 individuals.

Strikingly, we found WGD had almost no immediate effect on the relative gene expression pattern (**Figure 6**). The initial gene expression pattern of al-

polyploids was mainly determined by hybridization. Meanwhile, both hybridization and WGD had obvious effects on the phenotype (**Figure 7**). WGD may instantly affect phenotypes by altering the cell-size-related physical attributes without significantly distorting the relative gene expression pattern.

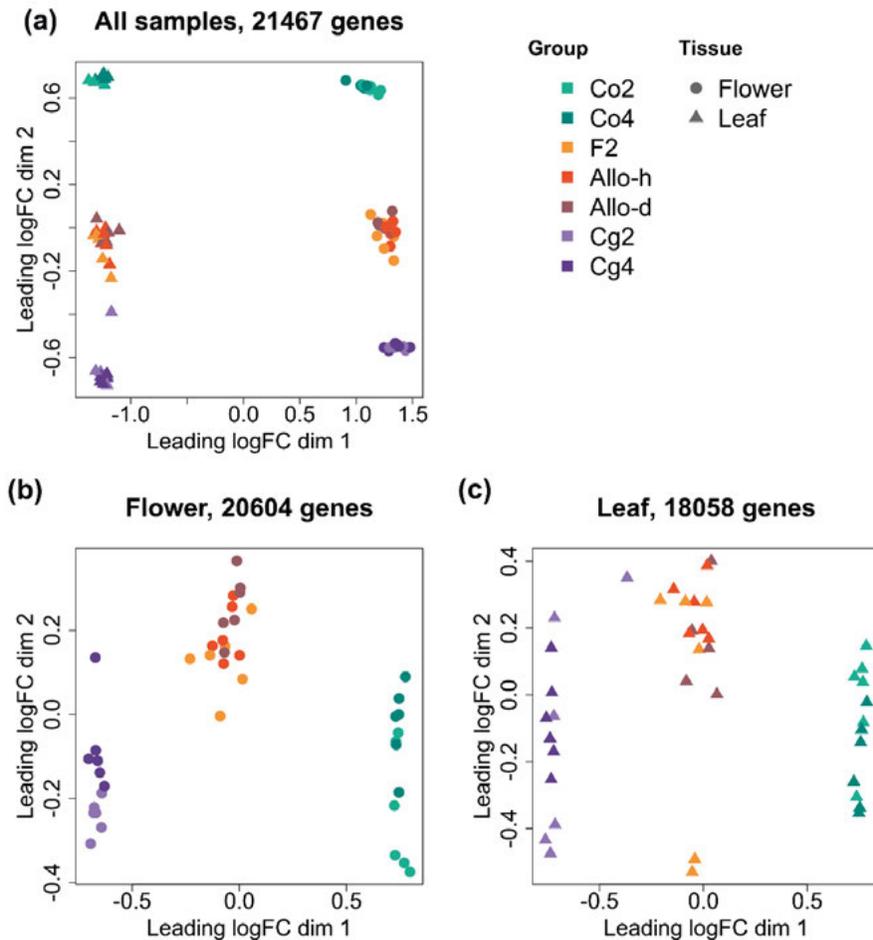


Figure 6. Transcriptome-wide expression pattern visualized by multidimensional scaling (MDS) plots. The plots were made with (a) all samples, (b) only the flower samples, or (c) only the leaf samples. Genes with transcripts per million (TPM) > 2 in at least three samples were used for the analysis, and the expression levels were normalized with the trimmed mean of M-values (TMM) method.

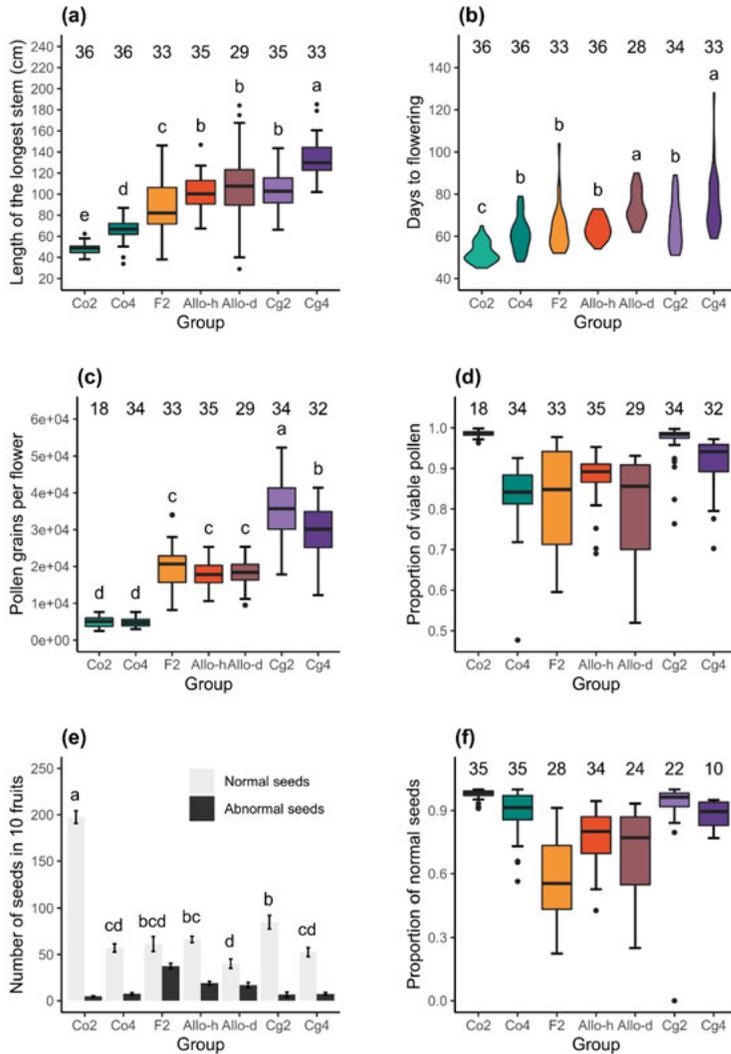


Figure 7. Phenotypes of the seven plant groups. (a) Stem length (b) Flowering time (c) Estimated pollen grain number per flower, averaged between the two flowers of each individual. (d) The proportion of viable pollen grains, calculated by examining > 300 pollen grains per flower, and averaged between two flowers. (e) The number of normal and abnormal seeds in ten fruits. Error bars show the group mean \pm standard error. (f) The proportion of normal seeds (normal seeds/total seeds). Individuals with less than ten fruits were excluded from the analysis. For boxplots and violin plots, sample size (number of examined individuals) was shown above the groups. When one-way ANOVA and Tukey's HSD test were applied (plots a, b and c and number of normal seeds in plot e), group differences at a significance level of $\alpha < 0.05$ were indicated by letters. Groups with the same letter are not significantly different. The seven groups are defined in **Figure 5**.

