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De novo domestication: retrace the history of agriculture to design future crops

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Certain crops were domesticated from their wild progenitors and have served as the major staple food since then, but now suffered from the limited genetic diversity in breeding.

Enormous wild species possess unique advantages such as stress tolerance, polyploidy, perennial habit, and natural nutrition. However, it remains a big challenge to utilize wild species in conventional breeding. With recent advances in biotechnologies, one new breeding strategy, *de novo* domestication, has emerged and been demonstrated by pioneer work. Here, we review the emergence and milestone progress of *de novo* domestication and discuss how wild relatives could be exploited into new types of crops. With the understanding of the genetic basis of crop domestication and the development of biotechnologies, various elite wild germplasms will be designed and practiced to fulfill particular breeding goals and create new types of crops. *De novo* domestication is paving a new way for breeding the future.

Addresses

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Introduction

In the past century, breeding strategies and biotechnologies have been evolving rapidly. Cross-breeding, heterosis and hybrid crop breeding, mutagenesis breeding, molecular marker-assisted breeding, transgenic breeding, and breeding by molecular design have made critical contributions to increase global grain

yield and ensure world food security. However, the narrow genetic background caused by the monoculture of elite varieties has become a bottleneck for germplasm innovation. New agricultural challenges, such as more frequent disasters and climate changes, extensive use of fossil-fueled products, including fertilizers and pesticides, along with the increasing world population, have driven the shift of breeding objectives. Therefore, new breeding strategies are eagerly needed for future agriculture.

Here, based on the recent progresses in *de novo* domestication, we overview new challenges in agriculture, summarize the emergence and development of *de novo* domestication, highlight the roadmap and key technical bottlenecks, and discuss the possible breeding goals that may be fulfilled by *de novo* domestication of certain wild species.

New agricultural challenges drive the shift of breeding objectives

The Neolithic Revolution and the Industrial Revolution were considered as two of the most important events in human history, which initiated the agriculture-driven and fossil fuel-driven civilizations [1,2]. The domestication of wild cereals can be tracked back to 12 000 years ago [3], and their grains have served as the major staple food since then. Crop domestication was accomplished by the long-term artificial selection and accumulation of beneficial natural mutations over hundreds or thousands of years. At this stage, the breeding objectives were to make plants fit the requirements of human cultivation, and various crops domesticated around the world shared similar characteristics known as 'domestication syndrome', such as less seed shattering, erect growth, shorter awn, larger seeds or fruits, reduced dormancy, and so on [4,5].

After the Industrial Revolution, agricultural products were no longer the sole source of human-consumable energy. The crops were cultivated with a large amount of extra industrial products, including fertilizers and pesticides, herbicides, and farm machinery. The breeding goal had shifted to develop high-yield and lodging-resistance varieties that adapt to new farming systems. As a result, roughly 90 times more energy subsidies per hectare of cropland were costly in 2000 than in 1900 [2]. These caused the new breeding objectives to decrease the agricultural input and make it

more sustainable, such as enhancing the biotic resistance for fewer pesticides, optimizing the plant architecture to improve the harvest index, and increasing the nutrient use efficiency for less fertilizer usage.

In foreseeable future, life-or-death challenges are in front of us for agriculture [6]. The world population is estimated to reach 10–12 billion by the end of this century, requiring at least a 60% increase in agricultural productivity [7]. The increase rate of grain yield has slowed down or even stopped, and whether the crop yield has reached a limit is unknown. Meanwhile, along with global warming, natural disasters have happened more frequently, such as extreme hot and cold weather, drought, flood, and so on, which all greatly harm agricultural production and require the crop with a higher ability of climate adaptation. New breeding strategies for these breeding objects are urgently needed [8].

