



Polyploidy before and after domestication of crop species

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Abstract

Recent advances in the genomics of polyploid species answer some of the long-standing questions about the role of polyploidy in crop species. Here, we summarize the current literature to reexamine scenarios in which polyploidy played a role both before and after domestication. The prevalence of polyploidy can help to explain environmental robustness in agroecosystems. This review also clarifies the molecular basis of some agriculturally advantageous traits of polyploid crops, including yield increments in polyploid cotton via subfunctionalization, modification of a separated sexuality to selfing in polyploid persimmon via neofunctionalization, and transition to a selfing system via nonfunctionalization combined with epistatic interaction between duplicated *S*-loci. The rapid progress in genomics and genetics is discussed along with how this will facilitate functional studies of understudied polyploid crop species.

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Introduction

Polyploidization¹ and its advantages and disadvantages in plants have historically attracted considerable attention [1–3]. Plants have undergone frequent polyploidizations in a lineage-specific manner, as exemplified by paleopolyploidizations (or ancient genome-wide duplications) in the Cretaceous–Paleogene boundary [4] or recent polyploidizations in crops [5]. Polyploidizations provided rapid phenotypic changes that are associated with variations in gene expression resulting from the combination of parental stress responses, novel allele dosages or regulatory interactions, or genetic and epigenetic rearrangements and modifications [6–10]. After polyploidization, duplicated gene pairs often undergo subfunctionalization, neofunctionalization, or nonfunctionalization over the long term, which releases them from functional redundancy or adaptive conflicts [11–13]. Empirical knowledge and some literature suggest the potential advantages of polyploidy for domestication or crop evolution, as represented by more edible parts (or yield), changes to selfing systems, and adaptation to new environments. Little is known about the detailed evolutionary paths and the molecular basis that are responsible for agriculturally favored traits and their roles in the establishment of polyploid crop species from their diploid (or lower ploidy) wild relatives.

Recurrent domestication events of diploids and polyploids

Domestication is an evolutionary process that occurs when wild plants are exposed to new selective environments for cultivation by humans after the last major glacial period, about 12,000 years ago [14]. Domesticated plant species have been improved in terms of seed shattering, edible part size, color, taste, and other agronomically important traits, and tend to be polyploid [5]. A recent database comparison of domesticated species and their suspected ancestral species generally supports this idea [5], but an inconsistent tendency has also been reported [15]. Table S1 lists 27 important polyploid crop species groups with their domestication pathways from putative progenitors or close wild relatives. Previous studies often categorized a crop species

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Keywords

Polyploidy, Domestication, Crops, Self-compatibility.

