



Accelerating crop domestication through genome editing for sustainable agriculture

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Abstract

With the establishment of human civilization, wild plant species were domesticated and cultivated at their centres of origin and further disseminated in different parts of the world. While being grown in the wild and on farms, innumerable mutations occurred over years creating new variations in their genome. Today's improved crop plants are the result of years of artificial selection for a few of those mutations, many times coupled with deliberate selection for desirable recombinants that originated in nature or developed through targeted breeding. Artificial phenotypic selection leaves footprints in the genome of crop species. Over the last three decades, researchers have identified numerous genes and causal mutations associated with domestication events, leading to a better understanding of how our forefathers and foremothers tinkered with plant development to meet their food and fodder needs. Our ability to script complex genetic information through efficient genome editing tools has enabled us to take a great leap forward to accelerate crop domestication. In this review, we have discussed how genome editing tools facilitate the domestication of wild and semi-domesticated species, the prerequisites for performing editing in wild genomes, and the potential future target loci for installing domestication syndrome rapidly in wild plant species. Genome editing technologies could help us bring wild and partially domesticated crop plants to mainstream agriculture to sustainably meet our current and future needs.

Keywords *De novo* domestication · CRISPR-Cas · Artificial selection · Domestication genes · Wild species · Crop wild relatives · Orphan crop

Abbreviations

CRISPR Clustered Regularly Interspaced Short Palindromic Repeats
Cas CRISPR-associated protein
DSB Double-strand break
HDR Homology-directed repair
CBEs Cytosine base editors

ABEs Adenine base editors
CGBEs C-to-G base editors
sgRNA Single guide RNA
PE Prime editing
SNPs Single nucleotide polymorphisms

Introduction

Our ancestors started a true revolution around 12,000 years ago through a societal transformation from being hunter-gatherers to farmers. They transformed many wild plant species into domesticated crop plants to best fit their needs. The first evidence of human-aided domestication of a large number of species was recorded in the 'fertile crescent' (present-day Iraq, Syria, Lebanon, Palestine, Israel, Jordan, Egypt, and a portion of Iran and Turkey) approximately 10,000–12,000 years ago. Several traits that are accumulated in domesticated crop plants are widely known as 'domestication syndrome'. This syndrome can clearly distinguish a

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modern crop from its wild progenitor (Hammer 1984). For example, food crop plants accrued characteristics like larger sink or grains, more determinate growth, increased apical dominance, loss of seed-dormancy and -shattering, more synchronized flowering, and modified photoperiod sensitivity compared to their progenitor (Doebley et al. 2006).

These predominantly productivity-oriented domestication efforts resulted in a severe loss of genetic diversity for other traits. Compared to neutral genes (i.e., genes that do not contribute to desirable phenotype), genes that influence favoured phenotype have undergone a more drastic loss of diversity since plant species harbouring desired alleles were only selected to raise the next generation. As a result, other alleles were lost from the population (Doebley et al. 2006). This allele loss has increased the vulnerability of our modern crop plants to abiotic and biotic stresses. Further, these modern high-yielding crop plants require more irrigation and fertilizers for desirable harvest, and agrochemicals for controlling diseases and pests. It has been estimated that about 30,000 plant species are edible and modern human cultivates only 150 species. Surprisingly, 70% of human calorie needs are fulfilled by only 15 crop plants, and 95% of the world's calories come from only 30 species (Fernie and Yan 2019). Hence, the lion's share of the edible species are left from utilization and can be brought into mainstream agriculture by modifying them for desirable characteristics. For example, *Ammophila arenaria*, commonly known as European beachgrass, can tolerate a high level of drought, cold, and salinity. However, *A. arenaria* has slender seeds; upon modification, it could be used as a cereal crop (Zhang et al. 2020).

The evidence discussed above shows that crop domestication has been crucial to the flourishing human population. However, it has also caused a massive loss of plant genetic diversity. In the wake of climate change and rising food demand, harnessing those lost diversities could play a significant role in global food security and sustainable agriculture. Furthermore, many wild and semi-domesticated plant species possess important traits desirable in a changing climate. Therefore, understanding the genetics of crop domestication and speeding up the process of domestication could help solve many problems in modern agriculture.

The natural process of domestication of wild species takes an extremely long time. For example, the domestication of modern-day maize from its wild ancestor, teosinte, took almost 9000 years. Genes that are identified to be associated with initial domestication are known as domestication genes, while genes that are associated with the subsequent spread and adaptation of domesticated/semi-domesticated crop plants to different local environments are called diversification genes (Meyer and Purugganan 2013). Many domestication traits have been reported to have arisen by disruption of gene function. Therefore, the availability of genome editing technologies gives us great hope to accelerate domestication.

The remarkable recent advancement in genome editing technologies, especially CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats)-Cas (CRISPR-associated protein), enables precise genome manipulation. CRISPR-Cas is a powerful genome editing technology that gave rise to diverse molecular tools to precisely modify targeted DNA sequences and regulate the expression of genes (Molla et al. 2020a). Overall, these tools, briefly described below, have tremendous potential in facilitating a rapid understanding of the genetics of crop domestication and eventually assisting the neo-domestication of wild and semi-domesticated species.

