REVIEW

Utilization of crop heterosis: a review

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Abstract Heterosis (or hybrid vigor) is a natural phenomenon whereby hybrid offspring of genetically diverse individuals display improved physical and functional characteristics relative to their parents. Heterosis has been increasingly applied in crop production for nearly a century, with the aim of developing more vigorous, higher yielding and better performing cultivars. In this review we present and compare three categories of crop heterosis utilization: intraspecific heterosis, intersubspecific heterosis and wide-hybridization heterosis, with particular focus on polyploid species. Different pollination-control systems used to breed for heterosis are also comparatively analyzed. Finally, we highlight problems involved in heterosis research and crop improvement. We aim to provide insight into best practices for amplifying heterosis potential.

Keywords Crop heterosis · Heterosis · Heterotic group · Wide hybridization · Polyploidy · Pollination-control systems

Introduction

Heterosis is a natural phenomenon whereby hybrid offspring from genetically diverse individuals show increased vigor relative to their parents (Coors and Pandey 1997; Shull 1948). Heterosis in crop species can be visualized in terms of increases in growth rate,

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total biomass, stress resistances, seed yield, and population fitness (Kalloo et al. 2006). Heterosis has the following specific characteristics: firstly, heterosis is highly variable; the degree of heterosis varies with respect to the genetic distance of the parents, their reproductive mode, the traits investigated (Zhou et al. 2012), the developmental stage of the plants (Groszmann et al. 2013) and the environment. With respect to environmental variation, biotic and abiotic conditions shown to affect heterosis include soil-type, topography, climate, solar energy, temperature and water availability (Munaro et al. 2011; Griffing and Zsiros 1971; Langridge 1962; Blum 2013).

Secondly, heterosis is largely universal and can increase crop yields by 15–50 % depending on crop type. Many of the major cereal crops as well as commercial varieties of vegetable and flower crops are populated using hybrid seeds for increased agricultural performance (Duvick 1999; Birchler et al. 2003). The earliest utilization of heterosis was in maize (*Zea mays*), followed by beet (*Beta vulgaris*), sorghum (*Sorghum bicolor*), onion (*Allium cepa*), eggplant (*Solanum melongena*), tomato (*Solanum lycopersicum*), peppers (*Capsicum*), rice (*Oryza sativa*), cotton (*Gossypium hirsutum*), sunflower (*Helianthus annuus*) and rapeseed (*Brassica napus*) (Melchinger and Gumber 1998). In maize, yield was increased by 15 % in hybrids relative to the superior open-pollinated varieties. By the late twentieth century hybrid maize accounted for 65 % of total maize cultivation and had contributed to a quadrupling of annual maize production (Duvick 1999; USDA-National Agricultural Statistics Service). Hybrid rice is grown widely in Asian countries including China and India, where it is the staple cereal (Lamkey and Staub 1998). In China, hybrid rice has a yield advantage of 20–30 % over the best available inbred rice cultivars, facilitating a 44.1 % increase in production (Cheng et al. 2007). Hybrid rapeseed accounts for at least 75 % of the total planted area in China, one of the biggest global producers of rapeseed (Fu 2009). Wheat (*Triticum aestivum*), as the most important cereal in the world, expresses 10–25 % heterosis levels (Hoisington et al. 1999). For grain sorghum, almost half of the global plantings at the end of the twentieth century used hybrid stocks, with genetic contributions accounting for yield gains of 35–40 % in the USA (Duvick 1999). In addition, hybrid sunflower accounts for 11.5 million of approximately 16.5 million hectares of sunflower planted globally each year (Miller and Fick 1997).