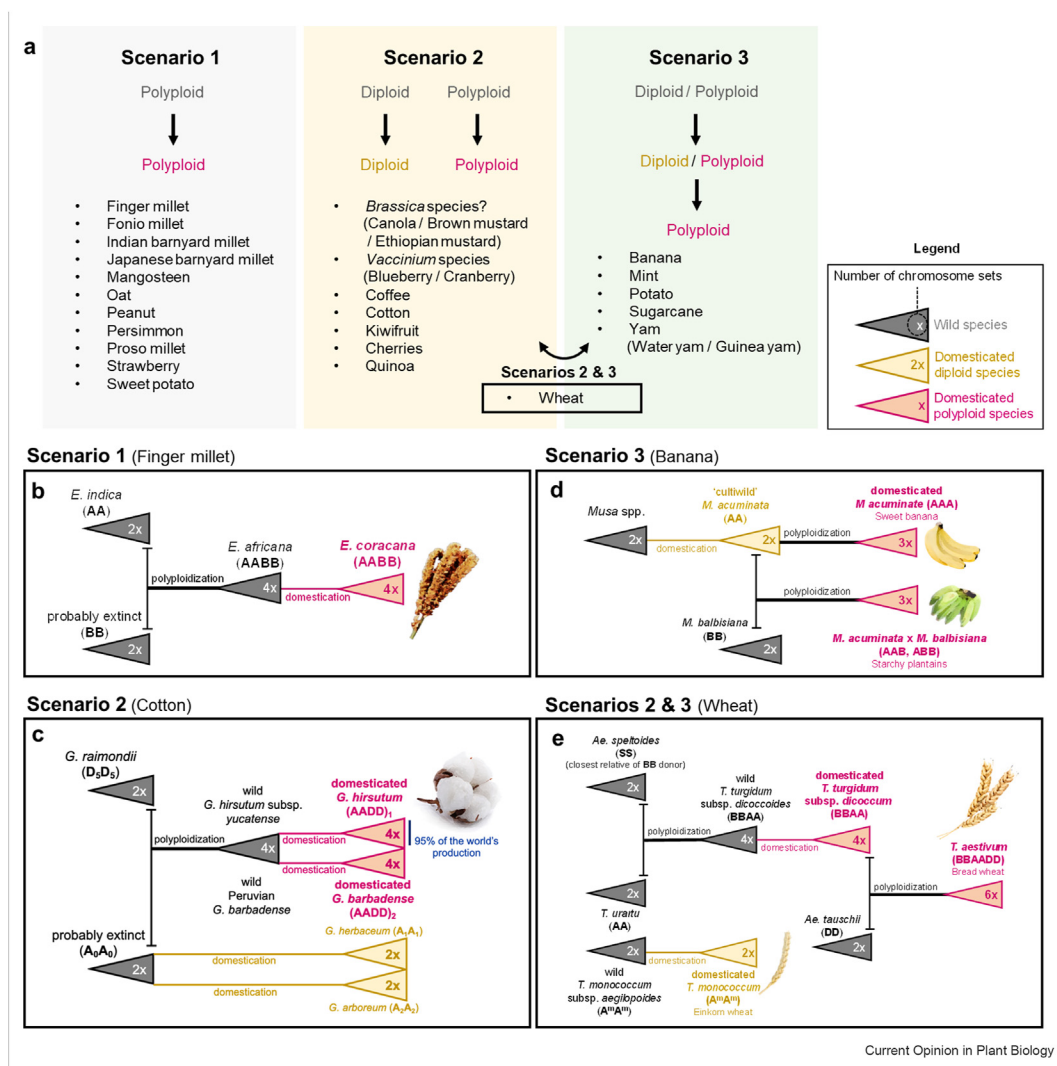
¹ Abbreviations: TE, Transposable element; SINE, Short interspersed nuclear element.

phylogenetically as either diploid or polyploid, and phylogenetic analysis at the species level supports the idea that polyploidy may have occurred before domestication [5]. However, domestication of diploid and polyploid species often coexists in a genus (or a closely related species), and gradual and complex polyploidization events are common, as represented by the following three scenarios (Figure 1a).

The first scenario is the simplest, in which a polyploid crop species was domesticated from a polyploid ancestor, and diploid species were not involved. Finger

millet (*Eleusine coracana*) is an allotetraploid crop species domesticated from a wild allotetraploid species (*E. africana*). One of its diploid progenitors is known (*E. indica*) but was never domesticated (Figure 1b) [16]. Similarly, oat (*Avena sativa*) is an allohexaploid (AACDD genome) domesticated from wild allohexaploid *A. sterilis* [17]. This scenario also includes fonio millet (*Digitaria exilis* and *D. iburua*), Indian barnyard millet (*Echinochloa frumentacea*), Japanese barnyard millet (*E. esculenta*), mangosteen (*Garcinia mangostana*), peanut (*Arachis hypogaea*), persimmon (*Diospyros kaki*), proso millet (*Panicum miliaceum*), strawberry (*Fragaria x*

