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Exploring and exploiting genetics and genomics for sweetpotato improvement: Status and perspectives

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ABSTRACT

Sweetpotato (*Ipomoea batatas* (L.) Lam.) is one of the most important root crops cultivated worldwide. Because of its adaptability, high yield potential, and nutritional value, sweetpotato has become an important food crop, particularly in developing countries. To ensure adequate crop yields to meet increasing demand, it is essential to enhance the tolerance of sweetpotato to environmental stresses and other yield-limiting factors. The highly heterozygous hexaploid genome of *I. batatas* complicates genetic studies and limits improvement of sweetpotato through traditional breeding. However, application of next-generation sequencing and high-throughput genotyping and phenotyping technologies to sweetpotato genetics and genomics research has provided new tools and resources for crop improvement. In this review, we discuss the genomics resources that are available for sweetpotato, including the current reference genome, databases, and available bioinformatics tools. We systematically review the current state of knowledge on the polyploid genetics of sweetpotato, including studies of its origin and germplasm diversity and the associated mapping of important agricultural traits. We then outline the conventional and molecular breeding approaches that have been applied to sweetpotato. Finally, we discuss future goals for genetic studies of sweetpotato and crop improvement via breeding in combination with state-of-the-art multi-omics approaches such as genomic selection and gene editing. These approaches will advance and accelerate genetic improvement of this important root crop and facilitate its sustainable global production.

Keywords: sweetpotato, polyploid genetics, genomics, breeding

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INTRODUCTION

Sweetpotato (*Ipomoea batatas* (L.) Lam., 2n = 6x = 90) is one of the most important root crops cultivated worldwide with an annual production of ~113 million tons (Food and Agriculture Organization of the United Nations, 2019). Because of its high yield potential and ability to adapt to a wide range of environmental conditions, sweetpotato has become an affordable source of dietary calories, protein, fiber, minerals, vitamins, and flavonoids (Woolfe, 1992; Padmaja, 2009), particularly in developing countries. Currently, orange-fleshed sweetpotato plays an important role in combating vitamin A deficiency in Africa (Kurabachew, 2015). Sweetpotato is not only cultivated for human food (storage roots and leaves) and animal feed but also as an industrial raw material to produce starch, alcohol, and natural pigments (Padmaja, 2009; Katayama et al., 2017). Development of cultivars that combine disease and pest resistance with high yields and enhanced nutritional value is essential to meet the increasing demands for quality foodstuff and industrial raw products.

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Research in genetics and genomics has enabled the application of molecular breeding strategies to many crop species (Liu et al., 2020; Nawaz and Chung, 2020; Mores et al., 2021). However, genetic analysis and breeding of sweetpotato have been challenging. First, sweetpotato is a highly heterozygous hexaploid (2n = 6x = 90) and has a large, complex genome approximately 2–3 Gb in size (Ozias-Akins and Jarret, 1994). The presence of multiple homoeo-alleles across homoeologous chromosomes and the resulting complex inheritance patterns complicate estimation of allele dosages (Dufresne et al., 2014). Accurate estimation of allele dosages is important for precise mapping of genetic loci (Rosyara et al., 2016; Bourke et al., 2018; da Silva Pereira et al., 2020). Second, a large number of possible genotypes are observed in segregating populations because of the diverse combinations of parental chromosomes provided by the male and female gametes (Cervantes-Flores et al., 2008a; Yamakawa et al., 2021). The number of potential allelic combinations in F_1 progeny plants is estimated to be 1.1×10^{39}, as calculated by $(C_6^3 \times C_6^3)^{15}$ if we consider sweetpotato to be an autohexaploid. The multitude of diverse combinations poses a significant challenge to genetic mapping and also results in laborious and time-consuming efforts to screen progeny. A large number of hybrid lines are needed in the early stages of a sweetpotato breeding program, and one cultivar is typically released every 10 years after extensive field evaluations and line selections (Kumagai, 2001). Third, sweetpotato plants are almost always self-incompatible and sometimes cross-incompatible. Cross-incompatibility restricts breeding progress when parental lines with desirable traits belong to the same incompatibility group (Vimala and Hariprakash, 2011; Gurmu et al., 2013). Finally, compared with diploid crops, the availability of genomics tools and resources for sweetpotato has lagged behind, mainly because of the complexity of the genome and the relatively small number of scientists working on sweetpotato.