The emergence and development of *de novo* domestication

The emerging concept of *de novo* domestication

The concept and progresses of *de novo* domestication have been developed rapidly in the past ten years (Figure 1). In 2013, the idea that the knowledge of cereal domestication would accelerate the rapid domestication of other crops was proposed by Tao Sang and Jiayang Li [5]. In the same year, Tao Sang and Song Ge elaborated that the discovery of valuable alleles from the cultivated and wild species, the collection of germplasms with allele pools might trigger the redomestication of rice varieties [9]. Meanwhile, in 2013, three works demonstrated that Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR)/CRISPR associated protein 9 (Cas9)-based genome editing can modify plant genomes with high efficiency [10–12]. In 2017, Lázaro Eustáquio Pereira Peres's group put forward that wild relatives harboring traits of interest could be *de novo* domesticated through advanced genome editing, and discussed a potential example of *Solanum galapagense*, a species tolerated to as high as 70% salinity, that editing six specific genes may achieve vegetative and reproductive ideotypes [13]. In 2017, Michael Palmgren's group proposed accelerating domestication of semi-domesticated or wild relatives to develop new crops and analyzed the feasibility and approaches [14].

Pioneer work in *de novo* domestication

In 2018, milestone progresses have been made to practice and prove the feasibility of *de novo* domestication with wild relatives of tomato cultivars. Cao Xu and Caixia Gao groups reported the achieved domestication in *Solanum pimpinellifolium* by genome editing, and the domesticated tomato retained natural resistance of interest [15]. Lázaro Eustáquio Pereira Peres and Jörg

Kudla's groups used CRISPR/Cas9 to achieve *de novo* domestication of wild tomato by editing six genes to combine agronomically desired traits [16]. In 2018, Zachary B. Lippman's group accomplished the rapid domestication of an orphan crop, *Physalis pruinosa* [17]. In 2021, Jiayang Li's group reported *de novo* domestication of elite wild allotetraploid rice, which proposed and developed a practical route toward creating a new staple crop with large biomass and high climate adaptation [18]. In 2022, a 'two-in-one' strategy allowed rapid exploitation by crossing the *de novo*-domesticated wild tomato species with modern cultivars to stack yield traits with stress tolerance [19].

Along with these research progresses, the concept of *de novo* domestication strategy has also been developed and become clear [4,20–24]. In summary, the route of *de novo* domestication strategy starts from the selection of wild or semi-domesticated plants with traits of interest, and follows by molecular design and rapid domestication by genome editing, conventional breeding and phenotypic screening, and field evaluation, and ultimately creates new crops that meet the policy assurance and biosafety assessment (Figure 2a). According to the characteristics of wild species, *de novo* domestication can be divided into three main directions (Figure 2b): (1) redomestication of the ancestors or relatives of cultivated varieties, which can quickly introduce the stress-resistant traits into cultivated varieties, and broaden the genetic diversity of cultivated varieties; (2) *de novo* domestication of wild plants, which can rapidly domesticate non-domesticated species with elite traits to create new crop types; (3) accelerating the domestication of semi-domesticated plants or orphan crops, which can improve the undomesticated traits of orphan crops with low input and develop regional agriculture.