Figure 1



Three proposed scenarios for the polyploidization and domestication processes in representative crops. **a**. List of crops categorized into the three scenarios. **b**. The simplest scenario in which a polyploid crop species was domesticated from a single polyploid species. The wild species *E. africana* (AABB genome) was derived from allopolyploidization long before domestication of finger millet. **c**. Parallel domestication from both diploid and polyploid progenitors in cotton. The vast majority of fiber is produced from the polyploid *G. hirsutum* despite four independent domestication events. **d**. After the domestication of diploid species, polyploidy contributed to agriculturally favored traits. Banana was (pre)cultivated as diploid (AA genome) and became triploid (AAA, AAB, or ABB) by subsequent polyploidization. **e**. The domestication of wheat involved scenarios shown in c and d. Both diploid and polyploid wheat were domesticated, but the production of the former is currently very limited. Domesticated tetraploid wheat (domesticated emmer wheat, which later produced durum wheat) further experienced allopolyploidization, and the resultant hexaploid bread wheat is widely cultivated.

amanassa) [18,19], and sweet potato (*Ipomoea batatas*) (Fig. S1).

In the second scenario, both diploid and polyploid species in a genus, in which polyploids often show advantages or specific characteristics, were domesticated independently. A typical example is the evolution of cotton (*Gossypium* spp.), which includes two diploid and two allotetraploid crops (Figure 1c). However, around 95% of worldwide natural fiber for cloth production is based on the allotetraploid species *Gossypium hirsutum*, also known as upland cotton [20,21]. Similarly, current data strongly suggest that a diploid *Coffea canephora* (Robusta coffee, CC genome) and an allotetraploid *C. arabica* (Arabica coffee, CCEE genome) were domesticated independently and that the polyploid form is responsible for 75–80% of the world's production [22]. In the section *Cyanococcus* of the genus *Vaccinium*, blueberry species *V. corymbosum* (4x) (or its hybrid 4x) and *V. virgatum* (6x) have been domesticated and are cultivated commercially. These are often called high-bush and rabbit-eye blueberries, respectively. By contrast, the other major sections in the genus *Vaccinium* are dominantly diploid and include some locally cultivated crops, such as cranberry and lingonberry [23,24]. Further examples of this parallel domestication of diploid and polyploid crops are kiwifruit (*Actinidia chinensis/deliciosa*), quinoa (*Chenopodium quinoa*), and cherry species (the subgenus *Cerasus* in the genus *Prunus*) which includes sweet and sour cherry.

In the third scenario, polyploidization events occurred after domestication and reinforced agricultural advantages. Recent bioinformatic and technological advances have enabled population genetic analysis of genome-wide polymorphisms [10] and have revealed more complex scenarios of polyploidy in crop species. The resequencing of 336 accessions of white Guinea yam (*Dioscorea rotundata*) and its relatives revealed that *D. rotundata* was initially domesticated as a diploid after the complicated hybridization of two progenitors, *D. abyssinica* and *D. praehensilis*. This was followed by further selection of triploid cultivated lines after hybridization with *D. togoensis* (Fig. S1) [25,26]. Water yam (*Dioscorea alata*) was also domesticated originally as a diploid and frequently migrated across Africa, South America, South Asia, and East Asia through clonal propagations [26,27]. This species often exhibits enrichment of triploidy or tetraploidy independently within the cultivation areas, presumably because of the artificial selection of better polyploid accessions [27]. The genus *Musa* (Figure 1d) includes domesticated bananas, which have been shown to be generally triploid, with genome constitutions of AAA (mainly sweet bananas) and AAB or ABB (predominantly starchy plantains). These triploidizations occurred independently in various regions through multiple hybridizations between preliminary domesticated (or “cultiwild”

[28]) diploid AA cultivars (*M. acuminata*) and BB cultivars (*M. balbisiana*) [28]. These triploidizations are thought to have contributed consistently to specific traits that are indispensable for banana cultivation, including plant vigor, yield, seedlessness (or increased proportion of edible parts), and hardiness [29].