Because of the development of next-generation sequencing (NGS) technologies, the availability of genomics resources, and advances in breeding methodologies, significant improvements to sweetpotato have been realized over the past two decades (Figure 1). The initial genetic map, constructed in 1997 (Ukoskit and Thompson, 1997), served as the basis for subsequent genetic studies that resulted in the identification of a series of agriculturally important traits. This was accomplished using various approaches, such as mapping of quantitative trait loci (QTLs) (Mwanga et al., 2002; Li et al., 2014; da Silva Pereira et al., 2020), application of bulked segregant analysis (BSA) (Nakayama et al., 2012; Suematsu et al., 2021; Yamakawa et al., 2021), and genome-wide association studies (GWASs) (Zhang et al., 2016; Okada et al., 2019; Chen et al., 2021). A genome sequencing project was formally initiated in 2012. In 2015, the first reference genome of the wild diploid sweetpotato relative *Ipomoea trifida* was published (Hirakawa et al., 2015), and the sweetpotato reference genome was released in 2017 (Yang et al., 2017a). Since then, the number of genetic and genomics studies has increased, and a number of bioinformatics tools/pipelines for sweetpotato have been developed. These include Ranbow, GBSapp, ngsAssocPoly, MAPpoly, QTLpoly, OutcrossSeq, and haplotype-based phylogenetic analysis (HPA) (Wadl et al., 2018; Moeinzadeh et al., 2020; Mollinari et al., 2020; da Silva Pereira et al., 2020; Yamamoto et al., 2020; Chen et al., 2021; Yamakawa et al., 2021; Yan et al., 2021). Over the past few decades, traditional breeding and molecular breeding approaches have been widely applied to sweetpotato and have resulted in the development of many new cultivars with improved yield, nutrient content, pest resistance, and other quality factors (Newell et al., 1995; Okada et al., 2001; Otani et al., 2003; Gao et al., 2011b; Wang et al., 2019). Several advances in sweetpotato breeding have been achieved; these include a synthetic hexaploid derived from wild species (Shiotani and Kawase, 1987), the first transgenic sweetpotato plant (Otani et al., 1998), an accelerated breeding scheme (ABS) (Grüneberg et al., 2009) and somatic hybrids (Yang et al., 2009), CRISPR-Cas9 (clustered regularly interspaced short palindromic repeats-CRISPR-associated protein 9)-mediated mutagenesis via genome editing (Wang et al., 2019), and, most recently, the development of genomic selection (GS) methods (Gemenet et al., 2020a).

GENOMICS RESOURCES IN SWEETPOTATO AND ITS WILD RELATIVES

Sweetpotato reference genomes

A high-quality genome sequence assembly is crucial for molecular breeding in any crop species. The initial sweetpotato genome sequence was obtained using the carotenoid-rich cultivar 'Taizhong 6' (Yang et al., 2017a). This genome sequence was assembled using only Illumina short DNA sequencing reads (Table 1). Fifteen pseudochromosomes were ultimately generated based on gene synteny between this haplotype-improved *I. batatas* assembly and the *Ipomoea nil* genome (Hoshino et al., 2016). The novel haplotyping method of Yang et al. (2017a) enabled the first successful genomic analysis of the complex hexaploid chromosomal composition of *I. batatas* using polyploid DNA sequencing data. This assembly (version 2017) is available at http://public-genomes-ngs.molgen.mpg.de/SweetPotato/. To improve the sweetpotato genome assembly, it was re-sequenced using nanopore sequencing (Oxford Nanopore Technologies) and 10X Genomics techniques (Table 1). The long-read assembly was then anchored onto chromosomes using the linkage map (Rastas, 2019). This assembly (version 2019) is available at http://sweetpotao.com/.

In 2012, six organizations from China, Korea, and Japan established the Trilateral Research Association of Sweetpotato genome sequencing consortium. In 2019, a draft genome of the sweetpotato cultivar 'Xushu 18' was assembled using PacBio and Illumina reads and chromosome-scale scaffolding using BioNano and high-throughput chromosome conformation capture (Hi-C) (Yoon, 2019). Yoon (2019) constructed a complete genome assembly of the sweetpotato cultivar 'Xushu 18' using DeNovoMAGIC. Their most recent assembly versions are currently unpublished.