Thirdly, increases in heterosis level diminish over time. On average, genetic gain for yield was gradually increasing by 1.5–2.0 % per year at the end of last century, albeit with a lessening of the heterotic increase (Hoisington et al. 1999). The average yield gain in rice went from 3.1 % per year in the 1980s to 1.4 % per year in the 1990s and then 0.8 % per year in the 2000s. Similarly, wheat yield gains were reduced from 2.9 % per year in the 1980s to 0.9 % in the 1990s and only 0.4 % in the 2000s (Phillips 2010). In maize, Duvick (1999) argued that heterosis has not contributed to crop improvement because it has been relatively constant for decades. Some studies have indicated that inbred lines have increased in y2009ield 1.9–3.5 times faster than hybrid lines, most likely because breeders primarily focus on inbred lines for enhancing quality traits, disease/pest/stress resistances (Troyer and Wellin 2009), and shoot architecture and flowering traits (Tollenaar and Wu 1999; Hammer et al.). Therefore, to maximize crop yields, breeders may focus on increasing heterosis level, improving the performance of inbred breeding lines, or both. Given the potential for heterotic gains, it is important that we understand how best to breed for heterosis. In this review, we classify heterosis into different categories according to the genetic distance between parents. We propose different breeding strategies, based on these categories and on different pollination-control systems, to facilitate selection of the optimal system for maximizing heterotic gain.

Classification and application of crop heterosis

Three categories of heterosis have been defined based on the genetic distance of parental lines. These are: (1) intraspecific heterosis, resulting from crosses between two accessions belonging to the same species, (2) intersubspecific heterosis, resulting from crosses between two subspecies, and (3) wide-hybridization heterosis, resulting from crosses between two individuals of a different species or genus. In certain contexts, there is a clear positive correlation between the genetic divergence of the parent lines and heterosis potential, which is evidenced in subtropical maize (Reif et al. 2003), winter rapeseed (Ali et al. 1995) and wheat

(Krystkowiak et al. 2009). In other contexts, little or no such correlation appears to exist, including in single-crosses of maize (Bernardo 1992), popcorn maize (*Zea mays* var. everta) (Munhoz et al. 2009) and resynthesized *B. napus* which is artificially created by crossing the modern diploid *Brassica* species carrying the rapeseed constituent 'A' and 'C' genomes (Girke et al. 2012). Thus, while genetic diversity is necessary, it is not sufficient to give rise to heterotic performance (Kaeppler 2012). Generally speaking, however, the genetic divergence and the probability of high levels of heterosis gradually increase from category 1 through 3 (East 1936; Karpechenko 1927; Li and Yuan 2010; Yuan 2006).

Intraspecific heterosis

Intraspecific heterosis is the favored choice of most breeders because it can be manipulated easily and results in lower breeding costs, higher breeding efficiency and better seed-set (for seed-based crops) compared with wide-hybridization heterosis (Fig. 1). To avoid the low levels of heterosis associated with crossing closely-related lines, crop breeders classify intra-species parental materials into heterotic groups based on molecular markers or physically testing combining ability. Each heterotic group fixes different alleles, which when combined with allele(s) from the opposite heterotic pool, can result in higher vigor. These positive interactions form the base for the superior performance of the heterotic pattern (Schon et al. 2010). Reciprocal crossing between these groups allows evaluation of the hybrid to determine the optimal combination of parents and establish a heterotic pattern and crossing regime (Melchinger and Gumber 1998).

The establishment of heterotic groups and patterns in crop species is dependent upon their evolutionary history and genetic diversity. The earliest and most successful establishment of heterotic groups and patterns was in maize, such as Stiff Stalk (SS) × Non-Stiff Stalk (NSS) in the US Corn Belt and Canada (Tracy and Chandler 2006). For practical simplicity, accessions of maize are currently classified into one of two general heterotic groups; A or B (Dhliwayo et al. 2009). In specific regions, breeders may also include additional classifications. In temperate Chinese maize germplasm, lines are generally classified into four to six major heterotic groups,

which have proven useful in hybrid breeding (Lu et al. 2009). Xie et al. (2008) classified 187 commonly used Chinese maize inbred lines into six subgroups, including BSSS (American BSSS including the cultivar 'Reid'), PA (group A germplasm derived from modern US hybrids in China), PB (group B germplasm derived from modern US hybrids in China), Lan (Lancaster Surecrop), LRC (Luda Reb Cob; a Chinese landrace, plus its derivatives) and SPT (Si-ping-tou, also a Chinese landrace, plus its derivatives). In another analysis, 288 Chinese inbred lines were subdivided into four subgroups: Lancaster, Reid, SPT and P (introduced from Pioneer hybrids) (Wang et al. 2008). Using high-throughput SNP genotyping, Wu et al. (2013b) also divided 367 maize inbred lines into two main groups: (1) introduced germplasm and (2) local germplasm, with five subgroups including Reid, Lancaster, P group, Tang Sipingtou (TSPT), and Tem-tropic I group. These studies show high consistency in the classification of maize heterotic groups.