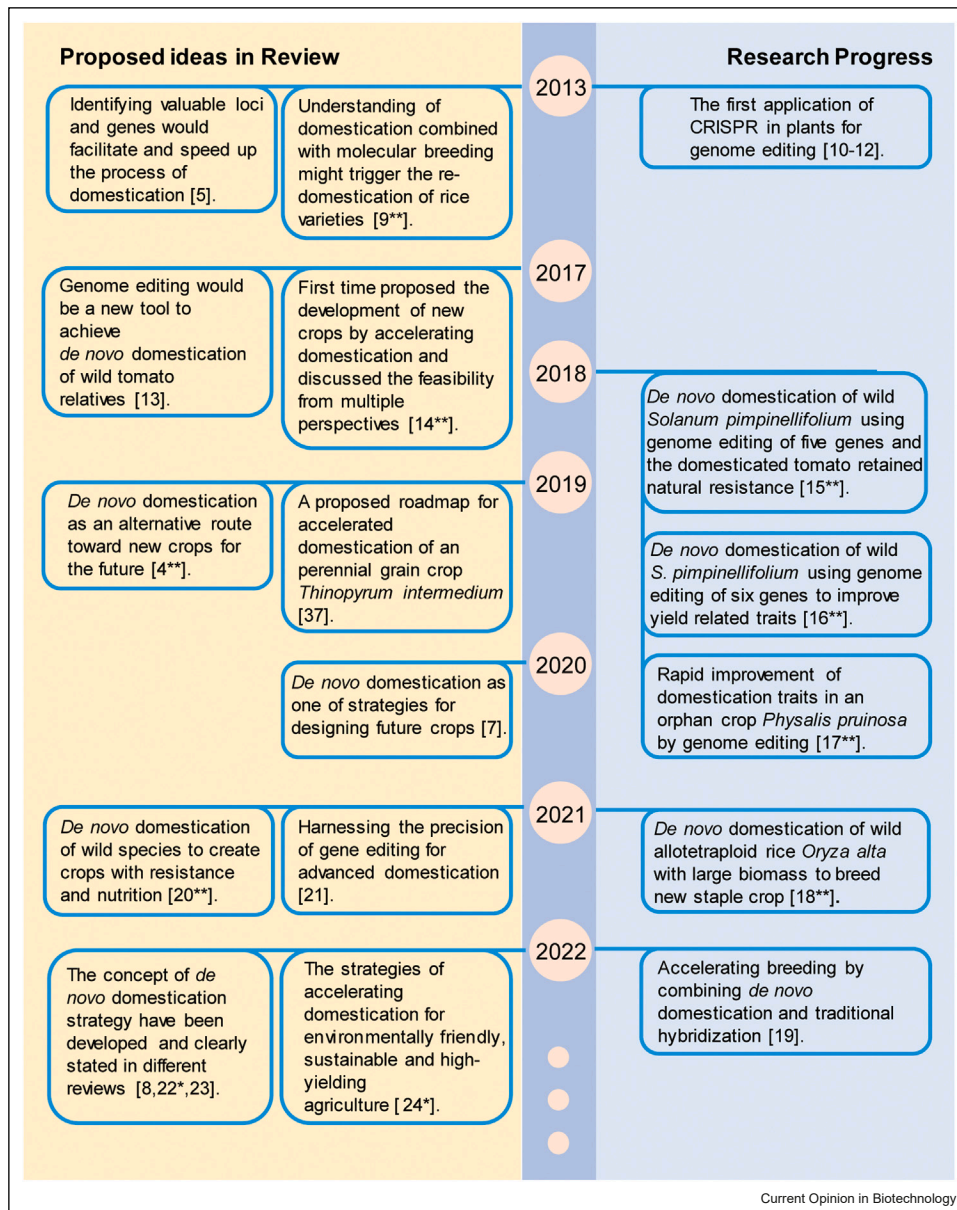
Utilization of wild species for agriculture goals

Based on the unique advantages of wild species, *de novo* domestication may achieve different breeding goals difficult for conventional breeding (Figure 3).

Stress tolerance for marginal land farming

Compared with cultivated crops, wild species usually possess stronger stress tolerance [20]. Owing to the narrow genetic diversity and the complicated regulatory mechanism underlying the stress responses, it is hard to introduce stress tolerance from wild species into cultivated crops, and thus *de novo* domestication of wild species is a promising alternative strategy. For example, *S. pimpinellifolium* accessions, the wild ancestor of cultivated tomato, are remarkably resistant to bacterial spot disease and salt-tolerant [15]. Genome editing of five or six genes achieved the improvement of its morphology, together with the size, number, and nutritional value of