A more complex but similar concept is applicable to the genus *Saccharum*, which includes the domesticated modern sugarcane cultivars (*Saccharum* spp.) and generally exhibits 10–13x ploidy levels [30]. An octaploid *S. officinarum* (called “noble cane”) was originally domesticated for its high sugar content. Modern sugarcane cultivars (10–13x) were later derived from multiple interspecific hybridizations between *S. officinarum* and the wild species *S. spontaneum* (5–16x), which displays greater hardiness [31], to balance the sugar content and environmental adaptive abilities. The same hybridization between *S. officinarum* and *S. spontaneum* also generated the other cultivated species, *S. barberi* and *S. sinense*, but they were less important than the 10–13x modern cultivars [32]. This third scenario also applies to potato (*Solanum tuberosum*) and mint (genus *Mentha*).

Some crop species have experienced a rich and very complex polyploidization history and, therefore, do not fit into only one of the single scenarios described above. One of these species is wheat, which shares the common patterns of scenarios 2 and 3 (Figure 1e). In the historical classification, wheat species were split into the nonmonophyletic genera *Triticum* and *Aegilops*. In the early Neolithic age in the Fertile Crescent, both diploid einkorn wheat (2x, A^mA^m genome) and tetraploid emmer wheat (4x, AABB genome) were domesticated [33]. There is now little commercial production of the former diploid, whereas durum wheat (tetraploid, derived from domesticated emmer wheat) is grown in Mediterranean climates for pasta, macaroni, and other foods. About 7000 years ago, the domesticated tetraploid wheat hybridized with a wild diploid species *Aegilops tauschii* (DD genome), and a new species of bread wheat (6x, AABBDD) emerged. Bread wheat constitutes the vast majority of current wheat production over a wide range of environments throughout the world [34]. A similar increase in ploidy also occurred independently in wheat. Timopheev's wheat (AAGG genome) was domesticated and then, by hybridization with diploid wheat (A^mA^m genome), the hexaploid Zhukovsky wheat (AAGGA^mA^m genome) emerged. Given that wheat is one of the most studied domesticated species, it is possible that future genomic studies of other plant groups will reveal a similar complex polyploidization history.

We note that, in any scenario, it is not trivial to systematically define whether domestication events had occurred before or after polyploidizations. For example,

because no truly wild population of the allotetraploid *Brassica napus* is known, it is difficult to determine whether *B. napus* was domesticated from wild allotetraploid populations that became extinct or was derived from polyploidization involving domesticated diploid crop species [35]. Furthermore, for tree or clonally propagated crops, wild accessions have often been introduced directly into commercial cultivation systems without clear genetic fixation. This situation has produced similar phenotypes with identical names for wild and crops species, which complicates the definition of crop species.

Although these scenarios often overlap, all three of them suggest that a simple dichotomy between diploid and polyploid crops may not be adequate to explain the role of polyploidization in domestication. Genomic data and population genetics study of domestication genes are useful for dissecting the role of polyploidy. A recent example is the population genetic analysis of the domestication genes of wheat, which has confirmed its known history, including independent domestication events. In wheat, the disruption of *Brittle Rachis 1 (Btr1)* is responsible for the non-shattering (or non-brittle rachis) trait, which is a hallmark of crop domestication that prevents the loss of grains until harvesting [36]. In the diploid crop einkorn wheat, haplotype analysis of population samples has shown that an amino acid change in *Btr1* was responsible for the non-brittle rachis trait [37,38]. The tetraploid domesticated wheat has two homoeologs *Btr1-A* and *Btr1-B*; the former was disrupted by a 2-bp deletion and the latter by a 4-kb insertion [39]. The presence of different mutation sites strongly suggests that the domestication of diploid and tetraploid wheat occurred independently, which supports scenario 2. By contrast, domesticated hexaploid wheat had the same mutations as tetraploid domesticated wheat, which is consistent with the idea that hexaploidization occurred after the domestication of tetraploid wheat [40] and supports scenario 3. These proof-of-concept studies in wheat suggest that similar population genetic analyses of domestication genes can be applied to other species.