Rapeseed has been divided into three heterotic groups: Asian rapeseed (including rapeseed from China and Japan), European winter-type rapeseed, and Canadian and European spring-type rapeseed. Hybrids obtained from crossing between Asian and European varieties exhibit stronger heterosis than hybrids obtained from crosses within the Asian or European groups (Charcosset et al. 1991; Qian et al. 2009). Crosses between spring rapeseed and Chinese semi-winter lines show great potential to increase seed yield (Qian et al. 2007). The cross of resynthesized *B. napus* to European winter oilseed rape also creates higher heterosis (Girke et al. 2012). In all, 86 oilseed rape cultivars have been divided into four distinct groups: I (mainly consisting of exotic cultivars), II (mainly composed of Chinese cultivars), III (mixed cultivars from China and Europe) and IV (mainly comprising exotic and newly synthesized yellow seeded lines) (Younas et al. 2012).

In rice, four heterotic patterns within two heterotic groups were identified in tropical hybrid rice from the International Rice Research Institute (IRRI) according to SSR markers and field trials (Xie et al. 2014). Heterotic groups of many additional crops have been classified, including Brazilian popcorn (Miranda et al. 2008), rye (Fischer et al. 2010b) and wheat (Fischer et al. 2010a; Zhang et al. 2011).

Future research into heterotic patterns and groups is suggested herein to have three major objectives: (1) to

Fig. 1 Classification and characteristics of heterosis utilization
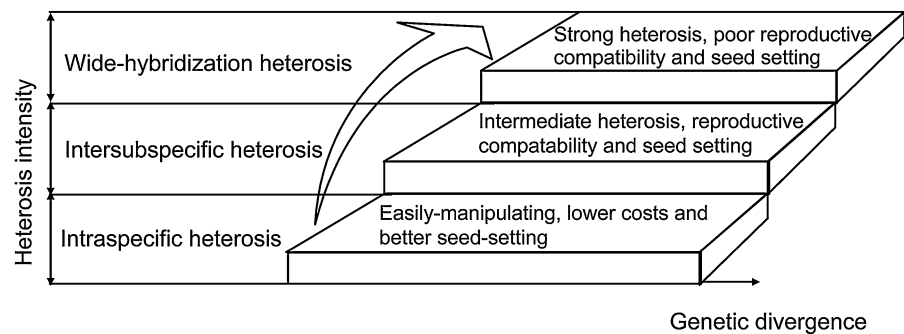
enrich the germplasm pool such that new heterotic groups and patterns can be detected and added to classical groups to meet breeding requirements; (2) to develop a simple, more efficient method of identifying heterotic groups and patterns with the help of molecular breeding tools; (3) to define the genetic interactions and molecular mechanisms involved in heterotic patterns.

Intersubspecific heterosis

Intersubspecific hybrids display 8–15 % more heterotic potential than intraspecific hybrids in rice (Li and Yuan 2010; Peng et al. 2008). Rice has three subspecies: *indica*, *japonica* and *javanica*. Superior heterosis between *indica* and *japonica* has been observed in China and elsewhere, with 30–50 % higher heterotic gains than that provided by intervarietal crosses (Yuan 2006). The *indica* and *japonica* subspecies of cultivated rice are genetically distant and each has excellent agronomic traits. The first generation (F$_1$) hybrid between *indica* and *japonica* rice exhibits later maturity, more luxuriance, larger spikes, more grains, higher tillering ability, a better root system, stronger stems, resistance to lodging, stronger regeneration, and higher biomass, than its parents (Gu 2010; Wei et al. 2013).