Figure 1



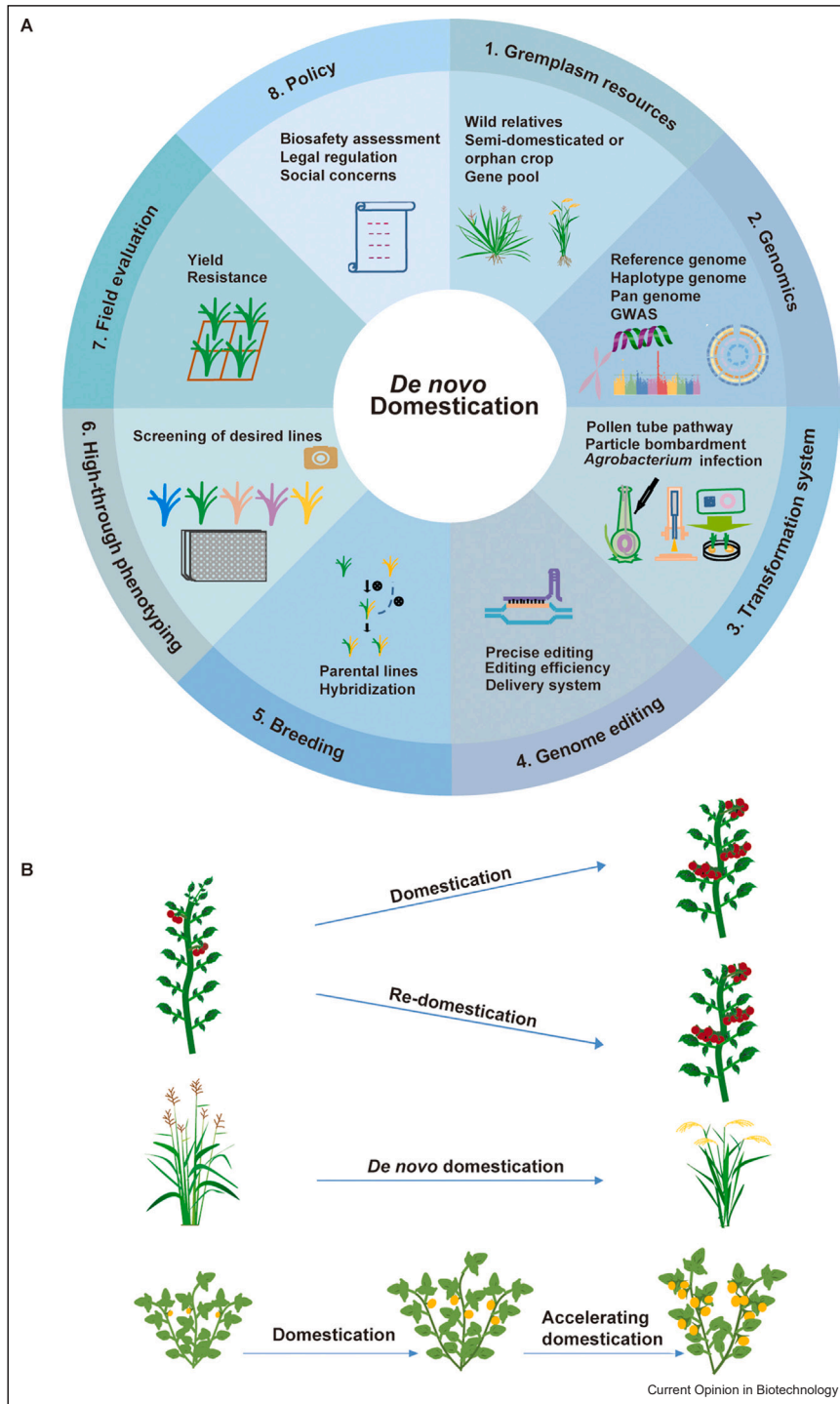
The development and pioneer work of *de novo* domestication.

the fruits while keeping its natural stress tolerance [15,16]. The wild halophytic plant *Oryza coarctata*, grown in the saline coastal regions of India and Bangladesh, is known to be naturally tolerant to salinity [25]. Different wild sorghum species have exhibited higher resistance to drought, high temperature, parasite, ergot, nematodes, insect, disease, and cold [26], and so do other species [27]. *De novo* domestication of such wild plants may create crops grown in marginal land such as saline-alkali land.

Polyploidy for high yield and environmental adaptability

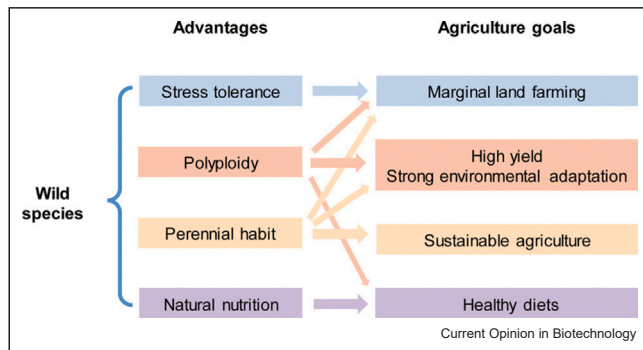
From the prospective of evolution, polyploidization, mostly resulting from whole-genome duplications or hybridization, is a common mode in flowering plants [28]. Polyploidy often shows genome buffering, vigourness, and environmental adaptability [29]. Recently, great efforts have also been made to improve crops by artificial induction of autopolyploidy [30,31]. Compared with this, *de novo* domestication of wild species with natural polyploidy usually has less fertility penalty and