Reference genomes of wild sweetpotato relatives

Crop wild relatives (CWRs) possess many agriculturally important traits and harbor a wealth of genetic diversity (Acosta-Gallegos et al., 2007). The CWRs of cultivated sweetpotato have the potential to contribute to breeding objectives. Over the last few decades, the CWRs of cultivated sweetpotato have been

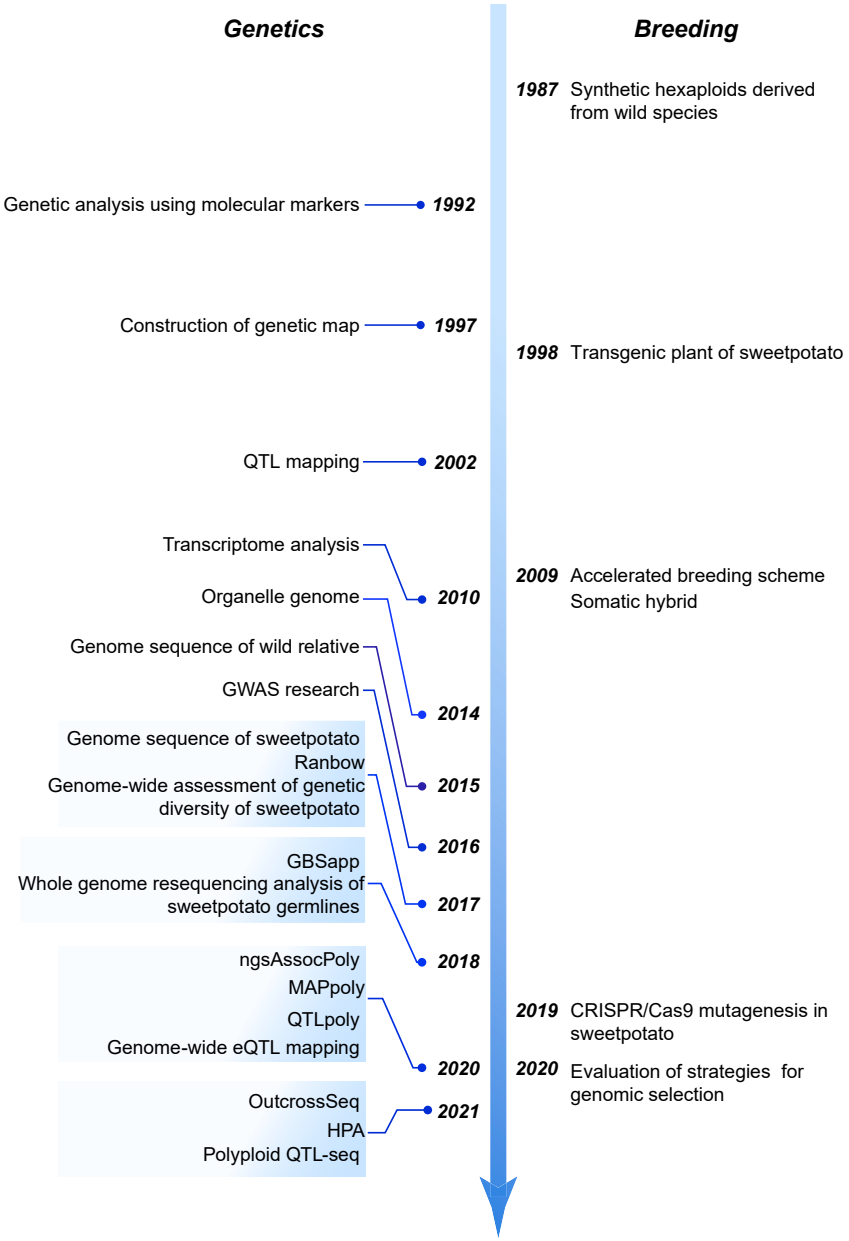

Figure 1. Milestones in sweetpotato genetics and breeding

Chronological achievements in the development of genetics tools/techniques and breeding are summarized. The references (Eserman et al., 2014; Schafleitner et al., 2010; Wang et al., 2010) are given in Supplemental Table 1. QTL, quantitative trait locus; GWAS, genome-wide association study; CRISPR-Cas9, clustered regularly interspaced short palindromic repeats-CRISPR-associated protein 9.