Despite the enhanced heterosis of many traits in intersubspecific crosses, it should also be noted that if the parents of intraspecific hybrids have higher adaptability or more favorable genes, intraspecific hybrids may surpass the heterotic potential of intersubspecific hybrids. Furthermore, discordance between parental genomes can lead to poor trait performance, for example with respect to seed setting and seed production, as a result of impaired pairing between homologous chromosomes during meiosis

(Li and Yuan 2010) (Fig. 1). Low and unstable seed setting and poor grain plumpness in the *indica* × *japonica* F$_1$ has limited the practical application of these hybrids (Lapitan et al. 2009; Zhu and Liao 1990). Though hybrid sterility is a major form of postzygotic reproductive isolation, it has been possible to find wide-compatibility genotypes that produce highly fertile hybrids when crossed to both *indica* and *japonica*. As such it is now possible to enhance *indica* × *japonica* hybrid fertility by manipulating a few allelic interactions at a small number of wide-compatibility loci (Chen et al. 2011; Ikehashi and Araki 1986).

The molecular basis for hybrid sterility is a beginning to be unraveled. The *S5* locus of rice is a major locus controlling *indica-japonica* hybrid sterility and encodes an aspartic protease involved in embryo-sac fertility. A large deletion in the N-terminus of the predicted S5 protein generates a wide compatibility gene variant, *S5-n*, resulting in the subcellular mislocalization of the presumably non-functional protein (Chen et al. 2008; Ouyang et al. 2009). The manipulation of wide-compatibility genes during hybrid rice breeding in China has resulted in normal seed setting rates in *indica* × *japonica* hybrids (Wei et al. 2013). Now hybrids of *indica* and *japonica* exhibit strong vegetative vigor with a normal rate of seed setting and grain plumpness (Luan et al. 2007; Ouyang et al. 2010). As such, more cultivars have been released and applied in breeding using *javanica*, or an intermediate type, as one parental line (Cheng et al. 2007; Zhong et al. 2005).

The *indica-japonica* hybrid system of rice may act as a model for intersubspecific hybridization heterosis of other crops. Future investigations should attempt to uncover additional genes involved in hybrid sterility, clarify the underlying molecular mechanisms and

utilize these findings to develop more inter-subspecific hybrids to increase productivity (Ouyang et al. 2009).

Heterosis from wide hybridization

Wide hybridization is defined as a cross between two individuals of at least species-level divergence. Examples include *Brassica oleracea* (cabbage/cauliflower) × *B. rapa* (Chinese cabbage), *B. oleracea* × *Raphanus sativus* (radish), *Zea mays* (maize) × *Oryza sativa* (rice) and *Secale* spp. (e.g. rye) × *Triticum* spp. (e.g. wheat). With respect to wide hybridization, as long as geographical and reproductive isolation exists between species, strong hybrid vigor is observed, but similarly to intersubspecific crosses, poor seed setting and genetic instability often occur.

Wide hybridization in vegetable crops is aimed directly at increasing vegetative growth, or biomass. For example, interspecific hybrids between *B. napus* and the less cultivated *B. campestris* display a midparent heterosis (MPH; difference between the hybrid and mean of the parents) of 35.6 % for biomass and 72.4 % for branch number (Wang et al. 2003). In another study, hybrids between *B. napus* and *B. campestris* or *B. rapa* showed approximately 34 % MPH for biomass production (Liu et al. 2002). Strong hybrid vigor was also achieved between the cultivated tetraploid cotton species *Gossypium hirsutum* and *Gossypium barbadense* (Basbag and Gencer 2007), which has been applied to cotton breeding in Xinjiang province, China.

One breeding strategy that utilizes wide hybridization involves finding methods to introgress an alien species' DNA into a genotype of another species to produce a novel, fertile accession with a normal chromosome number. Subsequent hybridization between this introgressed accession and natural accessions of the same species often give rise to stronger heterosis. For example, a hybrid between natural *B. napus* (amphidiploid genome AACC) and re-synthesized *B. napus* that carries genomic components from *B. rapa* (diploid AA) and *B. carinata* (amphidiploid BBCC) can exhibit stronger heterosis than an intraspecific natural *B. napus* hybrid (Qian et al. 2005). Resynthesized allotetraploid *B. napus* derived from a cross between *B. oleracea* (CC genome) and *B. rapa* was recently evaluated as a diverse *B. napus* germplasm for hybrid breeding

(Girke et al. 2012). While these resynthesized lines are not competitive with current elite cultivars for yield traits, hybrids between these lines exhibited heterosis for yield and seed oil content (Girke et al. 2012). However, genomic instability and unsustainable phenotypic variation may impede the application of this type of heterosis.