Inducing genetic variation by using CRISPR-Cas tools

Faster domestication by genome editing can be achieved with CRISPR-Cas tools. Conventional CRISPR-Cas tools can perform targeted gene knock-out with high precision. This system comprises two components, a single guide RNA (sgRNA) and a Cas9 nuclease protein. A sgRNA is designed to harbour a complementary sequence to the target DNA. The sgRNA guides Cas9 to make a double-strand break (DSB) at the target locus. During DSB repair, cellular machinery introduces small indels (insertions or deletions) at the breaking point, which frequently cause frameshift mutation, resulting in disruption of gene function. These tools are also suitable for knocking out multiple genes at once by simply constructing multiple sgRNAs. The technology has rapidly progressed beyond knocking out a gene through targeted DSB. For more precise sequence change, cytosine- and adenine-base editors (CBEs and ABEs) have been developed to perform targeted C-to-T and A-to-G conversion, respectively in the genome (Komor et al. 2016; Nishida et al. 2016; Gaudelli et al. 2018). More information on base editing technology and its applications is given in a comprehensive review (Molla and Yang 2019). The base editing toolbox has been recently enriched with C-to-G base editors (CGBEs) (reviewed by (Molla et al. 2020b)).

Another breakthrough in precise genome editing is the development of prime editing (PE) tools (Anzalone et al. 2019). PE can generate all kinds of base substitutions, small insertions and deletions, and the combination of those edits in the genome. Since the efficiency of PE is low in the plant system (Molla et al. 2021), significant improvement of PE tools and strategies is required before its routine use in domestication and other crop improvement program. Cas-mediated DSB and additional donor template supply could achieve targeted insertion of partial or entire gene and/or regulatory sequences in plant genome through homology-directed repair (HDR). Although HDR has the potential to install any simple to

complex edits in the genome, it suffers from extremely low efficiency of success in higher plant species (Molla et al. 2022). Nevertheless, these genome editing tools could be deployed for functional validation of any putative genes responsible for crop domestication. On the other hand, domestication alleles could be rapidly installed in wild relatives using those genome editing tools.

Imitating crop domestication

Many wild relatives of crop plants and semi-domesticated or orphan crop plants have better adaptability to harsh climates, greater resistance to pathogens, and superior nutritional quality than modern cultivars. However, farmers prefer to avoid cultivating them as they are beset with many undesirable characteristics. Crop domestication process has gone through artificial selection as per human food and fodder needs, purposeful cultivation, fixation of favourable alleles, geographic expansion, and decisive breeding (Gaut et al. 2018). It took thousands of years to domesticate a crop through repeated selections to avoid the inheritance of undesirable traits of the wild progenitor.

Negative epistatic interaction of favourable genes may lead to unsuitable phenotypic effects (Soyk et al. 2017). The introgression of a desired gene can bring in unwanted genes through linkage drags. Refining the best alleles from the allelic variation in wild relatives and new mutations are vital for domestication of some traits (Doebley et al. 2006). Next-generation high-throughput sequencing technology along with multi-omics strategies could help identify desirable genes/alleles in wild ancestors of crop plants. Identifying the mutation and searching orthologs of domestication genes contributing to a trait could help imitate crop domestication (Østerberg et al. 2017). Through modern molecular biology and genetics studies, our knowledge of domestication genes is enriching day by day (Table 1). The knowledge could guide genome-editing-mediated modification of homologous genes in wild species to turn them into suitable crops. Most of the domestication genes identified with characterized modifications could be targeted with the help of the latest genome editing tools. Since many domestication traits were identified as monogenic and involve loss-of-function mutation (Meyer and Purugganan 2013), genome editing is an attractive way to generate mutants for those genes rapidly. Genome editing tools can aid in developing looked-for traits in traditional orphan crop plants and help solve food security issues in a short span of time (Fig. 1). CRISPR-Cas engineered domestication could aid greater

nutritional benefits and better adaptation to climate change and various biotic stresses at an accelerated pace.

De novo domestication of wild species using genome editing

Traditional domestication took thousands of years, but with the advent of genome editing tools like CRISPR-Cas, domestication of wild species can be achieved in a few generations. Two pioneering studies reported using CRISPR-Cas tools for the domestication of the wild tomato, *Solanum pimpinellifolium* (Li et al. 2018; Zsögön et al. 2018). This wild tomato is well known for its stress tolerance ability but is poor in fruit production and yield. These studies showed targeted disruption of known tomato domestication genes by multiplex CRISPR-Cas editing. The genes: *SELF-PRUNING* (for determinate growth habit), *FASCIATED*, *CLAVATA3*, *WUSCHEL* and *FRUIT WEIGHT 2.2* (for fruit size), *SELF-PRUNING 5G* (for floral induction), *OVATE* (for fruit shape), *MULTIFLORA* (for fruit number), *LYCOPENE BETA CYCLASE* (for lycopene content), and *GDP-L-GALACTOSE PHOSPHORYLASE* (for vitamin C content) were edited in *S. pimpinellifolium* to accelerate the accumulation of traits suitable for cultivation (Li et al. 2018; Zsögön et al. 2018). Remarkably, the edited plants exhibited domesticated traits like compact plant architecture, increased fruit size and number, and improved lycopene and vitamin C content in fruits compared to the wild parents. Interestingly, the CRISPR-Cas-assisted domesticated tomato plants retained the stress tolerance characteristics. Similarly, another group of scientists performed the improvement of domestication traits in groundcherry (*Physalis pruinosa*) by disrupting three genes (Lemmon et al. 2018). *Oryza alta* is an allotetraploid wild rice with a CCDD genome, which possesses better biotic and abiotic stress resistance and higher biomass than the diploid rice, *Oryza sativa* (Wing et al. 2018). Polyploids have several advantages, like increased genome buffering, environmental fitness, and higher vigour. To domesticate *O. alta*, two genes *OaqSH1* and *OaAN-1* governing seed shattering and awn length characters were targeted with CRISPR-Cas. As a result, edited plants showed reduced seed shattering and decreased awn length. Similarly, editing was achieved in genes for heading date (*OaDTH7* and *OaGhd7*), plant height (*OaSDI*), and seed size (*OaGS3*) (Yu et al. 2021). Recent studies have used CRISPR-Cas technology to edit genes in the wild tetraploid *Solanum peruvianum* genome (Lin et al. 2022) and wild sea barley grass (Kuang et al. 2022). Figure 2 summarizes studies conducted to edit genomes of wild species.

