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Review

CRISPR/Cas Technology Revolutionizes Crop Breeding

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Abstract: Crop breeding is an important global strategy to meet sustainable food demand. CRISPR-Cas is a most promising gene-editing technology for rapid and precise generation of novel germplasm, and leads to revolutionary crop breeding innovation. In this review, we summarize recent advance of CRISPR/Cas technology in gene function analyses and generation of new germplasms with increased yield, improved product quality, and enhanced resistance to biotic and abiotic stress. We highlight their applications and breakthroughs in agriculture including crop de novo domestication, decoupling the gene pleiotropy tradeoff, crop hybrid seed conventional production, hybrid rice asexual reproduction, and double haploid breeding. Moreover, the challenges and development of CRISPR/Cas technology in crops are also discussed.

Keywords: CRISPR/Cas technology; crop; germplasm; breeding technology

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1. Introduction

In the future, agricultural production faces major challenges from a rapidly increasing human population and severe environmental stresses. Crop yield is a complex quantitative trait governed by many genes and environment factors, and some key genes and agronomic traits have gradually weakened or been lost during crop domestication. Traditional breeding methods have achieved increasing crop yield, but have many limitations in breeding superior varieties due to the lack of valuable natural germplasms, the obstacles of undesired genome incorporation or linkage drag, and their time consuming and laborious screening process (Razzaq et al. 2021). Compared with traditional methods, biotechnologies including transgene, gene editing, double haploid technique, and synthetic apomixis provide new crop breeding opportunities (Gao 2021; Razzaq et al. 2021; Xiong et al. 2023; Jacquier et al. 2020; Awan et al. 2022).

The advent of clustered regularly interspaced short palindromic repeats (CRISPR)-associated (Cas) (CRISPR/Cas) system provides a promising platform for genome editing in a site-specific manner, and initiates a new era in which we can rapidly and precisely manipulate genes responsible for agronomic traits to create novel germplasm (Wang and Doudna 2023). Based on the initial CRISPR-Cas9, multiple developed CRISPR/Cas systems (including spCas9-NG, base editing, prime editing, xCas9, Cas12a /Cpf1, Cas12b, Cas13 and Cas14) have greatly improved editing effectiveness, precision and specificity, and enabled their application in gene knockout, base editing, prime editing, gene insertion, epigenetic modulation, transcriptional regulation, and RNA editing (Koonin et al. 2023). CRISPR/Cas system iterative upgrades have provided unprecedented opportunities for gene function analyses and creation of desirable germplasms in different crops, which will lead to the third agricultural green revolution (Fernie and Yan 2019; Adeyinka et al. 2023). In this review, we summarize the application of CRISPR/Cas technology in crop de novo domestication, decoupling the tradeoff effect, conventional hybrid seed production, asexual reproduction and double haploid breeding.

2. Exploring gene functions and creating desired germplasms

CRISPR/Cas technology has unparalleled advantages in characterizing gene functions and faster generation of valuable crop germplasm resources (Ahmad 2023). Using CRISPR/Cas technology, KRN2 was well characterized as a convergent selected gene for the regulation of grain number in both maize and rice. Knockout of *KRN2* significantly increased their grain yields without affecting other agronomic traits, providing a feasible strategy for new germplasm generation and crop de novo domestication (Chen et al. 2022a). In maize, upright plant architecture is a practical choice for high-density planting and high yield (Kong et al. 2020). CRISPR-Cas9 editing *ZmRAVL1*, a positive regulator of leaf angle, engineered an upright plant architecture with increased yield under high planting densities, providing an option to develop density-tolerant high-yield cultivars (Kong et al. 2020; Tian et al. 2019). Now, specialty corns including sweet, waxy and baby corns have a growing consumer demand. Recently, supersweet and waxy corns and aromatic corns were created by simultaneously editing *ZmBADH2a /b*, *SH2* and *WX* (Wang et al. 2021b; Dong et al. 2019). In the USA, CRISPR-waxy corn hybrids with higher-yield and superior agronomic performance to conventional lines were pre-commercialized (Gao et al. 2020). Moreover, CRISPR-Cas9 editing *ChSK1* engineered maize with durable resistance to southern leaf blight (Chen et al. 2023). Recently, a gene discovery pipeline BREEDIT, combing multiplex genome editing of whole gene families with crossing schemes, has been used to identify valuable alleles for complex quantitative maize trait improvements (Lorenzo et al. 2023), providing a feasible tool to identify key genes and cultivate desired maize lines.