Triticale, a polyploid hybrid of both rye (*Secale* spp.) and wheat (*Triticum* spp.), exhibits heterosis for grain yield in the range of 20 % above the MPH (Oettler et al. 2001). Triticale is widely planted globally, with 15 million tons produced from 29 countries in 2009 (FAO Statistics Division 2010, http://faostat3.fao.org/). However, this hybrid also displays shrunken grains, late maturity and lodging in fertile soil. Furthermore, the stable reproduction of such tetraploid hybrids can be difficult due to meiotic abnormalities.

Overall, the gradual increase in genetic distance between parents, from intervarietal to intersubspecific crosses to wide-hybridization, enhances heterosis potential yet remains confounded by decreased seed setting and decreased genetic and phenotypic stability.

Specifics of heterosis in polyploid species

Heterosis in polyploids can be more complex than in diploids and requires specific considerations and applications (Washburn and Birchler 2013). Polyploids are classified into autopolyploids, containing multiple chromosome sets derived from the same species, and allopolyploids, comprising chromosome sets derived from different species. Progressive heterosis refers to a specific phenomenon in polyploid plants whereby the magnitude of heterosis is maximized by the diverse genomes in the polyploids. Progressive heterosis is not observed for every trait in polyploid species, suggesting that traits manifesting progressive heterosis are independently controlled and thus can only be exploited trait-specifically.

Heterosis in autopolyploids

In contrast to their diploid ancestral species, autopolyploids have been shown to have increased cell size and concentration of secondary metabolites (Lavania et al. 2012), higher seed germination (Hoya et al. 2007), higher genetic diversity (Wu et al. 2013a) and

Table 1 Comparative analysis of pollination-control systems in heterosis breeding

	Artificial emasculation	Residual heterosis of F$_2$	Cytoplasmic male sterility	Environment-dependent male sterility	Nuclear-encoded male sterility	Chemical emasculation	Transgenic technology	Self-incompatibility (SI)
Typical crop species	Maize, cotton and tobacco	Cotton and rapeseed	More than 150 species, including rice, rapeseed, green bean, pearl millet, sugar beet, carrot, maize, onion and sunflower	Rice, rapeseed, sorghum, soybean, millet, barley, maize and pigeon pea	Rapeseed, rice, tomato, maize sorghum, barley, wheat, cotton and sunflower	Rice, rapeseed and wheat	Tobacco and rapeseed	Widely distributed in Cruciferae (e.g. *B. rapa* and *B. oleracea*), Gramineae, Fabaceae, and Solanaceae
Characteristics	Suitable for dioecious crops with higher propagation coefficients, large floral organs and low quantity of seeds in planting	Suitable for crops with traits controlled by multiple genes and related hybrids with low inbreeding depression	Originating from rearrangements of mitochondrial DNA; especially suited to monoclinous crops; requires presence of stable sterile lines, maintenance lines and restorer lines	No maintenance line; male-sterility is generated by environment-induced fertility transition, such as temperature, photoperiod or both	Stemming from the mutation of nuclear genes; particularly suitable for monoclinous crops; restorer lines are needed if sterility genes are dominant genes	Sterility of plants obtained by spraying chemical hybridising agents (CHA), such as auxins/anti-auxins, halogenated aliphatic acids, gibberellins, ethephon (ethrel) and arsenicals; flowering time needs to be centralized	Requires sterility genes, restorer genes/mechanisms and mature genetic transformation systems for target species	Requires highly stable self-incompatibility lines and corresponding propagation approaches
Potential for strong hybrid combination	Very high	Low	Moderate	High	High	Very high	High	High in SI × SC (self-compatibility), but low in SI × SI