Table 1 An updated list of domestication genes in crop plants

Crop plants	Domestication genes	Traits	Molecular function/ Types of protein	References
Rice (<i>Oryza sativa</i> L.)	<i>Hd3a</i>	Transition to flowering under short-day conditions	Rice ortholog of <i>Arabidopsis</i> FT (mobile flowering signal)	Yamamoto et al. (1998), Komiya et al. (2008)
	<i>Hd6</i>	Delay of flowering under long-day conditions	CK2 alpha protein kinase subunit	Yamamoto et al. (2000)
	<i>LAX</i> <i>SPA</i>	Lax panicle	Transcription factor (bHLH)	Komatsu et al. (2003)
	<i>SD1</i>	Controls plant height	Gibberellin biosynthetic enzyme	Hedden(2003),Asano et al. (2011)
	<i>Rc</i>	Seed colour	Transcriptional regulator (bHLH)	Sweeney et al. (2006)
	<i>qSH1</i>	Shattering, abscission layer formation	Transcriptional regulator (homeodomain)	Konishi et al. (2006)
	<i>Sh4/Shal1</i>	Shattering, abscission layer formation	Transcriptional regulator (Myb3)	Li et al. (2006)
	<i>LAZY1(LA1)</i>	Tiller angle (Spreading)	Polar auxin transport	Li et al. (2007, Yoshihara and Iino (2007)
	<i>qSW5</i>	Seed size and weight	–	Shomura et al. (2008)
	<i>GIF1</i>	Grain filling	Cell-wall invertase	Wang et al. (2008)
	<i>PROG1/RPAD</i>	Plant/inflorescence architecture	Transcription factor	Jin et al. (2008), Tan et al. (2008), Wu et al. (2018)
	<i>Ghd7</i>	Heading date/Yield	Transcription factor	Xue et al. (2008)
	<i>HD1</i>	Heading date	Florigen	Takahashi et al. (2009), Huang et al. (2012)
	<i>BADH2</i>	Fragrant grains	Enzyme that catalyzes the oxidation of 2-acetyl-1-pyrroline(2AP)	Kovach et al. (2009), Shao et al. (2013)
	<i>GBSSI</i>	Waxy grains	Starch biosynthetic enzyme	Jeon et al. (2010)
	<i>GS3</i>	Grain size	Protein with plant-specific organ size regulation (OSR) domain	Mao et al. (2010), Lacchini et al. (2020)
	<i>Sdr4</i>	Seed dormancy	Zinc finger protein	Sugimoto et al. (2010)
	<i>AMT1;1</i>	Ammonium transport	Cis-regulatory element	Ding et al. (2011)
	<i>Bh4</i>	Seed colour	Amino acid transporter	Zhu et al. (2011), Vigueira et al. (2013)
	<i>Sh1</i>	Seed shattering, abscission layer formation	Transcription factor (YABBY-like)	Lin et al. (2012), Ishikawa et al. (2022)
	<i>LG1</i>	Panicle shape: closed panicle	SBP-domain transcription factor	Ishii et al. (2013), Zhu et al. (2013)
	<i>An1</i>	Awn morphology	Basic helix-loop-helix protein	Luo et al. (2013)
	<i>Ehd4</i>	Photoperiodic control of flowering	CCCH-type zinc finger protein	Gao et al. (2013)
	<i>LABA1/An2</i>	Awn morphology: short, barbless awns	Cytokinin-activating Enzyme	Gu et al. (2015), Hua et al. (2015)
	<i>RAE2/GAD1</i>	Awn morphology	EPF/EPFL family	Bessho-Uehara et al. (2016), Jin et al. (2016)
	<i>G</i>	Seed dormancy	Protease	Wang et al. (2018)
	<i>FZP</i>	More secondary branches per panicle	ERF transcription factor	Huang et al. (2018)
	<i>GLA</i>	Grain length and awn	EFPL protein	Zhang et al. (2019b)
	<i>qSH3</i>	Seed shattering, abscission layer formation	Transcription factor	Ishikawa et al. (2022)

Table 1 (continued)