Overall, neither WGD nor hybridization seemed to trigger a genomic shock *s.s.* in the synthetic *Capsella* plants. The relative total expression level of TEs was not elevated by WGD or hybridization. Regarding WGD, there is almost no gene significantly differentially expressed (DEGs) between diploids and the corresponding tetraploids. As for hybridization, most DEGs between hybrids and one parental species were also DEGs between the two parental species and were largely shared among the three hybrid groups. These results suggest that gene expression changes in hybrids are highly deterministic and possibly caused by the regulatory divergence between the parental species, rather than a global TE reactivation.

In addition, we found WGD and hybridization have instant beneficial interactions on pollen viability and the proportion of normal seeds. Both hybridization and WGD alone decreased pollen viability, but WGD was less deleterious for hybrids, and a similar interaction was also observed for the proportion of normal seeds.

In summary, while the initial relative gene expression pattern in neo-allotetraploids was almost entirely determined by hybridization, WGD only had trivial effects on relative expression patterns. Neither hybridization nor WGD was likely to cause a genomic shock even upon the formation of *Capsella* allopolyploids. The two processes interacted, and each had a strong impact on phenotypes.

Paper III: Assessing the short- and long-term outcomes of allopolyploidization

In Paper III we moved toward distinguishing the short- and long-term outcomes of allopolyploidization. Allopolyploidization can instantly alter gene expression patterns. Apart from “averaging” the gene expression levels of the parental species, genetic incompatibilities between the divergent subgenomes and a potential genomic shock *s.s.* could instantly cause non-additive gene expression and variation of homoeolog expression bias in allopolyploids. Alternatively, non-additive expression and homoeolog expression bias in allopolyploids could be established later during gradual evolution, as a neutral process or shaped by several forms of selection. From the phenotypic point of view, the initial phenotypic effects of allopolyploidization could be enhanced or counteracted by later evolution, and original phenotypes may also arise in long-term evolution as an indirect result of allopolyploidy (Bombliès, 2020). Regarding gene expression patterns and phenotypes in natural *C. bursa-pastoris*, how much of them can be attributed to the instant effect of allopolyploidization, and how much of them resulted from long-term evolution?

To answer this question, we compared gene expression patterns and phenotypes of resynthesized and natural allotetraploids with the diploid parental species. Again, we use the resynthesized allotetraploids from Paper 1, but we added data from six lines of natural *C. bursa-pastoris* (**Figure 8**). The natural *C. bursa-pastoris* plants were grown together with the other seven plant groups and were sampled and recorded simultaneously with the same strategies as in Paper I. To pay special attention to the selfing syndrome, measurements on floral morphological traits were also added.

We found that most phenotypic differences between resynthesized and natural *C. bursa-pastoris* reflected the establishment of a strong selfing syndrome (**Figure 9**). The floral morphology of resynthesized allotetraploids was more similar to that of the outcrossing parental species *C. grandiflora*, while the traits of natural allotetraploids were much more similar to that of the self-fertilizing *C. orientalis*. This result suggests that the selfing syndrome of *C. bursa-pastoris* was established progressively during long-term evolution.

Another aspect of the phenotypic difference between resynthesized and natural allotetraploids is the pollen and seed quality. Pollen and seed quality were largely improved in natural *C. bursa-pastoris* (**Figure 9**). As pollen viability is a good indicator of meiotic behavior, the result suggests that meiotic stability in natural *C. bursa-pastoris* has been improved during long-term evolution.

The instant effect of allopolyploidization contributed to the gene expression pattern of natural *C. bursa-pastoris*, as about 40% of ELDs in natural *C. bursa-pastoris* can already be found in resynthesized allotetraploids (**Figure 10**). However, the initial gene expression pattern of allotetraploids was largely reshaped by long-term evolution. Most transgressive gene expression (TRE) and down-regulated expression-level dominance (ELD) can only be found in natural *C. bursa-pastoris* but not in resynthesized allotetraploids. The major direction of ELDs was also preserved. Compared to resynthesized allotetraploids, natural *C. bursa-pastoris* had much more ELDs toward the selfing *C. orientalis*, especially in flowers. This pattern mirrored the phenotypic difference between resynthesized and natural allotetraploids.

In addition, we found abundant traces of the segregation and recombination of homoeologous chromosomes (homoeologous exchange, HE) in resynthesized allotetraploids (**Figure 11**), suggesting that disomic inheritance was not an instant outcome of this allopolyploidization event. HE was a major source of homoeolog expression bias or homoeolog-specific expression loss in the resynthesized allotetraploids. We were unable to assess the effect of HE in natural allotetraploids with only RNA-sequencing data. The evolutionary significance of HE variation in natural populations of *C. bursa-pastoris* remains to be assessed.