Table 1 continued

	Artificial emasculation	Residual heterosis of F₂	Cytoplasmic male sterility	Environment-dependent male sterility	Nuclear-encoded male sterility	Chemical emasculation	Transgenic technology	Self-incompatibility (SI)
Advantages	Freedom and ease of making hybrid combinations	Low cost of seed production; the diversity of F₂ genotypes enhance population resistance to disease, insect and other stresses	Natural, frequently occurring male sterility; high hybrid purity; beneficial to the protection of intellectual property	No need for maintenance line; reducing the cost of seed production	Freedom and ease of making hybrid combinations; higher breeding efficiency because sterility and maintenance lines are the same	Freedom and ease of making hybrid combinations; simple, labor efficient seed production; no need for restorer and sterility genes	Rapid establishment of pollination-control systems in new species; sterility is complete and the purity of hybrids is higher	Relatively easy to produce superior combinations
Disadvantages	Higher manpower cost in seed production	Low heterosis level; suitable for synthetic hybrid and single-cross hybrids with less divergence between two hybrid parents; not all hybrid combinations are suitable	Long breeding cycle due to selection of three lines; danger of disease susceptibility in cytoplasm when CMS hybrids are widely planted	Ideal, raw sterile materials are difficult to isolate; the unstable male-sterile phenotype may lead to failure of seed production; restricted to a given region and season	Removal of 50 % of lines for seed production results in higher manpower cost	Unsuitable for crops with longer flowering time (cotton and soybean); requires advanced training in hybrid production; different genotypes may be sensitive to chemical reagents	High cost of transgene development, screening and identification; requires efficient, easy transformation techniques; large time investment in transgene breeding	Requires method for efficient and low cost maintenance of self-incompatible parent; difficult to select ideal SI lines
Improvement direction	Mechanical emasculation and manpower reduction	Predict and identify combinations with low inbreeding depression based on molecular advances	Identify stable and complete sterility lines and excellent restorer lines	Identify improved sterile lines with manageable and stable sterility responses	Develop completely sterile sterility lines; exploit temporary maintenance line to decrease production cost	Increase efficiency, manageability and stability; reduce cost and toxicity without affecting stamen development	Improve understanding of genetic components of beneficial traits including sterility, yield and vigor; develop efficient and global transformation systems, maintenance and restorer lines	Identify stable incompatibility lines; improve methods for production of incompatibility lines

Table 1 continued

Artificial emasculation	Residual heterosis of F_2	Cytoplasmic male sterility	Environment-dependent male sterility	Nuclear-encoded male sterility	Chemical emasculation	Transgenic technology	Self-incompatibility (SI)
Relevant research topics							
Optimal planting pattern for mechanization	Mechanism of inbreeding repression	Cloning and characterizing sterility genes; mechanism of sterility restoration	Cloning and characterizing sterility genes; mechanism of sterility transition	Cloning and characterizing sterility genes	Biochemistry of reagent activity, basis of genotype and environment sensitivity	Transgenic technologies and trait efficiency, and sterility gene analysis	Mechanism and genetics of self-incompatibility

(1) Non-genetic systems, including artificial castration (Smith et al. 2004) and chemical hybridising agents (CHA) (Tu and Banga 1998; Guan et al. 2012); (2) biological pollination control technologies, including; the utilization of F_2 residual heterosis [e.g. in rice (Alam et al. 2004) and upland cotton (Yuan et al. 2001)], cytoplasmic-encoded male sterility (CMS) [e.g. S-, C- or T-system in maize (Vancetovic et al. 2010); Polima-, Shan2A- and Ogura-CMS systems in rapeseed (Fu 1995); wild abortive (WA)-, BT- and Honglian (HL) CMS systems in rice (Yuan 1994)], nuclear-encoded male sterility (NMS) (Kaul 1988), self-incompatibility (SI) [e.g. *B. napus*, *B. oleracea* and *B. rapa* (Tochigi et al. 2011; Rahman 2005)], environment-sensitive genetic male sterility [in particular temperature- and photoperiod-sensitive, or both (Kaul 1988; Yuan 1997)], and engineered pollination control systems. Engineered systems include; engineered CMS systems (Chase and Gabay-Laughnan 2004; Horn 2006; Schnable and Wise 1998), engineered nuclear-encoded pollination control systems, inducible pollination control systems, and pollination control by metabolic engineering (Kempe and Gils 2011; Engelke et al. 2011)