used in studies of yield, drought tolerance, and disease resistance (Khoury et al., 2015). There are approximately 800 species in the genus *Ipomoea* (Wood et al., 2020), and these are loosely considered to be the CWRs of cultivated sweetpotato. The New World *Ipomoea* species consist of five phylogenetic clades, designated clades A–E (Wood et al., 2020). The cultivated sweetpotato belongs to a subclade of clade A, clade A3, also known as *Ipomoea* section *Batatas*. Therefore, CWRs within section *Batatas* (such as *I. trifida* and *Ipomoea triloba*) are closely related to the sweetpotato (Diaz et al., 1996; Figure 2). The genetic relationships between sweetpotato and the CWRs in the other four clades decrease in order from clade B to clade E. Given their history of contributing to our understanding of the sweetpotato genome, reference genomes of its CWRs are important for evolutionary studies as well as improvement of the cultivated sweetpotato. At present, reference genomes of five sweetpotato CWRs are available (Table 1).

I. trifida, a wild species in section *Batatas* (Figure 2), is likely to be the diploid progenitor of sweetpotato (Jarret et al., 1992; Yang et al., 2017a). The assembly of the much smaller diploid *I. trifida* genome was used as an indirect means of viewing the much larger and more complicated genome of the hexaploid crop species *I. batatas*. Hirakawa et al. (2015) performed the first *de novo* genome assembly of two lines of diploid *I. trifida* (Mx23Hm and 0431-1) using Illumina DNA sequencing reads (Table 1). Although the genomes were not chromosome-level assemblies, they were the first reference genomes of any sweetpotato CWR and provided the foundation for future studies of the hexaploid sweetpotato genome (Hirakawa et al., 2015). Wu et al. (2018) published the first chromosome-level reference genome of *I. trifida* (Table 1). They used Illumina paired-end and mate-pair reads in the assembly. PacBio long reads and BioNano genome maps were used for gap filling and to improve the assembly, respectively. The total length of the pseudomolecules was 373.4 Mb (80.8% of the assembly in 461 scaffolds anchored to 15 pseudomolecules) (Wu et al., 2018). Li et al. (2019) also reported a chromosome-level genome assembly of an *I. trifida* variety (Y22) (Table 1). They integrated whole-genome shotgun reads, single-molecule long reads (PacBio RS II), and genotyping-by-sequencing (GBS) genetic maps. This *I. trifida* genome represents a vast improvement over previous genomes because of the high quality of the assembly (Li et al., 2019). For example, evidence of naturally occurring horizontal gene transfer was identified in this genome, and it therefore represents a vehicle for the analysis of genome evolution in the genus *Ipomoea*.

I. triloba also belongs to section *Batatas* and is a close CWR of sweetpotato (Figure 2). A chromosome-level reference genome of *I. triloba* has been published (Wu et al., 2018) (Table 1). This reference genome was assembled using Illumina paired-end and

Species	Ploidy	Materials	Sequencing platform	References	Total length of scaffolds[a] (bp)	N50 of scaffolds (bp)	Number of scaffolds	Genome size[b] (Mb)	Number of genes	Link
I. batatas	hexaploid	Taizhong6 (version 2017)	Illumina, Roche 454	Yang et al., 2017a, 2017b	836,316,092	200,728	35,919	851.4	78,781	*Ipomoea batatas* Genome Browser (http://public-genomes-ngs.molgen.mpg.de/SweetPotato/)
I. batatas	hexaploid	Taizhong6 (version 2019)	Nanopore, 10X Genomics	Rastas (2019)	728,240,131	77,499	3934	473.8	64,295	*Ipomoea* Genome Hub (http://sweetpotao.com/)
I. trifida	diploid	Mx23Hm	Illumina	Hirakawa et al. (2015)	512,990,885	42,586	77,400	515.8	62,407	Sweetpotato GARDEN (http://sweetpotato-garden.kazusa.or.jp/)
I. trifida	diploid	0431-1	Illumina	Hirakawa et al. (2015)	712,155,587	36,283	181,194	539.9	109,449	Sweetpotato GARDEN(http://sweetpotato-garden.kazusa.or.jp/)
I. trifida	diploid	NCNSP0306	Illumina, PacBio, Bio-Nano	Wu et al. (2018)	461,997,559	1,237,020	30,394	526.4	44,158	Sweetpotato Genomics Resource (http://sweetpotato.plantbiology.msu.edu/)
I. trifida	diploid	Y22	Illumina, PacBio	Li et al. (2019)	460,931,543	607,924	5264	476.4	30,227	NCBI (PRJNA362521)
I. triloba	diploid	NCNSP0323	Illumina, PacBio, Bio-Nano	Wu et al. (2018)	457,835,428	6,861,300	4008	495.9	47,008	Sweetpotato Genomics Resource (http://sweetpotato.plantbiology.msu.edu/)
I. nil	diploid	Tokyo Kokei standard	Illumina, PacBio	Hoshino et al. (2016)	734,061,355	4,082,476	3367	734.8	42,783	*Ipomoea nil* (http://viewer.shigen.info/asagao/)
I. purpurea	diploid	field sample	Illumina, PacBio, Sequel	Gupta et al. (2021)	-	5.77M	402	602.0	53,973	CoGe platform (https://genomevolution.org/coge/GenomeInfo.pl?gid=58735)
I. aquatica	diploid	HNUWS001	Illumina, PacBio	Hao et al. (2021)	513,191,976	2.75M	1392	550.0	30,693	BIGD (PRJCA002216)