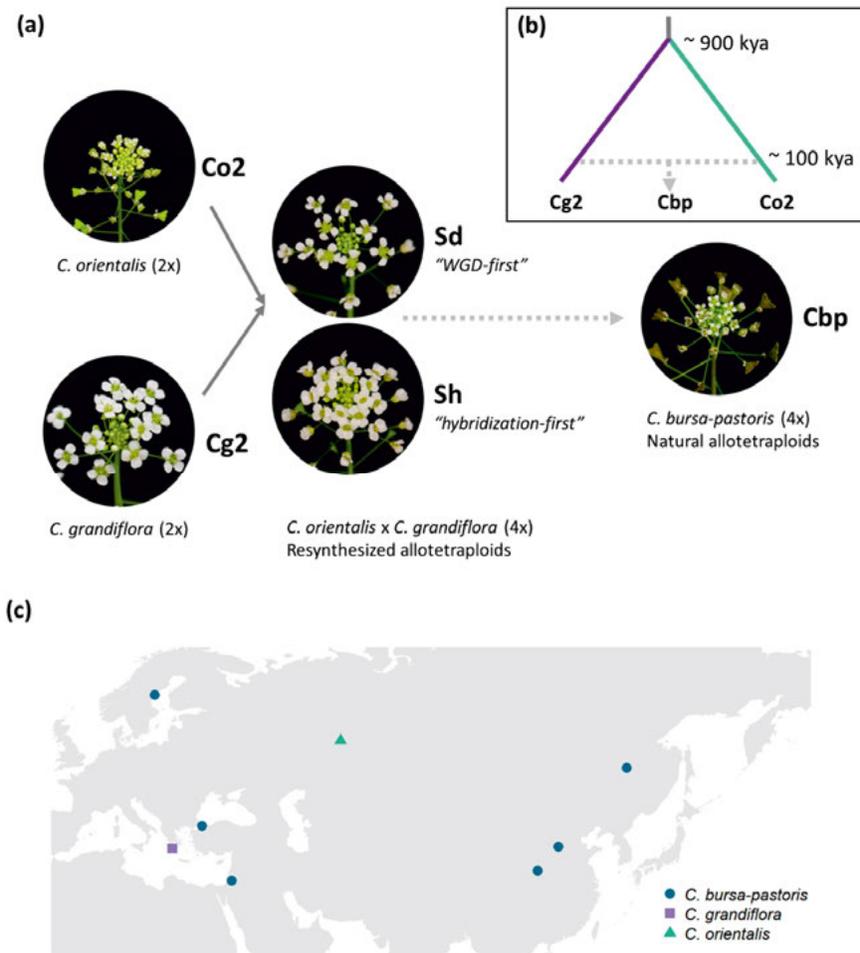


Figure 8. Plant material used in **Paper III**. (a) Five groups of *Capsella* plants. Diploid species (Co2 and Cg2 groups) and the second generation of resynthesized allotetraploids (Sd and Sh groups) are from Duan *et al.* (2022). Samples of natural allotetraploids, *C. bursa-pastoris*, were added to the present study. (b) Phylogenetic relationship of the three natural species, modified from Douglas *et al.*, (2015); kya: thousand years ago. (c) Geographic origin of the *Capsella* samples.

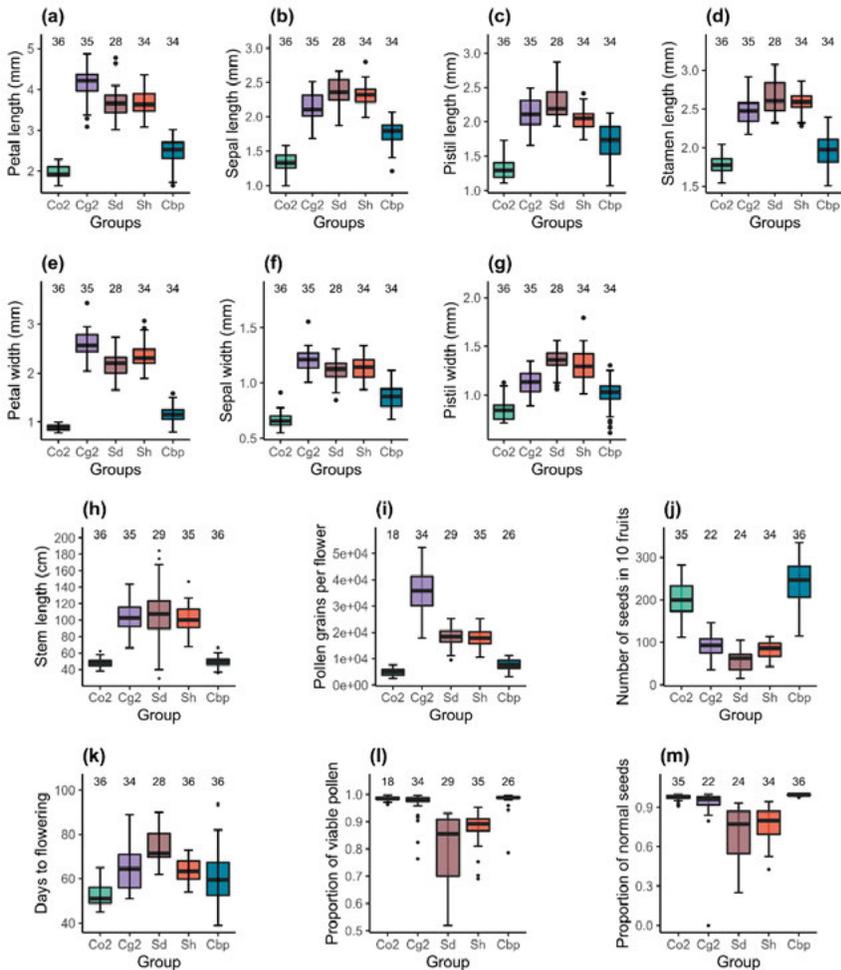


Figure 9. The establishment of the selfing syndrome in *C. bursa-pastoris*. Phenotypic traits of the five *Capsella* groups. Co2: diploid *C. orientalis*; Cg2: diploid *C. grandiflora*; Sd: WGD-first resynthesized allotetraploids; Sh: hybridization-first resynthesized allotetraploids; Cbp: natural allotetraploid *C. bursa-pastoris*. The measured traits were (a) petal length, (b) sepal length, (c) pistil length, (d) stamen length, (e) petal width, (f) sepal length, (g) pistil width, (h) length of the longest stem, (i) number of pollen grains per flower, (j) number of seeds in ten fruits, (k) number of days from germination to the opening of the first flower, (l) proportion of viable pollen grains and (m) proportion of normal seeds in ten fruits.