Crop plants	Domestication genes	Traits	Molecular function/ Types of protein	References
Wheat (<i>Triticum aestivum</i> L.)	<i>SPR3</i>	Panicle shape: closed panicle	Cis-regulatory element	Ishikawa et al. (2022)
	<i>EPFL2</i>	Awn Development	EFPL protein	Xiong et al. (2022)
	<i>KRN2</i>	Grain number	WD40 proteins	Chen et al. (2022)
	<i>Rht-1</i>	Controls plant height	Transcriptional regulator (SH2)	Peng et al. (1999)
	<i>Vrn1</i>	Flowering (Vernalisation)	Transcriptional regulator (MADS)	Yan et al. (2003)
	<i>Vrn2</i>	Flowering (Vernalisation)	Transcriptional regulator (ZCCT)	Yan et al. (2004)
	<i>WAP2(Q)</i>	Plant/inflorescence architecture	Transcriptional regulator (AP2)	Simons et al. (2006)
	<i>Btr1-A</i>	Shattering	–	Zhao et al. (2019)
	<i>LAX1</i>	Grain threshes ability	Basic helix loop helix transcription factor	He et al. (2021)
Tomato (<i>Solanum lycopersicum</i> L.)	<i>FW2.2</i>	Fruit size and weight	Like human RAS	Frary et al. (2000)
	<i>Style2.1</i>	Style length	Transcription factor	Chen et al. (2007)
	<i>SUN</i>	Fruit size and weight	–	Xiao et al. (2008)
	<i>Fasciated</i>	Fruit size and weight	Transcription factor (YABBY like)	Cong et al. (2008)
	<i>LC</i>	Locule number	Transcription factor	Rodríguez et al. (2011)
Maize (<i>Zea mays</i> L.)	<i>OVATE</i>	Fruit neck morphology	Transcription factor	
	<i>G</i>	Seed dormancy	Protease	Wang et al. (2018)
	<i>Sos1</i>	Inflorescence architecture	Cis-regulatory element	Doebley et al. (1995)
	<i>Tb1</i>	Apical dominance	Transcriptional regulator (TCP)	Doebley et al. (1997), Clark et al. (2004)
	<i>BA1</i>	Prevents axillary meristem development	Transcriptional regulator (bHLH)	Gallavotti et al. (2004)
	<i>Tga1</i>	Seed casing	Transcriptional regulator (SBP)	Wang et al. (2005), Guan et al. (2022)
	<i>Zag1l</i>	Increase in female ear length	Transcription factor	Weber et al. (2008)
	<i>PSY1</i>	Yellow endosperm	Cis-regulatory element	Fu et al. (2010)
	<i>Ra1</i>	Plant/inflorescence architecture	Transcriptional regulator (MYB)	Sigmon and Vollbrecht (2010)
	<i>Sh1-5.1-Sh1-5.2</i> <i>Sh1-1</i>	Shattering	Transcription factor (YABBY)	Lin et al. (2012)
	<i>MADS19(Tu)</i>	Ectopic expression in inflorescences, leads to kernels covered by glumes	Transcription factor	Wingen et al. (2012)
	<i>PBF</i>	Altered prolamin protein levels in seeds	Transcription factor	Lang et al. (2014)
	<i>SWEET4c</i>	Grain filling	Hexose transporter	Sosso et al. (2015)
	<i>CCT</i>	Earlier flowering	Transcription factor (CCT domain-containing)	Xu et al. (2017)
	<i>KRN2</i>	Grain number	WD40 proteins	Chen et al. (2022)

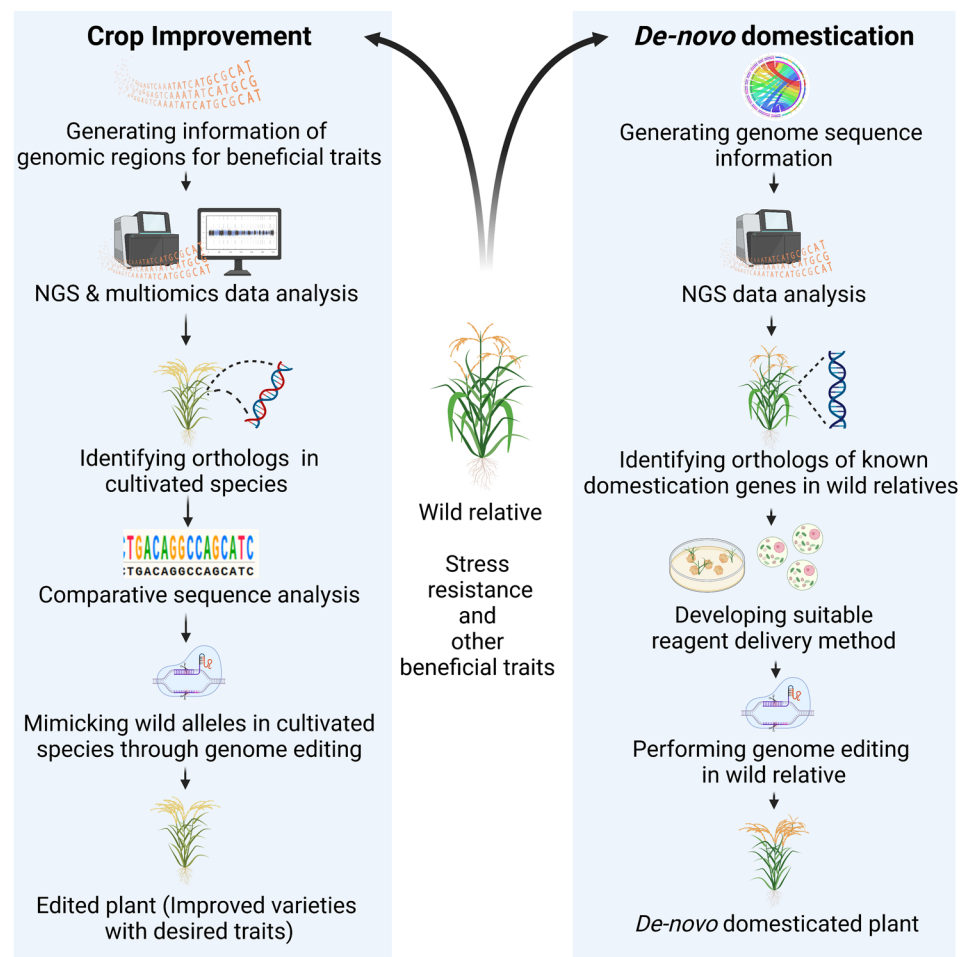
Table 1 (continued)