Table 1. Genomes and databases for the genus *Ipomoea*.

[a]Scaffold refers to the assembly version of contigs before chromosome-scale processing.

[b]Genome size and gene number are calculated based on the final assembly version (chromosome level, if available).

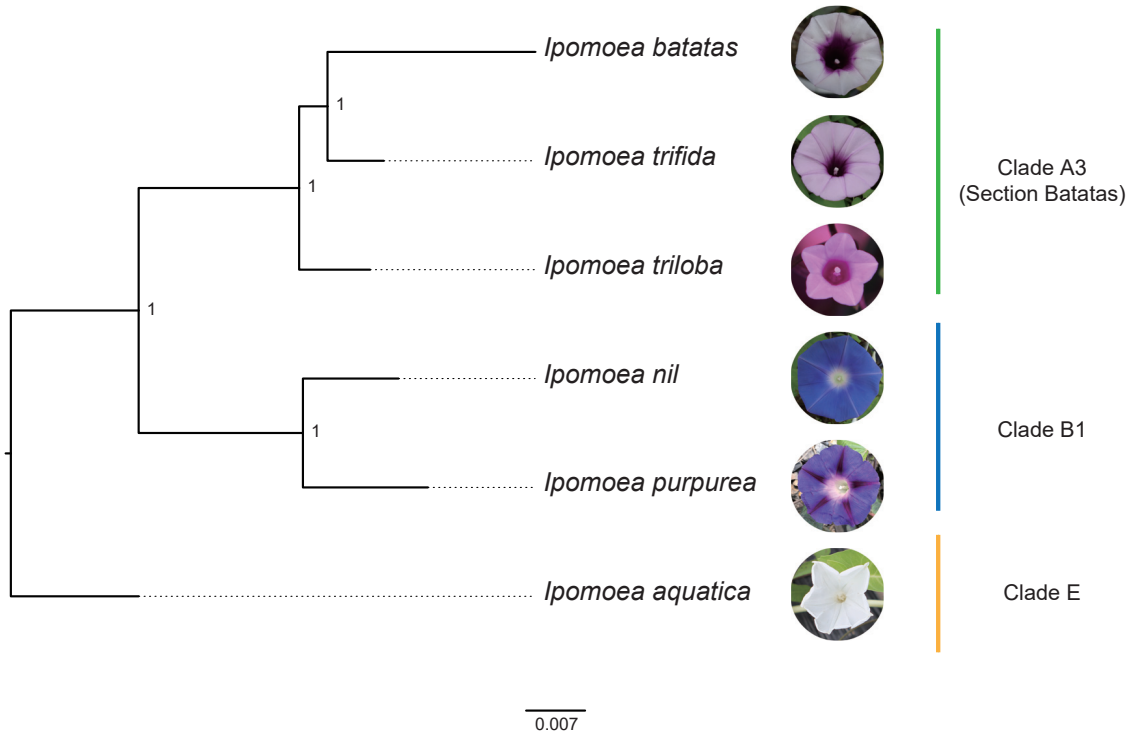

Figure 2. The phylogeny of sweetpotato and its wild relatives

The phylogenetic relationships were inferred from a concatenated alignment matrix of 9776 single-copy ortholog sequences across six *Ipomoea* species with published genomes. Values at the nodes indicate bootstrap support (1 = 100%). The phylogenetic clades are based on those of Wood et al. (2020). Shown are photographs of *Ipomoea* flowers by Yuqin Wang (*I. triloba* and *I. aquatica*), M.Y. (*I. purpurea*), and Ming Li (*I. batatas*, *I. trifida*, and *I. nil*).

mate-pair reads and was improved with PacBio reads, BioNano genome maps, and a linkage map. The total length of the pseudomolecules was 443.3 Mb (96.8% of the assembly in 216 scaffolds).