developmental differences (including slower growth rate, later flowering, reduced tassel branches, decreased stature and fertility) (Abel and Becker 2007; Yao et al. 2011). Variation of these traits may be exploited in breeding programs by making use of autopolyploid F_1 hybrids derived from either crossing autoployploids or the hybridization of two diploid progenitors followed by chromosome doubling. Such autopolyploid F_1 hybrids can combine the advantages of intra-species crosses with the manifestation of heterosis.

At present, however, autopolyploid F_1 hybrids often exhibit genome instabilities, regulatory incompatibilities, complex pairing patterns, polysomic inheritance, abnormal chromosome segregation and aneuploidy (Carvalho et al. 2010; Wei and Zhang 2010), hindering the application of seed-reproduced F_1 hybrid autopolyploids. Nonetheless, autopolyploid F_1 hybrids may be utilized in vegetatively propagated crops, such as sugarcane (*Saccharum* spp.) (Grivet et al. 1996), autotetraploid cultivated alfalfa (*Medicago sativa*) (Havananda et al. 2011) and potato (*Solanum tuberosum*) (Pendinen et al. 2012). Furthermore, the genome stability of autopolyploid F_1 hybrids can be genetically manipulated, with ability to select for autopolyploid lines with higher fertility. In the model species *Arabidopsis thaliana*, neo-tetraploid lines display great stability over at least three consecutive generations (Yu et al. 2009b).

In autotetraploids, homozygous tetraploid lines (AAAA, BBBB, CCCC and DDDD) are mutually crossed to generate single cross hybrids (AABB and CCDD), which are reciprocally crossed to give rise to a double cross hybrid (ABCD). This combination of the four different parental genomes exhibits greater heterosis than single cross hybrids (Groose et al. 1989; Levings et al. 1967; Mok and Peloquin 1975; Riddle and Birchler 2008). This progressive heterosis in autotetraploids has been observed for heterosis of forage yield and seed number per flower in alfalfa (*Medicago sativa*) (Groose et al. 1989; Bingham et al. 1994), tuber yield in potato (*Solanum tuberosum*) (Mok and Peloquin 1975) and the time to silk emergence, flowering time, plant height, and ear length in maize (Randolph 1942; Levings et al. 1967; Chase 1980; Sockness and Dudley 1989; Riddle and Birchler 2008). In rice, autotetraploid hybrids between the two subspecies *indica* and *japonica* can be obtained using tetraploidized parent lines followed by intensive selection, generating higher heterosis (Tu et al. 2007).

Overall, continued researches into autopolyploids will enhance the application of their F_1 hybrids in seed-reproduced crops. In the future, the aim is to obtain autopolyploid lines (or hybrids) with good fertility to further develop their potential.

Heterosis in allopolyploids

In contrast to autopolyploids, allopolyploid species are obtained by interspecific hybridization, which can generate interspecific heterosis and exhibit relatively higher genome stability. Allopolyploidization also enables heterosis fixation due to the ability to select lines with normal chromosome numbers during selfing.

One of the first reports of progressive heterosis was demonstrated in the crossing of the different allotetraploids *Nicotiana tabacum* (AABB) and *N. rustica* (CCDD), resulting in an ABCD hybrid with increased heterosis relative to intragenus crosses (AABB or CCDD) (East 1936). Therefore, accumulation of four different alleles at each locus resulted in greater heterosis (East 1936). One hypothesis is that the accumulation of diverse alleles in the F_1 may lead to multiple allelic interactions that facilitate adaptability towards complex and variable environments. This may hold true in higher-ploidy and higher-diversity genome species, such as in hexaploid wheat (Briggle 1963) and octoploid triticale, which is derived from the cross of wheat and rye (*Secale cereale*) and combines four sets of diverse genomes (Goral et al. 2005). This research further demonstrates the potential of progressive heterosis to maximize the heterosis level of polyploids.