Association between polyploidy and mass extinction periods

An association between polyploidy and mass extinction because of environmental changes has been suggested by the study of ancient polyploidy [4]. The estimated timings of ancient polyploidization events are significantly associated with the mass extinction at the Cretaceous–Paleogene boundary [41,42]. Moreover, polyploidization events in gymnosperm and in fish coincided with the Permian–Triassic mass extinction, the most severe in the history of the Earth [9]. These studies have prompted two mutually nonexclusive hypotheses: first, polyploidy can confer a broader

ecological tolerance, or environmental robustness [9,10], and second, the occurrence of polyploidy may have increased because of unreduced meiotic divisions induced by cold or other environmental stresses [9].

The contemporary period of thousands of years is considered the sixth mass extinction period of the Earth [43]. The prevalence of polyploidy in crop species at present provides evidence of another association between mass extinction and polyploidy, the latter of which has been attributed to artificial selection in agriculture. We hypothesize that agroecosystems provide open and disturbed unstable environments that are similar to those of past mass extinctions, in which polyploid species can earn better niches than diploid species. In other words, humans have forced crops both to survive in new extreme conditions and to express further traits beneficial for humans. This situation may be enhanced by novel polyploidization events, possibly reminiscent of scenario 3. The prevalence of polyploidy in invasive species [44] is consistent with this hypothesis.

Broader ecological tolerance has been suggested by the distribution range of polyploid species that are often distinct and broader than their progenitor species. A typical example is the broad distribution of polyploid wild potatoes, of which triploids tend to occur in warmer and colder areas, and higher-level polyploids tend to occur in colder areas compared with diploids [45]. Another good example is the gradual polyploidization in the genus *Fragaria* (strawberry), which may have contributed to its wider distribution [18] in which higher ploidy is more adaptive to heterologous and stressful environmental conditions [46]. More than 50 years ago, polyploids were proposed to be “general purpose genotypes” that could tolerate a wide range of environmental conditions [47]. Recent genome-wide studies of polyploid species suggest that the combination of adaptive traits inherited from progenitor species is a major molecular basis of the generalist niche [10].

Molecular basis for agriculturally favored traits of polyploid crops

In contrast to the theoretical assumptions about the benefits of polyploidy, the molecular mechanisms responsible for agriculturally favorable traits in plants have remained largely unknown until recently. We now review recent studies of the molecular mechanisms that have generated significant improvements in polyploid crops.

In cotton (*Gossypium* spp.), subfunctionalization of homoeologous genes via genomic rearrangement after allopolyploidization is suggested to have conferred an advantage of being a better crop. *MYB2*, which is

associated with fiber development, exhibits functional differentiation between the homoeologs located in the A and D subgenomes. Only *MYB2A*, which is derived from the A genome, promotes the development of spinnable fiber in the allotetraploid upland cotton. By contrast, *MYB2D*, which originated from the D genome, is associated with nonpreferred fiber development. This functional divergence is thought to have been mediated by a *trans*-acting siRNA, miR828, which targets only *MYB2D* to degrade the transcript, possibly because of variation in the sequences in the A/D alleles [48]. Differences in the quality of cotton fibers between tetraploid and diploid species may also be explained by functional differentiation between subgenomes involving transposable element (TE) insertions. This is thought to relate to a *Copia*, long terminal repeat retrotransposon (LTR) in *GhMYB25*, or a long interspersed nuclear elements retrotransposon (LINE) close to *GhERF* on the D genome. These insertions increase the expression level of the accompanying genes and may therefore stimulate stronger fiber growth [49]. In addition, the partitioning of the expression between homoeologs of the alcohol dehydrogenase A gene *adhA* can occur in different organs, including petals or styles. Interestingly, this subfunctionalization is similar in natural cotton polyploids and in two synthetic allopolyploids, which suggests that the epigenetic regulatory alteration may have been evolutionarily stable [50,51].

Polyploidization is frequently associated with changes in the mating system, especially if the progenitor has an outcrossing system. A newly polyploid individual, which undergoes reproductive isolation from the original outcrossed population, often immediately adjusts their mating system to selfing to produce the next generations properly. The diploid wild species in the genus *Diospyros* (widely called “persimmon”) exhibits an XY system (or heterogametic male) dioecious sex determination (or separated male and female individuals). By contrast, in a putatively autohexaploid cultivated Oriental persimmon (*D. kaki*), which is a major fruit crop in East Asia, a monoecious system (or both male and female flowers in a tree) evolved with Y chromosomes in genetically male plants [52,53]. In diploids, the Y-encoded small-RNA gene *OGI* can stably repress its targeted autosomal HD-ZIP1 homeodomain gene *MeGI* to be male.