Figure 2



Roadmap of *de novo* domestication. **(a)** The route of *de novo* domestication strategy starts from the selection of wild or semi-domesticated plants with traits of interest, and follows by molecular design and rapid domestication by genome editing, conventional breeding and phenotypic screening, and field evaluation, and ultimately creates new crops that meet the policy assurance and biosafety assessment. **(b)** According to the characteristics of wild species, *de novo* domestication can be divided into three main directions: (1) redomestication of the ancestors or wild relatives of cultivated varieties, (2) *de novo* domestication of wild plants, and (3) accelerating the domestication of semi-domesticated plants or orphan crops.

Figure 3



The advantages of wild species and proposed agriculture goals of *de novo* domestication.

possesses larger genetic diversity. A case study could be wild allotetraploid rice *O. alta*, which is originally distributed in south and central America and shows obvious polyploidy advantages in high biomass, resistance to several insects and diseases, and tolerance to salt. In addition to CCDD allotetraploid rice, *O. coarctata* (KKLL) showed large biomass and high photosynthetic efficiency under saline treatment [32]. It is foreseeable that *de novo* domestication of wild polyploid species might be a promising option to create new types of elite crops.

Perennial habit for sustainable agriculture

Compared with current annual cultivars, the perennial grain crop can develop a long and deep root system that improves nutrients and water utilization efficiency, and thus is more suitable for sustainable agriculture [33–35]. A recent study reported that after ~20 years of hard work, the perennialization of rice was successfully achieved by the hybridization of annual cultivated rice *O. sativa* with its wild perennial relative African *O. longistaminata* [36]. Still, it is very challenging to shift the life cycle from annual to perennial by conventional breeding, and *de novo* domestication of wild perennial relatives is an alternative approach. Michael Palmgren and his colleagues proposed that wheatgrass (*Thinopyrum intermedium*), a close perennial relative of wheat, was a candidate perennial grain crop for accelerated domestication [37].

Natural nutrition for healthy diets

Many wild species possessed unique beneficial metabolites for human health [38], and diversified nutrition food is one of the major parts for healthy diets. However, many wild species are undomesticated or semi-domesticated, leading to low production and labor-intensive. For example, orphan crop groundcherry *P. pruinosa*, grown in Central and South America for its subtly sweet berries and intense flavor. Rapid domestication in *P.*

pruinosa has improved productivity traits [17]. Right now, orphan crops have got less attention, and accelerating domestication of these orphan crops with new technologies will allow rapid improvement at a low cost, which will benefit local agriculture.

Essential technical basis for *de novo* domestication

Transformation and genome editing

Genetic transformation and genome editing are the fundamental technologies for *de novo* domestication to modify key genes as designed, and their efficiency directly determines the feasibility of *de novo* domestication for certain wild species. *Agrobacterium*-mediated transformation, particle bombardment transformation, and pollen-tube pathway transformation are widely used as DNA delivery tools for transgenic plants. Although the transformation efficiency can be very high in well-established systems in model plants such as rice, the generation of transgenic plants still remains a major obstacle for most of the wild species and many crops. It was estimated that fewer than 0.1% can be genetically manipulated among more than 370 000 higher plants in nature [39].

Recently, different strategies have been developed for genotype-free or tissue culture-free transformation systems, which greatly expanded the possible targets for *de novo* domestication. Overexpression of maize *Baby Boom 1* combined with *Wuschel 2* can improve transformation in maize, sorghum, sugarcane, and rice [40]. Overexpression of *Growth-Regulating Factor 4* (*GRF4*) and coregulator gene *GRF-Interacting Factor 1* (*GIF1*) can promote the regeneration ability of wheat, rice, and citrus [41]. A cut-dip-budding delivery method is developed for herbaceous, tuberous, and woody species [39]. RNA viruses were used to deliver editing reagents into apical meristem [42]. Nanotechnology coupled with CRISPR reagent is also encouraged for genotype-free transformation [43,44].