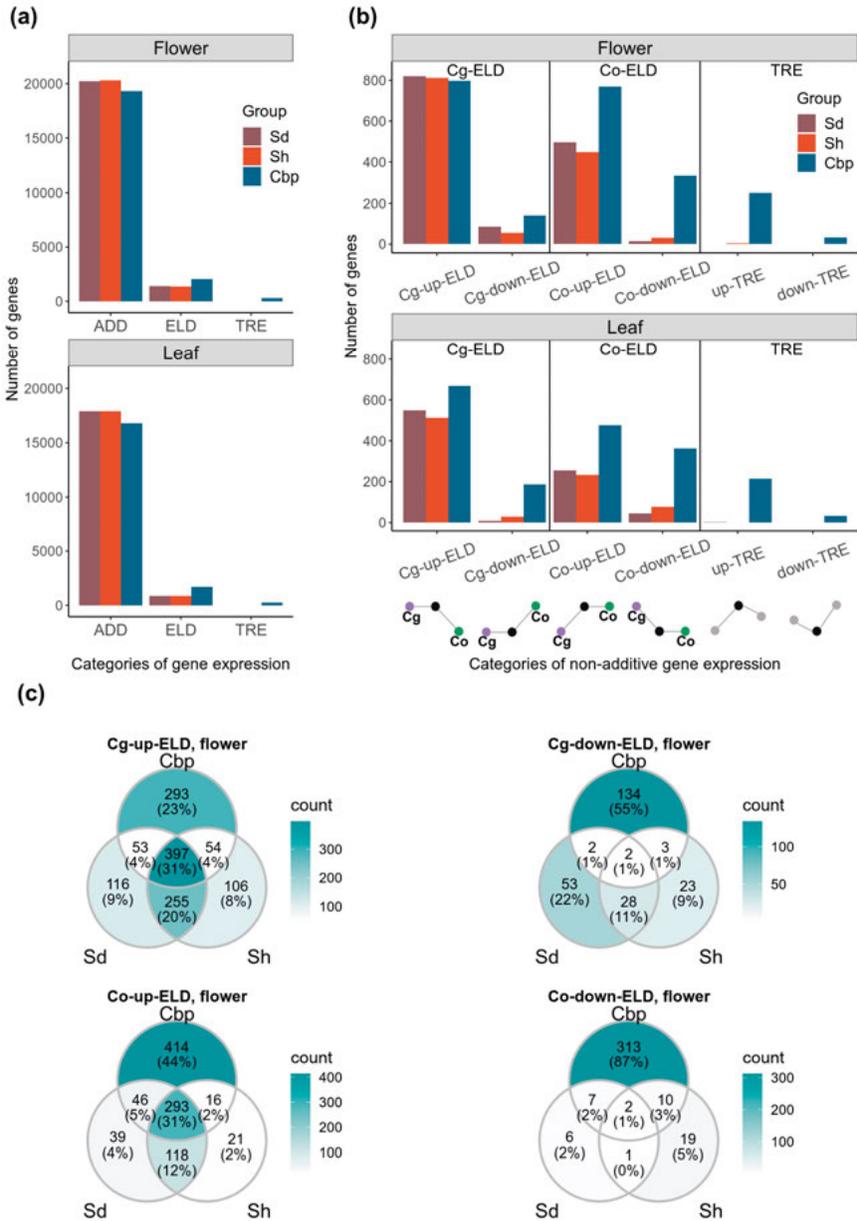


Figure 10. Additive and non-additive expression in allotetraploid groups. a) Number of genes that showed additive expression (ADD, including partial expression level dominance), complete expression level dominance (ELD), and transgressive expression (TRE) in each allotetraploid group. b) Genes with complete ELD or TRE were further classified by whether they were up- or down-regulated in allotetraploids, and whether the expression level in allotetraploids was similar to *C. grandiflora* (Cg-ELD) or *C. orientalis* (Co-ELD). c) Venn diagram of genes with complete ELD of the three allotetraploid groups in flowers, separated by directions of ELD.