Crop plants	Domestication genes	Traits	Molecular function/ Types of protein	References	
Soybean (<i>Glycine max</i> L.)	<i>PhyA3</i>	Early flowering	Phytochrome protein	Watanabe et al. (2009), Tsubokura et al. (2014)	
	<i>Dt1</i>	Growth habit	Signalling protein	Tian et al. (2010)	
	<i>TFL1b</i>	Inflorescence architecture	Transcription cofactor, PEN binding	Tian et al. (2010)	
	<i>Dt2</i>	Growth habit	MADS-domain factor gene	Ping et al. (2014)	
	<i>qPDH1</i>	Shattering	Dirigent (DIR)-like protein	Funatsuki et al. (2014)	
	<i>SHAT1-5</i>	Shattering	NAC (NAM, ATAF1/2 and CUC2) domain transcription factor	Dong et al. (2014)	
	<i>Hs1-1</i>	Hard seeds	PhoD-like phosphatase	Sun et al. (2015)	
	<i>FT2a</i>	Early flowering	PEBP family proteins	Zhao et al. (2016)	
	<i>J</i>	Early flowering	LUX-like proteins	Lu et al. (2017)	
	<i>WRKY15a</i>	Seed size	Transcription factor	Gu et al. (2017)	
	<i>B1</i>	Seed coat shininess	Transmembrane trans- porter like protein	Zhang et al. (2018)	
	<i>G</i>	Seed dormancy	Protease	Wang et al. (2018)	
	<i>PRR3A and PRR3B</i>	Early flowering	Transcription factors (TPL-related)	Li et al. (2019), Wang et al. (2020a)	
	<i>OLEO1</i>	Seed oil content	Putative OB protein	Zhang et al. (2019a)	
	<i>SWEET39/ SWEET10a</i>	Seed oil content	Sugar efflux transporter for intercellular exchange	Miao et al. (2020), Wang et al. (2020b)	
	<i>Tof12</i>	Flowering	Two-component response regulator-like APRR3	Lu et al. (2020)	
	<i>PDAT</i>	Seed oil content	Acyl-lipid metabolism	Liu et al. (2020)	
	Barley (<i>Hordeum vulgare</i> L.)	<i>Ppd-H1</i>	Delayed flowering time	Cis-regulatory element	Turner et al. (2005)
		<i>Vrs1</i>	Plant/inflorescence archi- tecture	Transcription factor	Komatsuda et al. (2007)
		<i>Nud1</i>	Naked Grain	Transcription factor (ERF family)	Taketa et al. (2008)
<i>GA20ox-2</i>		Controls plant height	Metabolic enzyme	Jia et al. (2009)	
<i>INT-C (HvTB1)</i>		Plant/inflorescence archi- tecture, apical dominance	Transcription factor	Ramsay et al. (2011)	
<i>Thresh-1</i>		Free threshing	–	Schmalenbach et al. (2011)	
<i>Rrs2</i>		Leaf scald resistance	Cis-regulatory element	Fu (2012)	
<i>APETALA2</i>		Plant height	Transcription factor (MADS-box)	Houston et al. (2013), Shoe- smith et al. (2021)	
<i>Btr1</i> <i>Btr2</i>		Non-brittle rachis	–	Pourkheirandish et al. (2015), Pourkheirandish and Komatsuda (2022)	
<i>Dep1</i>		Plant height	Heterotrimeric G protein γ -subunits	Wendt et al. (2016)	
<i>ELF3</i>		Earlier flowering time	Transcription factor	Prusty et al. (2021)	
Sunflower (<i>Helianthus annuus</i> L.)		<i>FT1</i>	Flowering	Transcription factor	Blackman et al. (2010)

Table 1 (continued)

Crop plants	Domestication genes	Traits	Molecular function/ Types of protein	References
Sorghum (<i>Sorghum bicolor</i> L.)	<i>Sh1</i>	Shattering	Transcription factor	Lin et al. (2012)
	<i>GBSSI</i>	Glutinous seeds	Starch biosynthetic enzyme	Kawahigashi et al. (2013)
	<i>qDor7</i>	Seed dormancy	Probable L-ascorbate peroxidase 4	Li et al. (2016)
	<i>Awn1</i>	Awn development	Transcription factor with the ALOG domain	(Zhou et al. (2021)
Foxtail millet (<i>Setaria italica</i> L.)	<i>GCI</i>	Naked grain formation	G protein γ subunit-like domain	Xie et al. (2022)
	<i>GBSSI</i>	Glutinous grains	Starch biosynthetic enzyme	Kawase et al. (2005)
Pearl millet (<i>Pennisetum glaucum</i> L.)	<i>Sh1</i>	Seed shattering	Transcription factor (YABBY-like)	Liu et al. (2022)
	<i>Tb1</i>	Plant/inflorescence architecture, apical Dominance	Transcription factor	Remigereau et al. (2011)
Foxtail amaranth (<i>Amaranthus caudatus</i> L.)	<i>MADS11, Hd3a and GI</i>	Earlier flowering time	Transcription factor	Clotault et al. (2012), Mar- iac et al. (2011)
	<i>GBSSI</i>	Waxy grains	Starch biosynthetic enzyme	Park et al. (2012b)
Red Amaranth (<i>Amaranthus cruentus</i> L.)	<i>GBSSI</i>	Waxy grains	Starch biosynthetic enzyme	Park et al. (2011)
Prince's-feather (<i>Amaranthus hypochondriacus</i> L.)	<i>GBSSI</i>	Waxy grains	Starch biosynthetic enzyme	Park et al. (2012a)
Adlay millet (<i>Coix lacryma-jobi</i> L.)	<i>GBSSI</i>	Waxy grains	Starch biosynthetic enzyme	(Hachiken et al. (2012)
Turnip rape (<i>Brassica rapa</i> L.)	<i>FLC1</i>	Flowering time	Transcription factor (MADS-box)	Yuan et al. (2009)
	<i>TT8</i>	Seed coat colour	Transcriptional regulator (bHLH)	Lou et al. (2020)
Common bean (<i>Phaseolus vulgaris</i> L.)	<i>TFL1y</i>	Determinate shoots with a terminal inflorescence,	Transcription cofactor, PEN binding	Kwak et al. (2012)
Rapeseed (<i>Brassica napus</i> L.)	<i>FLC.A10</i>	Flowering time	Cis-regulatory element	Hou et al. (2012)
	<i>FLC.A3b</i>	Flowering time	Cis-regulatory element	Zou et al. (2012)
Wild cabbage (<i>Brassica oleracea</i> L.)	<i>CAL</i>	Inflorescence architecture	Transcription factor	Purugganan et al. (2000)
	<i>FLCs</i>	Variation in flowering time	Transcription factor (MADS-box)	Okazaki et al. (2007)
Strawberry (<i>Fragaria</i> sp.)	<i>PINS</i>	Fruit flavour	Functionally characterised enzymes	Aharoni et al. (2004)
	<i>NES1</i>			
Woodland strawberry (<i>Fragaria vesca</i> L.)	<i>KSN</i>	Continuous flowering	Transcription factor	Iwata et al. (2012)
Grapes (<i>Vitis vinifera</i> L.)	<i>MYBA1</i>	Anthocyanin content variation	Transcription factor	This et al. (2007), Carrasco et al. (2015)
	<i>MYBA2</i>	Anthocyanin content variation	Transcription factor	Carrasco et al. (2015)
Pea (<i>Pisum sativum</i> L.)	<i>TFL1c</i>	Variation in flowering time	Signalling protein	Foucher et al. (2003)
	<i>PPO</i>	Hilum pigmentation	Biochemical enzyme	Balarynová et al. (2022)
Pumpkin (<i>Cucurbita moschata</i>)	<i>YABBY1</i>	Bushy habit and reduced stem length	Transcription factor	Wang et al. (2022)