In rice; many new germplasms with higher eating quality (e.g.; low amylose content; low glutelin content and grain aroma); improved agronomic traits (e.g.; grain shape; tiller number and grain yield) or stress resistance were generated by editing *FLO2*; *Wx*; Os*BADH2*; *GS3*,*TGW6*; *SSII-2*; *SSII-3*; *OsPLDα1*; *OsAAP3*; *OsAAP4*; *OsAAP5*; *OsSPMS1*; *OsRR30*; *Xa13* ; *Bsr-d1*; *Pi21*; *ERF922*; *OsSWEET1b*; *OsWRKY63*; and *JMJ710*; respectively (Hui et al. 2022; Song et al. 2023; Tian et al. 2023; Yang et al. 2022; Huang et al. 2021; Khan et al. 2020; Lu et al. 2018; Fang et al. 2021b; Tao et al. 2018; Li et al. 2022a; Li et al. 2022b; Zhou et al. 2022; Zhang et al. 2022b; Zhao et al. 2022a). Many wheat germplasms with enhanced grain yield; improved grain quality and disease resistance were created by editing *FT-D1*; *Gli-γ1-1D*; *Gli-γ2-1B*; *pinb*, *waxy*, *ppo* and *psy*, respectively (Zhang et al. 2021; Chen et al. 2022c; Liu et al. 2023b). New soybean lines with high-monounsaturated fatty acid and high resistance to several *P. sojae* strains were engineered by knocking-out *GmPDCTs* and *GmTAP1* (Li et al. 2023; Liu et al. 2023c). Moreover, key genes associated with yellow-green variegation of leaf (Zhu et al. 2023), plant architecture (Kong et al. 2023), and fatty acid anabolic metabolism (Zhou et al. 2023a) have been well characterized in soybean.

3. Ushering in a new era of crop de novo domestication

For a long time, crop domestication has mainly focused on selecting desirable traits related to yield, leading to the gradual loss of excellent traits in wild species such as pest and disease resistance, abiotic stress tolerance, and nutritional quality. Traditional wild crop domestication methods are still an option to create new germplasms, but they are time-consuming, labor-intensive, and difficult to aggregate multiple traits (Zhu and Zhu 2021; Zsogon et al. 2017). In 2017, a strategy for wild species de novo domestication was proposed using genome editing techniques (Zsogon et al. 2017). In particular, CRISPR/Cas technology has achieved rapid wild crop de novo domestication by simultaneously editing key genes controlling agronomic traits, showing attractive prospects for effectively developing elite varieties (Zhu and Zhu 2021; Zsogon et al. 2017; Kumar et al. 2022; Jian et al. 2022; Huang et al. 2022; Gasparini et al. 2021; Khan et al. 2019).

In tomato, desirable trait aggregations in wild *Solanum pimpinellifolium* were engineered by editing six important loci essential for yield and nutritional value in modern tomatoes. The engineered lines had significant increases in fruit size, fruit number and fruit lycopene (Zsogon et al. 2018). Novel germplasms with enhanced productivity were created in the orphan *Solanaceae crop 'groundcherry'* (*Physalis pruinosa*) by editing orthologues of modern tomato genes controlling plant architecture and yield related traits, realizing rapid creation of elite genomic resources in distantly related orphan crops (Lemmon et al. 2018). Stress-tolerant wild-tomato species with desirable traits were engineered using a multiplex CRISPR–Cas9 technology, which had domesticated phenotypes and retained parental stress-tolerant traits (Li et al. 2018). Moreover, a ‘two-in-one’ strategy for stress-tolerant and multi-scenario cultivation breeding in tomatoes was devised through combining wild species de novo domestication with CRISPR/Cas generating male-sterility in modern cultivars (Xie et al. 2022). Recently, rapid de novo domestication of wild allotetraploid rice was realized by editing *O. alta* homologs of the genes controlling various agronomic traits in diploid rice, providing an effective way to breed new varieties aggregating desired traits via wild rice de novo domestication (Zhu and Zhu 2021; Yu et al. 2021). These studies demonstrate that CRISPR/Cas technology is a powerful tool for wild species de novo domestication to create new desirable varieties, ushering in a new era of crop breeding to utilize wild species genetic diversity in major and orphan crops.