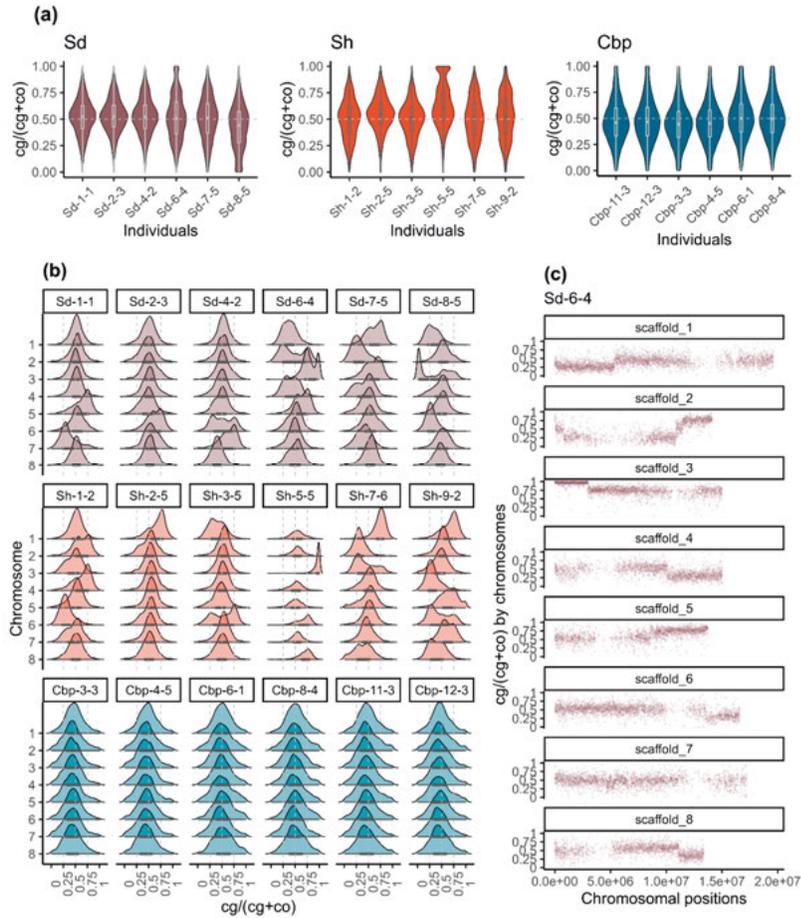


Figure 11. Variation of homoeolog expression bias (HEB) of the three allotetraploid groups in flowers. Gene HEB was calculated as the expression level of *cg*-homoeolog divided by the total expression level of both *cg*- and *co*- homoeologs ($HEB = cg/(cg+co)$). For each individual, HEB was calculated for 18,255 genes, which had count-per-million > 1 in all flower samples. The distribution of gene HEB was shown by (a) individuals and (b) chromosomes. (c) Gene HEB was also plotted along chromosome positions to show the sudden change of mean HEB between genomic blocks, taking individual Sd-6-4 as an example.

Paper IV: The molecular basis of the breakdown of self-incompatibility in allopolyploids

WGD has long been hypothesized to be associated with a transition to self-fertilization (Barringer, 2007; Robertson *et al.*, 2011), yet the association is controversial and may depend on the molecular basis of self-incompatibility (SI) system and whether hybridization has been involved (Mable, 2004;

Husband *et al.*, 2008). Our synthetic *Capsella* series provided an excellent system to dissect the direct effect of WGD and hybridization on mating system, and test if WGD or hybridization instantly causes the breakdown of SI in *C. bursa-pastoris*. In Paper II we observed that pure WGD could not directly cause the breakdown of SI in *C. grandiflora*, but hybridization between *C. orientalis* and *C. grandiflora* gave rise to both self-compatible (SC) and self-incompatible diploid hybrids or allotetraploids. This observation led to the main question of paper IV: What is the molecular basis of the variation of SI in *Capsella* hybrids?

SI in Brassicaceae is mainly determined by the interactions between the products of two genes: the *SRK* gene in stigma, and the *SCR* gene in anther (Shiba *et al.*, 2001; Takayama *et al.*, 2001). The two genes are tightly linked and located in a genomic region called S-locus. The S-locus has great polymorphisms in outcrossing species and S-alleles have a complex dominance hierarchy in anthers (Tarutani *et al.*, 2010; Durand *et al.*, 2014). The *SCR* gene on the relatively recessive S-allele can be transcriptionally silenced by small non-coding RNA (sRNA) generated by dominant S-haplotypes. One hypothesis is that the loss of SI in *C. bursa-pastoris* is immediately achieved by the dominance interaction of S-alleles in anthers (Bachmann *et al.*, 2021), but direct observation of the dominance relationship among *SCR* alleles is still lacking.

In paper IV we utilized the RNA-sequencing data from the synthetic *Capsella* hybrids (Paper II) and a newly developed bioinformatic pipeline, NGSgenotyp (Genete *et al.*, 2020), to formally test this hypothesis. First, we build a reference S-allele database of *Capsella*, using publicly available resequenced genomes of a large population of *C. grandiflora* (Josephs *et al.*, 2015). Second, we tested whether RNA-sequencing data can be used to identify S-alleles in *Capsella*, by applying the pipeline to the DNA- and RNA-sequencing data from Paper I. By comparing the *SRK* alleles identified with DNA and RNA data, we concluded that the co-dominant *SRK* expression in flowers can be reliably used for identifying S-alleles. Finally, we tested our core question: Can the dominance relationship of S-alleles explain the variation of self-compatibility in synthetic *Capsella* hybrids? We identify and quantify the expression of *SRK* and *SCR* alleles in the synthetic diploid or tetraploid *Capsella* hybrids, and compared the relative expression level of the non-functional S-allele (H4004) inherited from *C. orientalis* with seed production from autonomous self-fertilization.

We found that the predicted and observed dominance relationship of the functional and non-functional S-alleles could well explain the seed production

in both diploid and tetraploid hybrids (**Figure 12**). Our results, for the first time, formally verified the hypothesis of the role of dominance interaction of S-alleles in SI phenotype by linking the relative expression level of *SCR* alleles to the seed production in *Capsella* hybrids. The results suggest that the breakdown of SI in natural *C. bursa-pastoris* could be an instant result of the hybridization involving an SC parental species. Nonetheless, the fixation of self-compatibility in the allopolyploid species may also be facilitated by WGD-related selection, i.e., self-compatibility may be favored by selection due to the polyploid-specific challenge: meiotic cytotype exclusion. In the latter case, hybridization still plays a critical role as it introduces variation of self-compatibility to polyploid populations and enables WGD-related selection to promote self-compatibility.