The CRISPR/Cas-based genome editing systems have been rapidly developed, such as deletion, base editing, insertion, replacement, and prime editing [45], which all benefited the efficiency of *de novo* domestication. Still, *de novo* domestication has special demands. As many desired traits need to be stacked in one germplasm, editing of many designed genes together was especially important, which requires efficient multiplex genome editing and high-throughput low-cost genotyping of multiple editing targets. Moreover, genome editing may result in heterozygous and chimeras, and for multiplex genome editing, this will lead to laborious work to obtain desired homozygous lines in the offspring. Meanwhile, many domestication-related genes require gain of function to acquire the desired trait, but it is still very

challenging to create gain-of-function mutations. Knock-in system is anticipated for this intention. For example, the knock-in of the elite allele of *5-enolpyruvylshikimate-3-phosphate synthase* conferred glyphosate tolerance in rice [46]. Although strategies have been developed to improve knock-in efficiency, such as geminivirus-derived CRISPR system, retrons, and Cas-associated transposases, the efficiency of precise gene knock-in is still a bottleneck [47–49]. Meanwhile, it is argued whether knock-in products, especially with foreign gene knock-in, should be regulated as transgenic organisms. Therefore, the development of specific genome editing systems is important for *de novo* domestication.

Identification of domestication-related gene

The decoding of the genome of targeted germplasm provides fundamental information for *de novo* domestication. Nowadays, newly emerged sequencing technologies and algorithms have largely accelerated genome assembly as well as the exploitation of genes and genetic variants associated with important traits. Update to 2020, 788 plant species have been sequenced, of which 47 species have genomes assembled to the chromosomal level [50], and this number is rapidly increasing. However, compared with well-assembled genomes, the identification of domestication-related genes is still very challenging. Sequence alignment is normally used to identify the genes homologous to the known domestication-related genes, but it usually hits many candidates and further validation will cost a lot of time. Meanwhile, great efforts have been made to study domestication-related genes in the past twenty years [51,52], but many domestication traits have still not been fully investigated such as heading uniformity, which requires great efforts in cloning new genes controlling certain traits.

Perspective on *de novo* domestication

Crop breeding is a rapidly developing science and technology driven by individual innovations and their integrations of multiple disciplines, including germplasm resources, genetics, biochemistry, molecular biology, genomics, functional genomics, biostatistics, genetic engineering, computational biology, synthetic biology, genome editing, and so on. Recently, a *de novo* domestication strategy is developed by integrating unexplored genetic resources of wild species, the elucidated molecular mechanisms of domestication-related traits, and the advanced tools of genetic manipulation, which enables us new opportunities to breed unprecedented crops to fulfill special breeding goals and face the coming challenges.

Although the practical route of *de novo* domestication has been demonstrated, a series of key questions remain to be addressed for the realization of *de novo*-domesticated crops. Whether the created crops can truly surpass the current crops? Whether the efficiency, the cost, and the breeding cycle of *de novo* domestication are acceptable? Tremendous efforts still need to be made in the future. The wild species should be carefully evaluated to identify the best candidate worthy to be *de novo* domesticated, which ultimately determines the success of its domestication. Moreover, in addition to highly efficient genome editing for a specific wild species, to minimize the breeding cost and time, effective breeding also requires the comprehensive utilization of conventional breeding technologies, the breeder's experience, and good luck.

Even after an elite new material could be generated, additional steps are necessary for realizing it as a new crop in commercialization. First, the regulatory policies are primarily to be considered. In particular, *de novo* domestication is based on genome editing, and some wild species are previously unexploited. Second, a suitable production system for new crops is needed to make it economically practical, including cultivation techniques, farm machinery, processing machinery, and food recipes. Third, public concerns and acceptance of new crops require time and publicity. All these works cover multiple disciplines and require extensive and in-depth cooperation from all sectors of society.

Conclusion

It has been estimated that 2500 species, spanning 160 taxonomic families, have undergone domestication, but only 250 species are fully domesticated [3]. With a deep understanding of the molecular genetic basis of domestication events and multiple genome editing systems, proof-of-concept studies in crop domestication have been realized. Domestication-driven breeding can greatly expand available genetic resources and be applied to meet emerging breeding goals for sustainable agriculture. The achievements of this strategy will promote a new round of agricultural revolution.

Conflict of interest statement

Nothing declared.

Data Availability

No data were used for the research described in the article.

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