4. Breaking breeding bottlenecks of tradeoff effects

Due to linkage drags or gene pleiotropy, crop breeding is often subject to complex trade-offs between traits, such as high yield and stress/disease resistance, yield and nutritional quality, and yield and plant architecture. In particular, the trade-off effect caused by gene pleiotropy has become the bottleneck of multi-traits pyramiding breeding (Nelson et al. 2018; Takatsuji 2017; Wang et al. 2021a; Song et al. 2022). Recently, CRISPR/Cas-mediated editing of cis-regulatory regions was used in different crops to generate novel beneficial alleles with improved stress resistance, yield and quality (Saeed et al. 2022; Okita and Delseny 2023). Unlike editing coding region, editing cis-regulatory region can fine-tune the expression level or profile of the target gene without disrupting its function, and thereby optimizing the trade-off effects of pleiotropic gene (Saeed et al. 2022; Zafar et al. 2020).

In rice, OsSWEET14 has a trade-off effect on disease resistance with plant height, tiller number, and seed size (Li et al. 2012; Chen et al. 2010; Antony et al. 2010). Using CRISPR/Cas technology, a broad-spectrum resistant rice with normal tiller number and seed size was developed by editing the TALE-binding elements in *OsSWEET11* and *OsSWEET14* promoters (Xu et al. 2019). *IPA1*, a pleiotropic gene regulating various agronomic traits and stress resistance, has a trade-off effect on rice yield related traits such as panicle size and tiller number (Jia et al. 2022b; Jia et al. 2022a; Liu et al. 2019; Wang et al. 2018; Song et al. 2017; Zhang et al. 2017; Wang et al. 2017; Lu et al. 2013; Jiao et al. 2010; Miura et al. 2010). New rice germplasms with enhanced yield were created by deleting a key cis-regulatory region controlling *IPA1* expression pattern, which subtly decoupled its tradeoff effect on grains per panicle and tiller number (Song et al. 2022; Dwivedi et al. 2021). *SLG7* is a key gene regulating grain slenderness and low chalkiness. By editing the AC II element-containing region in the promoter, CRISPR/Cas edited *SLG7* alleles with increased expression levels exhibited better appearance quality without affecting yield and eating quality (Tan et al. 2023). Similarly, in hybrid rice, editing the regulatory regions of *HEI10*led to an altered expression level and genetic recombination, which may be used for developing elite varieties (Wei et al. 2023). Recently, a CRISPR-Cas12a promoter editing (CAPE) system has been developed to improve rice agronomic traits by editing specific gene promoters. A high yield rice with better lodging resistance as Green Revolution *OsSD1* mutant was generated by editing *OsD18* promoter (Zhou et al. 2023b). Moreover, a high-efficiency prime-editing system was used to create resistant alleles with broad-spectrum resistance by knocking-in TAL effector binding elements from Os*SWEET14* into the promoter of dysfunctional *xa23* (Gupta et al. 2023). These research examples provide alternative strategies for the creation of quantitative variations of agronomic traits.

In maize, although the key components of CLAVATA-WUSCHEL signal pathway impact yield formation due to their tradeoff effects on ear meristem activity and ear development, their weak alleles show few yield effects (Bommert et al. 2005; Bommert et al. 2013; Taguchi-Shiobara et al. 2001; Rodriguez-Leal et al. 2019; Il Je et al. 2016; Basu and Parida 2021). Recently, elite weak alleles with increased grains per ear and maize yield were created by editing the key regulatory regions of *ZmCLE7* and *ZmFCP1* (Liu et al. 2021b). In wheat, *Mildew resistance locus O* (*MLO*), a pleiotropic susceptibility gene, has trade-off effects on disease resistance and yield related traits (Wang et al.