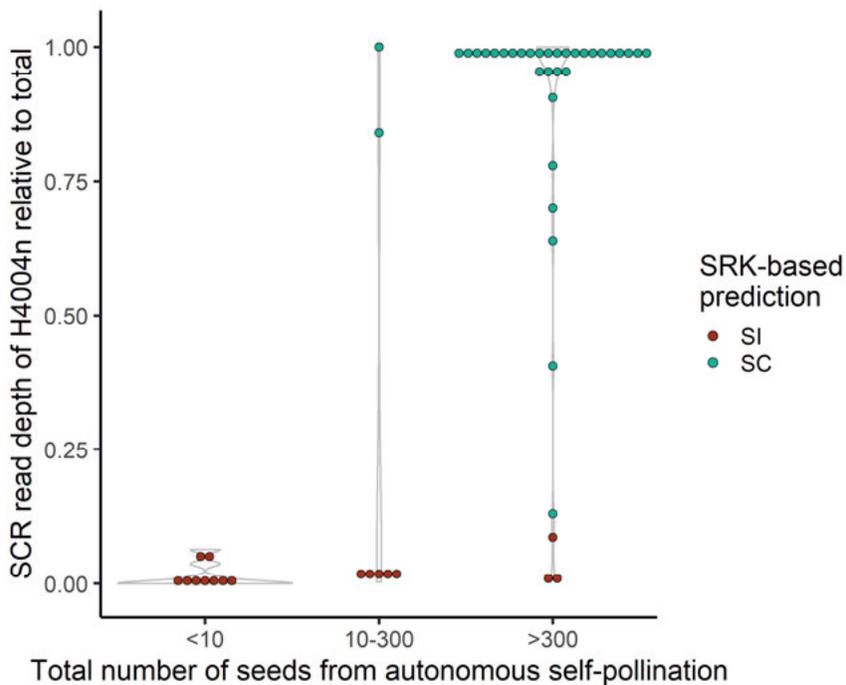


Figure 12. Relationships of the *SRK*-predicted dominance of the H4004n *SCR* allele, the observed relative expression level of the H4004n *SCR* allele and seed production in the diploid and tetraploid *C. grandiflora* x *C. orientalis*.

Conclusions and future perspectives

Instant genomic and transcriptomic changes may come with allopolyploidization in *Capsella*, but do not constitute a genomic shock

TE activities were often thought to play a central role in the genome evolution of allopolyploid species (Parisod *et al.*, 2009; Woodhouse *et al.*, 2014; Pont & Salse, 2017). A very common hypothesis is the TE-mediated genomic shock (McClintock, 1984; Baduel *et al.*, 2018), in which WGD or hybridization serves as genomic stress for globally reactivating previously silenced TEs, and further causes rapid genomic and transcriptomic changes. However, in the case of *C. bursa-pastoris*, we did not find any evidence for the genomic shock *s.s.* scenario. The expression level of TEs was not elevated in the resynthesized *C. bursa-pastoris*-like allotetraploids (paper II). Regarding the possible consequences of genomic shock *s.s.*, we found that non-additive gene expressions and homoeolog-specific expression loss were rare in both resynthesized and natural *C. bursa-pastoris* (Paper I, II and III). In addition, non-additive gene expression in resynthesized allotetraploids are highly deterministic, and expression level dominance was mainly caused by the expression change of the expression-level-recessive homoeolog (paper II and III). All these observations contradict the expectation of genomic shock *s.s.*

On the other hand, about 40% of the expression level dominance in the natural *C. bursa-pastoris* can already be observed in resynthesized allotetraploids, and striking variation of homoeologous expression bias was found in the resynthesized allotetraploids (paper III). In this sense, instant genomic and transcriptomic changes did come with the allopolyploidization event. But neither the magnitude nor the mechanism of these changes fits the concept of “genomic shock” anymore. These instant changes can be well explained by basic genetic mechanisms: the interaction, segregation and recombination of the divergent subgenomes (i.e., genomic incompatibility and homoeologous exchanges).

Similar to our results, recently the prevalence and influence of homoeologous exchanges have been recognized in more and more allopolyploid species (Lashermes *et al.*, 2016; Hurgobin *et al.*, 2018; Bertioli *et al.*, 2019; Li *et al.*, 2019; Zhang *et al.*, 2020). In nascent allopolyploids, homoeologous ex-

changes seem to be a paradigm rather than an exception. The effect of homoeologous exchange may be confused with chromosomal rearrangements, silencing of homoeologous genes, or gene flow from parental species. Despite being such a common and influential form of genetic variation, the evolutionary significance of homoeologous exchanges has not been fully studied in natural allopolyploid species.

WGD and hybridization played distinct roles in allopolyploidization

WGD and hybridization are often confounding factors for each other, due to the high prevalence of allopolyploid species. We used a full-factorial design to dissect the instant effects of WGD and hybridization in allopolyploidization.

The relative gene expression pattern in resynthesized allotetraploids was mainly shaped by hybridization, and WGD had almost no effect on relative gene expression pattern. Meanwhile, both hybridization and WGD instantly affected phenotypes. WGD may affect phenotypes through changing the cell-size-related physical attributes, rather than distorting the relative gene expression pattern. We found neither WGD nor hybridization significantly increased TE expression in the synthetic polyploids and hybrids, hence neither of them was likely a cause of genomic shock *s.s.* in *Capsella*. (paper II)

Regarding the change of mating system, we found WGD alone did not cause a breakdown of self-incompatibility in *Capsella*, but hybridizing involving the self-compatible *C. orientalis* enabled the majority of diploid hybrids and allotetraploids to produce seeds with autonomous self-fertilization (paper II). We further investigated the molecular basis of the self-incompatibility in *Capsella*. The seed set of the synthetic hybrids can be well explained by the expected dominance relationship of S-alleles and the observed relative expression level of the non-functional *SCR* allele in hybrids. The result showed that the dominance interaction of S-alleles may instantly create a variation of self-compatibility in allopolyploid offspring and enable selection to promote self-compatibility.

The role of interspecific hybridization and WGD in evolution reminds me of many features of the Parallel Metropolis coupled Markov chain Monte Carlo algorithm ((MC)³, Altekari *et al.*, 2004). The adaptive walk of a population on an n-dimensional genotype-fitness landscape (De Visser & Krug, 2014) is very similar to the Markov chain Monte Carlo (MCMC) algorithm in which a Markov chain walks on an n-dimensional posterior probability distribution, aiming to explore all peaks in a probability landscape. In this context, the function of hybridization is a bit similar to the replicate exchange process in (MC)³. Species (multiple Markov chains in (MC)³) independently evolved for a short while and then exchange their current alleles (states or heats in