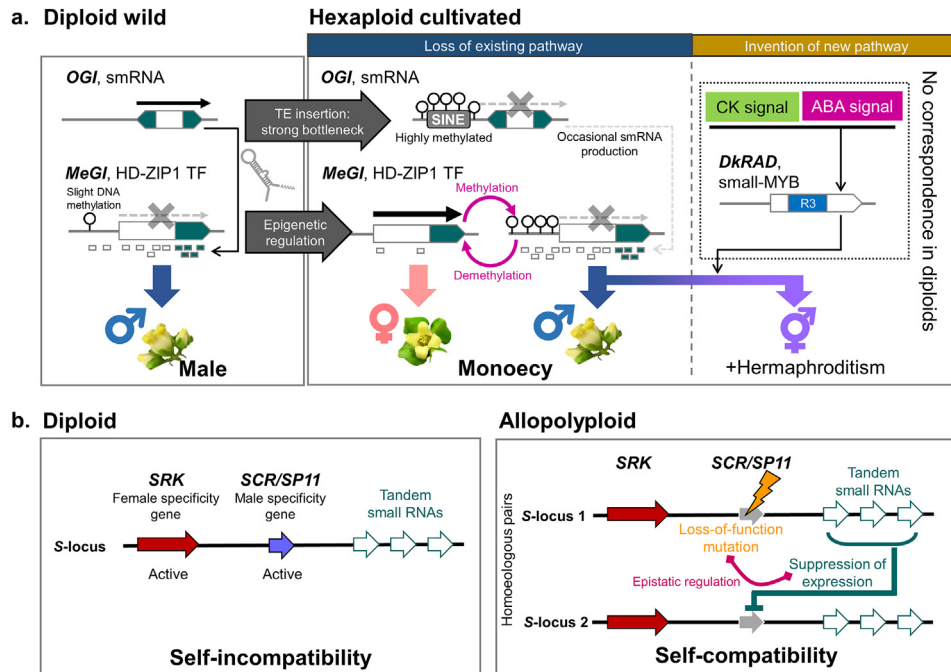
In the hexaploid Oriental persimmon, a short interspersed nuclear element (SINE)-like TE was inserted into the promoter region of the *OGI* allele and fundamentally silenced the expression of *OGI*. By contrast, *MeGI* has established an epigenetic switch in its promoter region that regulates its expression pattern, which resulted in a monoecious sex determination system [53,54]. Importantly, the SINE-like insertion in the *OGI* allele underwent a strong bottleneck in the

hexaploidization event, which suggests that the transition into selfing (to monoecy) was triggered via a polyploidization event (Figure 2a) [53]. In addition to this monoecious system with loss of the existing pathways, hexaploid Oriental persimmon has invented a new pathway of occasional conversion of male to hermaphrodite flowers, which has not been observed in its diploid wild relatives (Figure 2a). This sex conversion is caused by hexaploid-specific activation of the cytokinin- or abscisic acid-responsive signaling pathways and their putative integrator, *RADIALIS*-like *DkRAD* [55]. *RADIALIS* genes regulate flower morphology widely, particularly petal architecture [56], but their involvement in sexuality is specific to persimmon, which is reminiscent of neofunctionalization. Although hermaphroditism is thought to be the ancestral state of sexuality in plants, the reversion from male to hermaphrodite in hexaploid persimmon occurred through the use of a novel pathway independent of the existing sex determinants, *OGI* and *MeGI*.