Fig. 1 Pipelines to utilize wild plant species and crop wild relatives for rapid domestication and crop improvement



Prerequisite for de novo domestication

Genome information









Selection is the key driving force of domestication and has resulted in molecular footprints in crop genomes (Meyer and Purugganan 2013). The availability of reliable information on the identification and characterization of domestication genes would enable us to choose genes that could be readily targeted with the available genome editing tools. Genome editing of wild species requires several resources, for instance, good quality genome information and functional annotation of genes. The information is necessary to find proper orthologs of domestication genes that are to be targeted. For example, Yu et al. (2021) generated high quality genome assembly of allotetraploid wild rice (*Oryza alta*) prior to genome editing. Similarly, the genome of sea barley grass (*Hordeum marinum*), a wild Triticeae plant with a high level of waterlogging and salinity tolerance, was sequenced and annotated to carry out genome editing (Kuang et al. 2022). High-quality whole genome assemblies

are available for eight wild *Oryza* species, *Leersia perrieri* (from *Oryza* Tribe), *Solanum pennellii*, *Triticum turgidum*, *Prunus yedoensis*, and *Glycine soja* (Bolger et al. 2014; Avni et al. 2017; Brozynska et al. 2017; Baek et al. 2018; Stein et al. 2018; Zhao et al. 2018; Xie et al. 2019; Shenton et al. 2020), making them suitable candidates for de novo domestication. With the rapid advancement and the availability of low-cost sequencing platforms, a platinum standard genome sequence for all ‘crop wild relatives’ would be available sooner or later (Mussurova et al. 2020).

Regeneration and transformation protocol

Another crucial factor is to have a well-established genetic transformation and regeneration system for the species that need to be modified. The major bottleneck to apply the rapid domestication approach is the unavailability of genetic transformation and regeneration systems for wild species. Most of them are recalcitrant to tissue culture and produce a small number of seeds. To standardize a genetic transformation system, the supply of an adequate number

Fig. 2 Reported editing of targeted traits in wild species genomes for crop *de novo* domestication

Wild species	Targeted trait	Gene	Reference	
 Currant tomato <i>(Solanum pimpinellifolium L.)</i>	Compact plant architecture, synchronized fruit ripening	<i>SP</i>	(Li et al. 2018)	
	Day-length neutrality	<i>SP5G</i>		
	Enlarged fruit size	<i>SICLV3, SIWUS</i>		
	 Ground cherry <i>(Physalis pruinosa L.)</i>	Increased vitamin C level	<i>SIGGP1</i>	(Zsögön et al. 2018)
		Growth habit	<i>SP</i>	
		Fruit shape	<i>OVATE</i>	
		Fruit size	<i>FAS, FW 2.2</i>	
		Fruit number	<i>MULT</i>	
Nutritional quality		<i>CycB</i>		
 Ground cherry <i>(Physalis pruinosa L.)</i>	Primary and axillary shoot flowering	<i>SP5G</i>	(Lemmon et al. 2018)	
	Locule number	<i>CLV1</i>		
 African rice <i>(Oryza glaberrima Steud.)</i>	Plant height	<i>HTD1</i>	(Lacchini et al. 2020)	
	Seed size/ yield	<i>GS3, GW2 and GN1A</i>		
 Green foxtail <i>(Setaria viridis L.)</i>	Seed shattering	<i>SvLes1</i>	(Mamidi et al. 2020)	
 Wild rice <i>(Oryza alta Swallen)</i>	Shattering	<i>OaqSH1</i>	(Yu et al. 2021)	
	Awn length	<i>OaAn-1</i>		
	Heading date	<i>OaGhd7</i> <i>OaDTH7</i>		
	Seed size	<i>OaGS3</i>		
	Plant height	<i>OaSD1</i>		
 Wild tomatoes <i>(Solanum peruvianum L.)</i>	Plant RNA silencing pathway	<i>SpRDR6</i> <i>SpSGS3</i>	(Lin et al. 2022)	
	Pathogen resistance peptide precursors	<i>SpPR-1</i> <i>SpProSys</i>		
	Powdery mildew resistance	<i>SpMlo1</i>		
 Sea barley grass <i>(Hordeum marinum Huds.)</i>	Salinity tolerance	<i>HmSOS1</i>	(Kuang et al. 2022)	

of seeds is also crucial. It is recommended to use a significant number of lines as starting material in tissue culture because the responsiveness to tissue culture techniques can vary between different accessions of wild germplasm. In an earlier study, Yu et al. (2021) started with 28 tetraploid wild rice lines and selected one line for editing experiments based on the highest tissue culture responsiveness. Recently, three lines H508, H559, and H560 were taken for developing efficient *Agrobacterium*-mediated transformation method and genome editing system in sea barley grass (Kuang et al. 2022). Since H559 showed the highest regeneration

efficiency, it was selected for genetic transformation with CRISPR-Cas reagents.