(MC)³) with interspecific hybridization. The beneficial alleles from the other species may be retained in the follow-up non-random diploidization, just like the swapping of states would be accepted only if the foreign state is on a higher probability peak. The replicate exchange process releases the Markov chains that are trapped in local optima and greatly reduces the time for crossing low-probability valleys, while interspecific hybridization may release species from evolutionary constraints (Patton *et al.*, 2022) by enabling the trapped genotypes to access areas that cannot be reached by adaptive mutational paths and reduce the time of independent adaptation. Meanwhile, one attribute of WGD is similar to the idea of “heated chain” in (MC)³. With an extra copy of the genome, the temporarily relaxed purifying selection allows some alleles to more freely walk on the fitness landscape, similar to the heated chain that walks on a flattened version of the probability landscape in (MC)³. The “wonderous cycle” (Wendel, 2015) of WGD-diploidization is like the joint use of cold chains (diploids and paleopolyploids) and heated chains (young polyploids) in (MC)³, except that the cold and heated chains are not parallel but alternate in time. Even the general benefits seem similar: (MC)³ allows Markov chains to reach multiple peaks within a reasonable time, while hybridization and WGD may facilitate lineages quickly reaching more empty niches.

These metaphors do not cover all the important attributes of hybridization or WGD. For example, different from the time cost of adding additional parameters in (MC)³, hybridization and WGD have their unique penalties, such as hybrid incompatibility, meiotic abnormalities, and minority cytotype exclusion. Metaphors are always wrong in details and are not very useful until being developed into formal models. Nonetheless, the accumulating evidence has suggested that both hybridization and WGD are critical parameters for the populations that are wandering in the changeable fitness landscape and continually chasing fitness optima. This thesis focuses more on the outcome of allopolyploidization rather than its role in evolution. Understanding the direct outcome of allopolyploidization and disentangling the confounding factors would provide solid prior information for better modeling and elucidating the evolutionary significance of hybridization and WGD.

Svensk sammanfattning

De flesta växtarter är eller har varit polyploider, vilket betyder att varje enskild cell innehåller fler än två uppsättningar av kromosomer. Organismer ”polyploidiseras” genom en duplikation av hela genomet (WGD, ”whole genome duplication”). Duplikation av hela genomet är ofta, men inte alltid, förknippad med en hybridisering mellan arter. Beroende på hur det är med den saken kategoriseras polyploider som autopolyploider (endast duplikation av genomet), och allopolyploider (duplikation av genomet och hybridisering). Det är fortfarande lite känt i vilken ordning duplikation av genomet och hybridisering sker, och vilket som är det vanligaste vägen till allopolyploidisering, men icke-reducerade gameter, gameter vars DNA innehåller inte reducerats under meiosen är sannolikt inblandade i de flesta fall. Det har länge funnits ett stort intresse för allopolyploidisering eftersom den utgör en fundamental och betydelsefull evolutionär övergång hos växter, men också för att allopolyploidisering ansetts öka potentialen för anpassning och diversifiering, och därmed identifierats som ett viktigt verktyg i växtförädling.

I min avhandling har jag fokuserat på de genomiska och fenotypiska förändringar som sker vid allopolyploidisering. Mer specifikt, har jag undersökt om evolutionen av polyploidi inbegriper en första chockartad förändring av genomfunktion följt av en stabilisering, eller om den snarare innebär en mer gradvis förändring. Ett andra mål har varit att separera effekter av genomduplikation och hybridisering, för att förstå hur var och en av de två processerna bidrar till allopolyploiders egenskaper.

Som studiesystem har jag valt lomme (*Capsella bursa-pastoris*), en av världens vanligaste växter. Lomme är ett oansenligt ogräs med små vita blommor. Frukterna liknar en penningpung och har givit upphov till artens engelska namn ”shepherd’s purse”. Lomme är en ruderväxt som återfinns i mänskligt påverkade miljöer. Överallt där det finns människor kan man hitta lomme, förutom vid polerna och nära ekvatorn. Lomme är en tämligen ung allopolyploid som uppstod för cirka 100 000 år sedan som ett resultat av hybridisering mellan föregångare till de två diploida arterna *C. grandiflora* och *C. orientalis*. Den förra arten är korsbefruktande med stora blommor och har en begränsad utbredning. Idag återfinns den bara i bergstrakter i nordvästra Grekland och Albanien. Den självbefruktande *C. orientalis* förekommer däremot vitt spridd över de omfattande stäppområdena i Centralasien. Precis som lomme, är *C. orientalis* en ruderväxt med mycket små blommor. Det finns

en fjärde art i släktet: *C. rubella*, som också är självbefruktande och har mycket små blommor. Den återfinns runt Medelhavet och har indirekt spelat en viktig roll för mina studier: dess genom är sekvenserat och annoterat och den informationen har varit viktig.

Det finns åtminstone två olika sätt att söka förstå evolutionen av allopolyploida arter. För det första, kan man provta och studera individer i naturliga populationer av allopolyploiderna och dess föräldrararter. Man kan karaktärisera deras genom, genuttrycksmönster och fenotyp och från dessa data föreslå och testa olika hypoteser rörande deras evolution. Alternativt, kan man använda sig av en mer experimentell ansats och återskapa allopolyploider genom korsningar, vilket gör det möjligt att undersöka olika aspekter av polyploidiseringsprocessen i en kontrollerad miljö. Genom att jämföra återskapade allopolyploider med artificiella diploida hybrider och autopolyploider, kan man särskilja effekter av genomduplikation och hybridisering. Genom att jämföra återskapade allopolyploider med den existerande lommen blir det möjligt att särskilja polyploidiseringens omedelbara effekter på genom och fenotyp från de förändringar som skett under allopolyploidens vidare evolution. I min avhandling har jag och mina kolleger använt oss av båda dessa angreppssätt.