Self-compatibility is generally considered to be a desirable trait in crop species that ensures a high fertilization rate and uniform crop, and reduces the need for pollination by humans or insects [57]. Polyploidy can promote domestication because a common characteristic of polyploid species is self-compatibility [2,58]. However, mutational robustness derived from the redundancy of homoeologs may slow phenotypic evolution, such as the loss of self-incompatibility; that is, each homoeolog may require independent mutations in allopolyploids, and the fixation of an advantageous allele may occur more slowly in autopolyploids [47]. Interestingly, this potential contradiction can be reconciled by an epistatic interaction between homoeologous loci in the evolutionary loss of self-incompatibility in two self-incompatibility systems; this concept is reviewed in the following two examples.

The first system is the self-incompatibility system of Brassicaceae. *B. napus* (4x, AACC genome) is a self-compatible crop species derived from two self-incompatible diploid species. This raises the question of whether two independent loss-of-function mutations (or nonfunctionalization) at the homoeologous *S*-loci were necessary for the allotetraploid species to have become self-compatible. In the *S*-locus of Brassicaceae, the female specificity gene *SRK* encodes a receptor kinase, and the male specificity gene *SCR/SP11* encodes the pollen surface ligands [59]. Tandem arrays of small RNAs are also located at the *S*-locus and confer self-incompatibility dominance by epigenetically repressing the expression of recessive *SCR* (Figure 2b) in diploid heterozygous plants. The state of allotetraploidy corresponds to permanent heterozygosity, and the same mechanism can confer epistasis or the interaction between different loci. In this case, the small RNAs from

Figure 2



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Molecular mechanisms underlying polyploidy-specific transitions to selfing systems in the genus *Diospyros* (persimmon) and family Brassicaceae. **a.** In diploid *Diospyros* species with dioecious sex expression (or male and female individuals), stable production of small RNAs (smRNAs) of *OIG* from the Y-chromosome, which can degrade the autosomal counterpart, *MeGI*, generates male individuals. By contrast, in hexaploid cultivated species (*D. kaki*), insertion of a short interspersed nuclear element (SINE)-like retrotransposon (named *Kali*) in the *OIG* promoter region, which has a high level of DNA methylation, silences *OIG* expression. This insertion has been conserved in wide cultivars through strong bottleneck selection. Alternatively, the downstream *MeGI* establishes an epigenetic switch to release or maintain DNA methylation in its own promoter, which establishes monoecious sex expression (or male and female flowers in a tree). Hexaploid *D. kaki* also exhibits occasional conversion from male to hermaphrodite flowers caused by activation of *DkRAD* in response to cytokinin (CK) and abscisic acid (ABA) signals in a hexaploid-specific manner. **b.** Simple model of a self-compatible mutation of a polyploid species of Brassicaceae. The self-incompatibility system of Brassicaceae is characterized by a dominance relationship, in which tandem small RNAs of a dominant haplogroup suppress the expression of the male specificity gene *SCR* in a recessive haplogroup. Although an allopolyploid species has two duplicated *S*-loci, the function of one of the *S*-loci is suppressed by small RNAs. Thus, a single loss-of-function mutation in a dominant haplogroup may be adequate to confer self-compatibility.

one of the duplicated *S*-loci can suppress the function of another.

Four different self-compatible mutations were identified from the *SRK* and *SCR* sequences of 45 *B. napus* lines [60,61]. In all four mutations, the dominant *S*-haplogroup (termed class I) at one of the two *S*-loci had a loss-of-function mutation in *SRK* or *SCR* (Figure 2b). The function of another *S*-locus was suppressed by the dominance relationship. Thus, a single mutation of nonfunctionalization was sufficient to repress the function of two *S*-loci. An interesting difference between natural and domestication selection is the prevalence of mutations in the female specificity gene *SRK* in crop species, in contrast to the male specificity gene in natural species, which is consistent with the theoretical study of sexual asymmetry [59,62,63]. Farmers may have selected self-compatibility at the level of

individuals, whereas, for natural species, mutations in male specificity genes can be advantageous for spreading within the population. In addition, a recent report suggested that the self-incompatibility of *B. napus* involved factors that have yet to be studied [64].