I. nil, the Japanese morning glory, is a popular ornamental plant with significant commercial value that has been used as a model species for analysis of the photoperiodic flowering response (Hoshino et al., 2016). *I. nil* nests in phylogenetic clade B1 and is therefore relatively distantly related to sweetpotato (Figure 2). Hoshino et al. (2016) sequenced and assembled the genome of this species using PacBio long reads (Table 1). Residual errors were identified and corrected using Illumina reads. The authors constructed linkage maps for all 15 chromosomes using single-nucleotide polymorphisms (SNPs) as markers. This assembly was the first pseudochromosome-level genome assembly in the botanical family Convolvulaceae.

Ipomoea purpurea, a species that also belongs to clade B1 (Figure 2), is a common noxious field weed that is distributed worldwide. Its genome was assembled from PacBio Sequel whole-genome shotgun data (Gupta et al., 2021; Table 1). In total, the 602-Mb genome assembly consists of 402 scaffolds with a scaffold N50 of 5.77 Mb. The assembly was collapsed into the expected 15 haploid chromosomes by performing pseudomolecule scaffolding with a Phase Genomics Hi-C map. Approximately 53,973 genes were annotated from the *I. purpurea* genome.

Ipomoea aquatica (also known as water spinach) is consumed as a popular vegetable in East, South, and Southeast Asia (Wu et al., 2018). *I. aquatica* is a semi-aquatic tropical plant that has medicinal value (Malalavidhane et al., 2001, 2003). *I. aquatica* belongs to clade E in the phylogenetic tree (Figure 2) and is a distant CWR of sweetpotato. The *I. aquatica* genome was assembled *de novo* using PacBio sequencing and 10X Genomics reads (Hao et al. 2021). The 162 scaffolds (415.77 Mb) were anchored to 15 pseudochromosomes using a high-density genetic map (Table 1).

Databases

Ipomoea *batatas Genome Browser*

The *Ipomoea batatas* genome browser (http://public-genomes-ngs.molgen.mpg.de/SweetPotato/) is an early database created by the Max Planck Institute for Molecular Genetics that provides access to the sweetpotato genome (version 2017) published by Yang et al. (2017a). Genomic sequences and RNA sequencing (RNA-seq) data are available to download. A browser for the sweetpotato genome and BLAT (the BLAST-like alignment tool) can be used to search for required information (Supplemental Table 2).

Ipomoea *Genome Hub*

The phased sweetpotato genome (version 2019) is available through the *Ipomoea* Genome Hub (http://sweetpotao.com/), which was jointly established by the Shanghai Chenshan Botanical Garden, the Max Planck Institute for Molecular Genetics, and the Chinese Academy of Sciences. It provides optimized reference genome annotation, RNA-seq, and expressed sequence tag (EST) data for sweetpotato. The JBrowse genome browser, haplotypes of sweetpotato, and the *Ipomoea* Atlas are available

on this platform, which has descriptions and photos of 146 species in the genus *Ipomoea* (Supplemental Table 2).

Sweetpotato GARDEN

This database (http://sweetpotato-garden.kazusa.or.jp/), built by the Kazusa DNA Research Institute, contains the reference genome of the wild diploid species *I. trifida* which was published in 2015 (Hirakawa et al., 2015). Two different lines (Mx23Hm and 0431-1) are available for Basic Local Alignment Search Tool (BLAST) searches. It also provides genetic and Kyoto Encyclopedia of Genes and Genomes (KEGG) maps for further application (Supplemental Table 2).

Sweetpotato Genomics Resource (SGR)

This database (http://sweetpotato.plantbiology.msu.edu/) contains the reference genomes and gene expression profile information for two wild diploid species, *I. trifida* and *I. triloba* (Wu et al., 2018). The SGR database was built by the Genomic Tools for Sweetpotato team. The pseudomolecules, annotation, RNA-seq data, and gene expression data for these two species can be downloaded from this database. A JBrowse genome browser and many tools, such as BLAST, Gene Ontology (GO), ID and keyword search, and pfam accession ID search, are also available (Supplemental Table 2).