Vi började med att undersöka genom och genuttryck i naturliga accessioner av lomme och dess föräldrararter, den korsbefruktande *C. grandiflora* och den självbefruktande *C. orientalis*. Genuttryck undersöktes i tre vävnadstyper: blommor, blad och rötter. Tidigare studier har funnit viktiga genomiska och transkriptomiska (genuttrycks-) förändringar i allopolyploider, medan andra däremot hittat tydliga spår av föräldrararternas egenskaper och bara mindre förändringar. Hur skulle det se ut hos den allopolyploida lommen? Kom genetisk variation i de delgenom som ärvt från de två föräldrararterna att utvecklas på liknande vis, och började genuttryck att regleras gemensamt? Hos lomme visade sig den relativa styrkan i genuttryck för de flesta homeologer (genkopior som stammar från olika arter) att likna den hos föräldrararterna, vilket indikerade en stark effekt av ursprung. Men det fanns flera undantag. Många gener visade tecken på gemensam reglering: homeologer som var uttryckta i olika grad i föräldrararterna hade likartat genuttryck i lomme. Anmärkningsvärt var att dominansförhållanden skiljde mellan olika vävnader: genuttryck i blommor var mer likt det i den självbefruktande föräldern *C. orientalis*, medan genuttryck i rötter och blad var mer likt det i den korsbefruktande föräldern *C. grandiflora*. Att genuttryck i blommor hos lomme var mer likt det hos *C. orientalis* speglar det faktum att de två arterna båda är självbefruktande och har likartade blommor. Sammanfattningsvis, var förändringar i genuttryck tämligen modesta och förutsägbara vilket inte är i enlighet med vad som skulle förväntas om allopolyploidisering leder till chockartade förändringar i genomfunktion. Kan vi ha missat tecken på genomisk chock på grund av att vi här undersöker slutresultatet av 100 000 år av evolution? För att kunna särskilja effekter av hybridisering och genomduplikation, och av

omedelbara interaktioner i genomet respektive långsiktiga evolutionära förändringar, skapade vi med korsningar en serie av återskapade Capsellalinjer.

I ett första steg inriktade vi oss på att särskilja de omedelbara effekterna av genomduplikation och hybridisering. Vår serie av återskapade Capsellalinjer inkluderade diploida hybrider, autotetraploider av de två föräldrararterna, och två typer av allotetraploider där genomduplikation föregått hybridisering eller tvärtom. Hybridisering spelade stor roll för uppkomsten av relativt genuttryck i neo-allopolyploiderna, medan genomduplikation inte hade någon omedelbar effekt på relativt genuttryck men påverkade ändå fenotyper. We observerade inte något tecken på genomisk chock orsakad av transposoner i vare sig neo-hybrider eller neo-polyploider. För att sammanfatta: relativt genuttryck i neo-allotetraploider kunde nästan helt förklaras av hybridisering och påverkades endast marginellt av genomduplikation. Samtidigt var det så att fenotyper påverkades av båda processerna och deras interaktion.

För att undersöka hur lommens egenskaper utvecklats jämförde vi lommen med de återskapade allotetraploiderna. Den jämförelsen visade otvetydigt att egenskaper associerade med anpassning för självbefruktning ("självbefruktningssyndromet"), såsom små blommor, men också egenskaper som hög pollen- och frökvalitet i naturliga allotetraploider är resultatet av evolution över lång tid. På liknande sätt återfanns en del mönster i genuttryck bara i naturlig lomme. En del mönster i genuttryck i den naturliga allotetraploiderna liknade mer dem hos den självbefruktande föräldrararten än hos nyskapade allotetraploider, vilket kan kopplas till att lomme också är självbefruktande. Till sist fanns också tecken på att omedelbara förändringar kan vara av betydelse; en del mönster i genuttryck hos lomme observerades också i de nyskapade allotetraploiderna. Sammantaget visar resultaten att mekanismer som verkar över kort såväl som lång tid har bidragit till förändringar i genuttryck och fenotyp i naturliga allotetraploider. De initiala förändringarna i genuttryck har dock starkt modifierats under efterföljande evolution vilket lett fram till mer markanta morfologiska förändringar. Inga tecken på "chockartade" förändringar kunde observeras, vilket visar att evolutionen av allopolyploider kan vara jämn och gradvis.

Till sist, hur kom lommens parningssystem till? Lommen har två föräldrararter, den korsbefruktande *C. grandiflora* och den självbefruktande *C. orientalis*. Det är därför inte självklart att lommen skulle vara självbefruktande, även om förmåga till självbefruktning kan ge en nybildad art en fördel (det räcker med en individ för att en population ska kunna etableras). Hur och när blev lommen självbefruktande? Var det resultatet av hybridiseringen eller genomduplikationen? För att besvara dessa frågor använde vi på nytt våra neopolyploider. Växter som tillhör familjen Brassicaceae har sporofytiskt självinkompatibilitet som styrs av två kopplade loci, *SCR* och *SRK*, belägna i en liten genomisk region kallad S-locuset. Hos självinkompatibla arter, segregerar som regel ett stort antal S-alleler. Efter att ha karakteriserat S-alleler i en stor population av *C. grandiflora* kunde vi genotypa både *SRK* och *SCR* gener och

kvantifiera deras expressionsnivåer på basis av RNA-sekvensdata. Vi fann att en del av de återskapade diploida hybriderna och allopolyploiderna var självkompatibla, medan genomduplikation inte hade någon direkt effekt på självkompatibilitet. De återskapade allopolyploidernas självkompatibilitet kunde enkelt förklaras utifrån teoretiska och observerade dominansförhållanden bland *SCR* alleler. Resultaten tyder på att lommen blev självkompatibel främst för att den ärvde en tämligen dominant icke-funktionell S-allel från sin självkompatibla förälder, medan selektion kopplad till genomduplikationen kan ha hjälpt till att fixera denna egenskap hos arten.

Sammanfattningsvis har våra studier av allopolyploidi hos lomme visat att allopolyploidi kan uppkomma till följd av en gradvis och förutsägbar evolutionär process, i vilken genomduplikation och hybridisering har sina unika roller. Även om genomduplikation och hybridisering innebär en formidabel utmaning, behöver allopolyploidisering inte innebära en dramatisk genomisk chock eller något som kräver en omfattande omkoppling av det genomiska maskineriet. Tvärtom, tycks det som ett nytt normaltillstånd uppnåddes efter en tämligen stillsam revolution i det här fallet!

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