Knowledge of gene regulatory elements

Once high-quality genome information and efficient regeneration and genetic transformation systems become available, it is straightforward to go for domestication using genome editing tools. However, it is also vital to have information on the level of functionality of gene regulatory elements (promoters and terminators) in the

wild species. In order to achieve high efficiency and simultaneous editing at multiple genes in wild species, basic information on promoters that govern a high level of expression would be beneficial. Additionally, the characterization of more and more genes that played crucial roles in the domestication process of a particular species will further facilitate de novo domestication through genome editing.

Future targets: characterized genes responsible for domestication

The discovery of the domestication genes unlocked the doors for crop improvements. The maize *tb1* is the first isolated domestication gene (Clark et al. 2004). The *tb1* mutation was due to a selective sweep of ~60–90 kb at the upstream to the *tb1* coding sequence, causing an increase in apical dominance in domesticated maize when compared with the wild ancestor teosinte (Clark et al. 2004). In teosinte, the kernels were protected by hardened casing; an alteration in the gene *tg1* (*teosinte glume architecture*) produced naked kernels, making them suitable for consumption (Wang et al. 2005). A recent study revealed that strigolactones interact with the domestication gene *tg1* to regulate maize domestication phenotypes (Guan et al. 2022). After the *tb1* gene identification, numerous genes have been identified as domestication and diversification genes in diverse crop species, although most of them are in cereal species (Table 1). While updating the compilation provided earlier (Meyer and Purugganan 2013), we have made a comprehensive list of domestication and diversification genes provided in Table 1.

Rice (*Oryza sativa* L.) is one of the extensively studied cereal crop plants. The *Oryza* genus is composed of 26 authenticated species, containing 11 different types of genomes and four species complexes (Brar and Khush 2018; Dalai et al. 2021). Along with other wild species, two domesticated species, *O. sativa* and *O. glaberrima* fall under the *O. sativa* complex. Species from *O. sativa* complex are inter-crossable, although with low cross-fertility and low F₁ seed germinability. Genotypes from other species complexes are highly cross-incompatible with the cultivated species, making it extremely difficult to harness the wild rice gene pool's beneficial traits. Wild rice species have been identified to harbour many important traits. For example, *Oryza logistaminata* for perenniality, high outcrossing ability, and bacterial blight resistance (Song et al. 1995) *O. meyeriana* (Molla et al. 2018a) for bacterial blight resistance, *O. coarctata* for salt tolerance (Mondal et al. 2018), *O. neocaledonica* for drought tolerance (Molla et al. 2018b), and *O. australiensis* for heat tolerance (Atwell et al. 2014). Thus, keeping these valuable

traits intact, the wild species are attractive to be subjected to rapid domestication by CRISPR-Cas.

Mussurova et al. (2020) recently reviewed ten well-studied rice genes that are responsible for domestication traits such as seed shattering, daylight sensitivity, erect growth, high yield, flowering time, panicle shape, seed hull color, and awn morphology. During cereal domestication, the loss of seed shattering was a crucial step. Seed shattering results from forming an abscission layer between the seed and the pedicel. The genes responsible for seed shattering are responsible for the regulation of the abscission layer and disruption of the cell wall during seed shattering. In rice, genes like *qSH1*, *qSH3*, *Sh4/Sh1*, and *OsSh1* are responsible for seed shattering (Konishi et al. 2006; Li et al. 2006; Lin et al. 2012; Ishikawa et al. 2022). Low lignification induces seed shattering. Plant laccases are considered to play a role in lignin biosynthesis (Wang et al. 2015). A recent study revealed that loss of miRNA-mediated laccase silencing is responsible for domestication phenotype in Indica rice (Swetha et al. 2018).

Similarly, the seed shattering genes like *Btr1-A* in wheat (Zhao et al. 2019), *qPDH1* and *SHAT1-5* in soybean (Dong et al. 2014; Funatsuki et al. 2014), and *Sh1* in sorghum (Lin et al. 2012) have been reported. A recent study reported that transposons and the associated gene *Sh1* played a major role during the evolution of seed shattering in foxtail millet (Liu et al. 2022). The easy detachment of seed from sticky glumes is important for threshing. In wheat, *soft glume* (*Sog*) and *tenacious glume* (*Tg*) loci are involved in the toughness of glumes and act as major threshability genes (Sood et al. 2009). *GCI* is responsible for the production of naked grains in sorghum as it negatively regulates the sorghum glume coverage (Xie et al. 2022).

Certain traits that humans have selected during crop domestication, such as yield, have been found to have convergently evolved in different crops. For example, *KRN2/OsKRN2*, which encodes a WD40 protein, has been identified as a convergently selected gene in both maize and rice. Knockout lines of these genes have been shown to increase grain yield by 10% in maize and 8% in rice (Chen et al. 2022). Other genes that have played significant roles in rice domestication include *RAE2/GAD1* (awn length) and *GLA* (grain length and awn development) (Jin et al. 2016; Zhang et al. 2019b). Xiong et al. 2022 reported that out of 11 genes encoding EPF and EPFL type proteins in rice, *OsEPFL2* is highly expressed in young panicles and is responsible for awn development. Generally, red pericarp appears in wild rice varieties, and genes like *Rc* and *Rd* are responsible for the colouration (Sweeney et al. 2006; Furukawa et al. 2007). White pericarp arises from a 14 bp deletion in *Rc* gene. In rice varieties with white pericarp, restoration of open reading frame in *Rc* gene can give red colouration (Zhu et al.