2014; Acevedo-Garcia et al. 2017; Chen et al. 2022c). Using CRISPR/Cas technology, a *mlo* resistance allele (*Tamlo*-R32) with normal growth and yield was engineered in multiple varieties by deleting a large fragment in the *MLO*-B1 locus, which led to ectopic activation of *TaTMT3B* and thereby rescued growth and yield penalties caused by *MLO* disruption (Chen et al. 2022c). These studies provide effective strategies for developing high-yielding crop varieties with stress resistance by decoupling the tradeoff on different traits caused by gene pleiotropy.

5. Accelerating conventional production of crop hybrid seed

Heterosis is a breakthrough in crop breeding which has greatly improved crop yield. However, since offspring cannot maintain their heterosis due to genetic separation of traits, it is a time-consuming, laborious and costly process to produce hybrid seeds every year (Wang 2020; Yu and Li 2022). The use of male-sterile lines has greatly enhanced hybrid seed yield and quality. Recently, CRISPR/Cas technology has shown its unique advantages in unravelling the mechanism of male sterility and developing male sterile lines (Barman et al. 2019). Many male-sterile related genes have been well characterized in maize (Wang et al. 2022c), rice (Zhang et al. 2022a; Ni et al. 2021; Han et al. 2021; Xiang et al. 2021; Wang et al. 2020), wheat (Zhang et al. 2023a), and soybean (Fang et al. 2021a), enriching the molecular mechanisms of male sterility in crops. Importantly, increasing CRISPR-edited male-sterile lines have been generated in maize (Wang et al. 2022c), rice (Fang et al. 2022; Chen et al. 2022b; Pak et al. 2021; Song et al. 2021; Barman et al. 2019; Li et al. 2019; Li et al. 2016), wheat (Li et al. 2020; Okada et al. 2019; Singh et al. 2018), foxtail millet (Zhang et al. 2023b) and soybean (Nadeem et al. 2021), which will greatly promote commercial hybrid seed production in different crops.

Unlike male-sterility, thermo-sensitive female sterility has been rarely reported due to a lack of desired germplasms, but it is very important for promoting crop hybrid seed production (Li et al. 2022c). Using CRISPR/Cas technology, a thermo-sensitive female sterility gene, *AGO7*/*TFS1*, was identified to engineer a female sterility line. As a restorer line, its field trial showed high seed-setting rate of hybrid panicles, paving a new path for fully mechanized hybrid seed production like conventional rice (Li et al. 2022c; Yu and Li 2022).

6. Promoting hybrid rice asexual reproduction

Recently, genome editing mediated apomixis technology has realized heterosis fixation in hybrid offspring. In rice, clonal progeny retaining parental heterozygosity was obtained by CRISPR-editing *BABY BOOM1* (*BBM1*), *BBM2*, and *BBM3*, and its asexual-propagation traits can be stably inherited in multiple generations of clones (Khanday et al. 2019). Similarly, by combining heterozygosity fixation with haploid induction by simultaneous editing *REC8*, *PAIR1*, *OSD1* and *MTL*, Wang et al. generated hybrid rice plants that could propagate clonally through seeds, realizing self-propagation and stable transmission of elite F1 hybrid crops (Wang et al. 2019b; Liu et al. 2023a). Excitingly, in hybrid rice, high-frequency synthetic apomixis was achieved by simultaneous editing *PAIR1*, *REC8* and *OSD1*, and clonal progeny could stably retain the phenotype and genotype of F1 hybrid in successive generations (Vernet et al. 2022). These studies provide efficient ways to utilize F1 hybrid heterosis and convert hybrids to apomixis in a sustainable way.