The second system is the *S-RNase* system, which is prevalent among angiosperms, including agriculturally important families of Solanaceae [59]. Its *S*-locus harbors *S-RNase* and the tandemly duplicated *S*-locus F-box gene *SLF*. *S-RNase* protein in female tissue is harmful for male pollen tubes, whereas the arrays of *SLF* detoxify non-self *S-RNase*. As a result of this non-self-recognition system, when polyploidization results in two *S*-loci in a single pollen tube cell, both duplicated *S-RNase* are detoxified and, thus, self-compatibility can emerge without a new mutation. A clear correlation between self-compatibility and

polyploidy was reported in natural Solanaceae species [65]. A crop example is the autotetraploid and self-compatible potato (*S. tuberosum*). Its diploid wild relative *Solanum chacoense* can be a breeding resource, but its self-incompatibility is a barrier [66]. In this case, the *S*-locus inhibitor (*Sli*) in *S. chacoense* may be a tool to overcome this barrier [67]. Recently, two groups have demonstrated that *Sli* encodes a non-*S*-locus F-box protein that obtained new function (neofunctionalization) [68,69]. These studies indicate that self-compatibility was important for ancient domestication and plays a significant role in modern breeding.

Perspectives: genomics and genetics of polyploid crop species

In the past, a major difficulty in studying polyploid crop species related to their complex genomic structures. It was difficult to distinguish highly similar homoeologous sequences in genome assembly, transcriptome, polymorphism, and epigenome analyses. In recent years, the quality of the genome assembly of polyploid species has improved significantly [70]. For example, the values for N50 (a common index of assembly quality) in the genome assembly of the two allopolyploid species, bread wheat (genome size 16 Gb, 6x) and finger millet (genome size 1.5 Gb, 4x), were previously less than 10 kb [71] and 24 kb [72], respectively. With new sequencing and bioinformatics innovations, the N50 values improved by about three orders of magnitude to 2.6 Mb for finger millet [73] and to 20 Mb for bread wheat [74–76]. The genomes of some autopolyploids have also been sequenced, and information for all chromosomes is available for sugar cane [77] and potato [78]. However, high-quality assemblies alone may not be adequate for accurate transcriptome, epigenome, and polymorphism analyses [10].

Most analytic tools and programs target diploid species and, when applied to polyploid species, the error rate in mapping sequencing reads and statistical methods should be customized to each species [79–81]. Several groups have developed subgenome classification methods, for example, HomeoRoq, PolyCat, and EAGLE-RC, the last of which is based on probability theory and has been shown to be the best method in benchmark studies [79–81]. The remaining challenges include the assembly of some totally or partially autopolyploid genomes (such as strawberry) and tandemly duplicated genes, in which some copies have been assigned to the wrong subgenome [82–84]. Very recently, single-molecule long-read technology, such as the PacBio HiFi reads approach, has improved assembly quality further [85] and reduced the cost, and is expected to facilitate the analysis of difficult genomic regions.

Numerous issues have arisen in research on the genetics of polyploid crops, mainly because of the complicated inheritance modes, especially in autopolyploid species,

which make both systematic breeding and genetic mapping analyses difficult. Recent progress in bioinformatic methods will facilitate genetic studies of polyploidy-specific quantitative genotypes/haplotypes or inheritances. Such programs include updog [86], OutcrossSeq [87], and PopPoly [88] for genotyping, or GWASpoly [89] and StAMPP [90] for population genetic approaches. The genetic study of polyploids provides evidence in support of the new concept of allele dosage or balances, which is not considered to have occurred in diploids, but often leads to the expression of novel traits [91,92]. Better harnessing of polyploidy genetics may provide more variations for use in the current breeding systems.

These advances in understanding the genomics and genetics of polyploid crop species will help to expand the identification of genes responsible for agriculturally favored traits and domestication, and for population genetic analysis. These advances will also help to facilitate the discovery of recurrent patterns and the significance of polyploidy among diverse crop species.

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Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pbi.2022.102255>.

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- * of special interest
- ** of outstanding interest

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