2019). In tomatoes, a new approach to target a switch between homobaric and heterobaric leaves was possible by targeting *AUXIN RESPONSE FACTOR 4 (ARF4)* (Moreira et al. 2022). Recent studies suggest that the improvement of photosynthesis is associated with increases in CO₂ diffusional capacities during the process of domestication. The variation of cell wall thickness drives the increase of mesophyll conductance per mass (Huang et al. 2022). In the case of cucurbits, long trailing vines represents wild characters and compact plant architecture can increase yield and save labour cost. Recently, a natural allele of a transcription factor gene *YABBY1* with 76 bp deletion in the 5' untranslated region (UTR) responsible for bushy habit has been identified in pumpkin (*Cucurbita moschata*) (Wang et al. 2022). The allele has been mimicked by CRISPR-Cas in Cucumber, watermelon and pumpkin for reducing stem length (Wang et al. 2022). The agricultural production efficiency of cucurbits, especially in a controlled environment, could be greatly enhanced through this approach.

Despite being locally important in providing nutrition, many orphan crops suffer from undesirable characteristics that prevent them from becoming popular in wider region. CRISPR tools have a high potential to remove those undesirable characteristics and facilitate wider domestication of orphan crops. All our major cereal crops (rice, maize, and wheat) are annual and developing perennial version of them is an attractive strategy to save money, labour cost, and reduce environmental footprint. For example, a recent attempt to turn rice into a perennial crop has been successful by hybridizing annual *Oryza sativa* with perennial *Oryza longistaminata* (Zhang et al. 2022). However, since wide hybridization is difficult, a similar approach has been unsuccessful for making a perennial wheat (Cui et al. 2018). Alternatively, genome editing could assist direct domestication of perennial wild grasses by targeting known homologous domestication genes of cereals (Zhang et al. 2020).

Given the information available on domestication genes, obtaining targeted mutants with the CRISPR-Cas approach is easier. Hence, domestication syndrome can be mimicked in wild species of interest with multiplex genome editing in a relatively much shorter time.

Concluding remarks and future perspectives

CRISPR-Cas system and its variants provide ample opportunities for accelerating *de novo* domestication of wild species of major crop plants of agricultural importance. For addressing the challenge of sustainably feeding the projected 10 billion people by 2050 (United Nations 2017), the crop wild relatives represent attractive genetic resources as they possess traits related to climate resilience, disease resistance, and better nutritional quality, in addition to high yield

potential. Our efforts must be directed to generate desired quality genome informations of selected crop wild species, identify domestication genes and genetic elements, and develop reliable genotype-independent transformation systems for undertaking genome editing of target traits. Editing horticultural crops are more strenuous since they are primarily polyploid. Methodologies are to be developed for a high expression level of editing reagents to achieve robust genome editing in polyploids.

Pre-breeding could also be accelerated by generating advantageous knock-out alleles or decoupling unwanted traits from the desired trait through genome editing. On the other hand, if a novel wild allele governing an economically important trait is characterized to have a small sequence variation (SNPs, small insertion, deletion, or combination of those) with the cultivated allele, we can recreate a wild allele in a cultivated genomic background by applying advance tools like base editing, prime editing, and HDR. Sometimes, the favourable allele of a gene is present in a few landraces or wild species, but that corresponding gene remains absent in the significant cultivated genotypes. For example, *Xa7* or *Sub1A* genes are absent in many cultivated rice (Xu et al. 2006; Wang et al. 2021). In many cases, favourable allele for such a useful gene is present in wild species only and a few cultivated accessions carry unfavourable alleles. In such scenario, the cultivated accessions can be edited to mimic favourable wild alleles and then transferred to elite cultivated genotypes through backcrossing. This can help avoid the difficulties of wide hybridization and linkage drags. Even the problem of lack of availability of a wild species or even a cultivated germplasm in a country due to restricted germplasm exchange can be overcome through the genome editing strategies.

Although a great deal of knowledge is available on domestications genes and alleles, we must keep in mind that domestication is complex and needs to be understood completely. Domestication involves complex changes in plant architecture and biology as well as human culture. Indigenous knowledge and communities could provide crucial inputs in *de novo* domestication programs (Bartlett et al. 2023). Hence, fair and equitable sharing of benefits should also be taken into consideration.

Genome editing tools need to be applied to exploit the rich genetic diversity of crop wild relatives, through the process of rapid domestication. Only 0.4–0.57% of plant species have been subjected to some form of domestication from ~300,000 vascular plant species available in the wild (Milla et al. 2018; Marks et al. 2021; Royal Botanic Gardens 2021). These untapped wild genetic resources could be utilized to address future food and nutritional security challenges. Once successfully adopted for rapid domestication of as many wild species as possible, the CRISPR-Cas-assisted system could facilitate the development of high-yielding,

climate-smart, and nutrient-rich crop plants leading to global food security and environmental sustainability. The need of the hour is to identify more and more useful genes or alleles from the wild. This would be possible only through developing more backcross inbred lines or structured segmental substitution lines from wild species, precise phenotyping, mapping, cloning, and validation using the available editing tools. At every stage, the complementary role of genetics, breeding, and editing tools can comprehensively enhance the speed of neo-domestication, resulting in an accelerated and multiplicative genetic gain.

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Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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