Heterosis utilization and pollination-control systems

New, superior cross combinations should have simple, low-cost, high yielding and stable seed production techniques. In order to control hybrid production in many species, floral castration methods are required, which can be classified into: (1) non-genetic castration, or, (2) biological pollination control technologies. Non-genetic castration includes artificial castration and the use of chemical hybridising agents (CHA) such as tribenuron-methyl (a sulphonylurea herbicide) (Yu et al. 2006) and amidosulfuron (Yu et al. 2009a), both of which have been used to induce

male sterility in rapeseed. Biological pollination control systems make use of cytoplasmic-encoded male sterility (CMS) (involving a cytoplasmic genetic male sterile line, a maintainer line and a restorer line), nuclear-encoded male sterility (NMS), self-incompatibility (SI), environment-sensitive genetic male sterility, and F_2 residual heterosis. F_2 residual heterosis occurs when the yield of the F_2 generation in some hybrids is still likely to be higher than the control (Lamkey and Edwards 1999). Genetic and metabolic engineering of such pollination control systems can also be applied, which may involve manipulation of CMS, nuclear-encoded pollination control genes and inducible pollination control genes (Kempe and Gils 2011; Engelke et al. 2011). The characteristics, advantages, disadvantages and research trends of different pollination control systems in crops are summarized in Table 1.

The selection of pollination control technology is dependent on the species involved. A good pollination control system takes into consideration species-specific propagation methods, ploidy, flower size, flowering habits, manpower requirements, economic cost, mating type (hermaphrodite or dioecism), the presence or absence of genetic sterility (NMS, CMS and SI), the fertility and restoration ability of restorer lines, transformability, the degree of inbreeding depression (reduced vigor or yield due to inbreeding) and the sensitivity towards chemical hybridising agents. Generally, CMS is the preferred choice for pollination control and is considered first if the sterility and fertility genes are found in related species, since it occurs naturally and has higher seed quality control. NMS also widely occurs in nature and is the second most popular pollination control system, as breeders can more easily obtain superior combinations. Environment-conditioned CMS and NMS are also widely applied, however, as the name implies, the seed production and growth of environment-conditioned CMS or NMS lines are limited by the regional or seasonal environment. Environment-conditioned CMS and NMS thus also have a higher danger of generating sterile lines in F_1 hybrids than other types of pollination control systems.

Chemical hybridising agents are not restricted to particular species and do not require the laborious practise of transferring sterility and fertility genes from one species/line to another species/line, making it a promising alternative. Furthermore, these can enable

breeders to develop hybrids with higher heterosis level in a shorter time. Genetic engineering for pollination control also shows promise, particularly in new species, providing that these are amenable to genetic transformation and the regulation of genetically-modified crops can be accepted. Pollination control by artificial emasculation is mechanically intensive and difficult to apply in regions where the expense or limited availability of manpower is prohibitive.

Problems and future directions in hybrid breeding

Some problems remain in hybrid breeding. Firstly, not every hybrid combination exhibits strong heterosis. This can occur when few heterotic loci, or low genetic diversity, exist in parent lines, emphasizing the need to select diverse lines enriched with heterotic loci. Additionally, negative heterotic loci may occur simultaneously in the F_1 generation and must be removed in subsequent generations without compromising the degree of positive heterosis. Furthermore, as discussed, although the degree of heterosis tends to increase with increasing genetic diversity of the parents, this also increases the likelihood of meiosis abnormalities, such as poor chromosome pairing. Indeed, aberrant chromosomal rearrangements and transposon activations have been detected following wide hybridization (Chen and Ni 2006; Nicolas et al. 2007). Hence, the divergence and stability of both parental and F_1 genomes influence seed yield and the stable inheritance of agronomic traits.

In light of the current problems in our capacity to utilize heterotic potential, there remains a need to: (1) identify and manipulate additional wide-compatibility genes to support stable genome compatibility between distant species; (2) identify and functionally characterize positive heterotic loci; (3) pyramid wide-compatibility genes and positive heterotic loci into a common genetic background; (4) deepen our understanding of the mechanisms involved in genomic structural instability in the F_1, and (5) develop high efficient pollination control technologies on a species-specific basis.

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