7. Facilitating double haploid breeding technology

Double haploid technology, including haploid induction and double haploid development, can greatly accelerate breeding processby rapidly generating homozygous plants, and has been widely applied in various crops (Eliby et al. 2022; Jacquier et al. 2020; Dwivedi et al. 2015). Using CRISPR/Cas genome editing technology , many advances have been made in the mechanisms and application of haploid induction in different crops (Shen et al. 2023). In maize, increasing key genes involved in haploid induction such as *ZmPOD65*, *ZmPLD3*, *ZmDMP7*, and *ZmMTL*/*ZmPLA1* have been characterized and show potential for breeding haploid inducers (Zhong et al. 2019; Li et al. 2021; Jiang et al. 2022). In rice, haploid induction was triggered by editing *OsMATL*, *OsECS1* and *OsECS2*, respectively (Liu et al. 2021a; Zhang et al. 2023c; Yao et al. 2018; Wang et al. 2019b; Xie et al. 2019). In *Brassica*, editing homologues of *DMP9* triggered haploid induction in *B. oleracea* and polyploid *B. napus*, offering haploid induction materials for efficient breeding (Zhao et al. 2022b; Zhong et al. 2022). In *Medicago truncatula*, haploid plants were generated by editing *DMP* homologues (Wang et al. 2022b). Moreover, editing *TaPLA*, *TaMTL* and *TaCENH3α* could trigger haploid induction in wheat, indicating that CRISPR/Cas mediated haploid induction could be extended from diploid crops to polyploid species (Liu et al. 2020a; Liu et al. 2020b; Lv et al. 2020; Sun et al. 2022). These findings provide available methods for haploid induction in different crops.

Recently, CRISPR/Cas9 technology mediated haploid induction systems have been developed in different crops. In maize, a haploid induction editing technology (HI-EDIT), a Haploid-Inducer Mediated Genome Editing (IMGE) system, an approach combining haploid induction with a robust haploid identification marker, and a CRISPR/dCas9-mediated gene activation toolkit were established to effectively generate genome-edited haploids (Kelliher et al. 2019; Dong et al. 2018; Wang et al. 2019a; Qi et al. 2022). Using a CRISPR/Cas9 vector with an enhanced green fluorescent protein expression cassette, an efficient haploid induction system was developed by editing *BnaDMP* genes in *Brassica napu*(Li et al. 2022d). In foxtail millet, haploid induction has been achieved by CRISPR-Cas9 mediated mutation of *SiMTL*, providing a possible application of double haploid technology in its breeding (Cheng et al. 2021). Importantly, a fast technique for visual screening of wheat haploids was developed by combining the haploid inducer generated by editing *TaMTL* and embryo-specific anthocyanin markers, providing a promising strategy for a large-scale haploid inducer in different crops (Tang et al. 2023). Recently, a RUBY reporter system, a background-independent and efficient marker for haploid identification, has been established that enables easy and accurate haploid identification in maize and tomato, which will be promising in double haploid breeding in different crops (Wang et al. 2023a).

8. Conclusions

The advent and updating of CRISPR/Cas technologies have paved the way for gene function analysis and crop breeding, providing unprecedented opportunities for generation of novel genetic variation, rapid crop de novo domestication, breeding technology innovation, and precise pyramiding breeding. In particular, the upgrade and integration of genome editing, haploid induction and apomixis technologies will usher in a new crop breeding era (Wang et al. 2019b).

Excitingly, CRISPR-edited products such as a CRISPR/Cas9 waxy corn (Gao et al. 2020) and a CRISPR-edited GABA-enriched tomato have been commercialized and are entering the market (Waltz 2022). Notably, many CRISPR/Cas products have only been tested for their characters under simulated conditions, and there is a lack of field trials to evaluate their final field performance, which seriously hinders their application in production (Wang et al. 2022c). Thus, it is urgent to focus on field trials of CRISPR-Cas edited crops and thus promote their commercial production.

Low efficiency and high genotype dependency are the major bottlenecks limiting widespread application of CRISPR/Cas technology in different crops and elite varieties (Altpeter et al. 2016; Wang et al. 2022a). Recently, developed genotype-independent transformation systems by enhancing *TaWOX5* and *Wus2*/*Bbm* could significantly increase transformation efficiency in wheat, rye, barley, maize and rice, providing new ways to expand genetic transformation and genome editing across the Poaceae (Wang et al. 2022a; Wang et al. 2023b). Further optimizing transformation methods will advance genome editing on a wider range of crop species and varieties. Moreover, it is imperative to develop CRISPR/Cas systems with higher editing efficiency, lower off-target activity, more editing ways and wider editing range, which will make them more effective and flexible in crop breeding. Recently, an optimized Cas12a base editor (Cas12a-ABE) has been established to introduce inheritable multiplex base edits in wheat and maize, which will assist in optimizing genome editing systems in a wide range of crop species (Gaillochet et al. 2023). With the continuous development of CRISPR/Cas technology, it will become a popular strategy for breeders to precisely generate novel germplasms in different crops.

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