Ipomoea nil

This site (http://viewer.shigen.info/asagao/) provides access to the *I. nil* genome assembly (Hoshino et al., 2016). This database was established by The Morning Glory Genome Consortium. The JBrowse, BLAST/BLAT, and keyword searches are available. This database enables users to download genome, gene, annotation, RNA-seq, and transposon data for *I. nil* (Supplemental Table 2).

POLYPLOID GENETICS OF SWEETPOTATO

The origin of sweetpotato

The origin of sweetpotato and its polyploid genome have been debated for years. Three polyploidization hypotheses have been proposed.

(1) The autopolyploid hypothesis posits that sweetpotato is an autopolyploid and that *I. trifida* is its only wild ancestor (Figure 3A and 3B). This hypothesis is supported by polysomic inheritance based on genetic linkage analysis (Ukoskit and Thompson, 1997; Kriegner et al., 2003; Cervantes-Flores et al., 2008a; Zhao et al., 2013a; Mollinari et al., 2020), phylogenetic analysis (Roullier et al., 2013; Muñoz-Rodríguez et al., 2018), and cytogenetic analyses (Shiotani, 1988; Shiotani and Kawase, 1989). Based on a phylogenetic analysis of chloroplast genomes, a hybridization event between sweetpotato and *I. trifida* that occurred after speciation of sweetpotato resulted in chloroplast capture from *I. trifida* (Roullier et al., 2013; Muñoz-Rodríguez et al., 2018; Figure 3B).

(2) The second origin hypothesis suggests that sweetpotato is a segmental allopolyploid that carries three partially differentiated subgenomes originally from *I. trifida*, *Ipomoea tenuissima*, and *Ipomoea littoralis*, based on an analysis of 811 conserved single-copy genes (Gao et al., 2020; Figure 3C).

(3) The third allopolyploid hypothesis suggests that sweetpotato was formed by hybridization between two progenitor species but that the identities of the progenitor species are controversial. This allopolyploid hypothesis is supported by cytogenetic evidence because two of the genomes show closer homology to one another than to the third (Magoon et al., 1970). Nishiyama (1971) suggested that sweetpotato originated from *I. trifida* 3x, which is a hybrid between *Ipomoea* × *leucantha* and *I. littoralis* based on cytogenetic analysis (Figure 3D). Based on morphological data, Austin (1988) concluded that the cultivated sweetpotato is derived from a hybridization event between *I. trifida* and *I. triloba* (Figure 3E). From an analysis of nucleotide sequence variation in the *Waxy* gene intron, Gao et al. (2011a) suggested that sweetpotato arose via hybridization between *I. tenuissima* and *I. littoralis* (Figure 3F). Based on phylogenetic analyses of homologous haplotypes, it is likely that sweetpotato arose from a cross between *I. trifida* and tetraploid *I. batatas* 4x (Yang et al., 2017a; Yan et al., 2021; Figure 3G). Recently, Muñoz-Rodríguez et al. (2022) described an autotetraploid relative from Ecuador as a new species, *Ipomoea aequatoriensis*, and identified it as the tetraploid progenitor of sweetpotato based on morphological and phylogenetic analyses (Figure 3H).

A phylogenetic analysis based on a haplotype-resolved genome showed that the six sets of sweetpotato chromosomes are divided into two clusters that, in turn, are composed of two sets and four sets (Yang et al., 2017a). This is consistent with the $B_1B_1B_2B_2B_2B_2$ genomic formula of sweetpotato proposed by Shiotani and Kawase (1987) based on cytogenetic analyses. Genomic and cytogenetic analyses suggest that sweetpotato arose from a cross between a diploid and a tetraploid progenitor (Shiotani and Kawase, 1987; Yang et al., 2017a). The diploid progenitor is most likely *I. trifida*, whereas the identity of the tetraploid progenitor remains under debate. An extant tetraploid relative (tentatively identified as *I. batatas* 4x) shows a closer relationship with sweetpotato than does *I. trifida* (Jarret et al., 1992; Jarret and Austin, 1994; Rajapakse et al., 2004; Srisuwan et al., 2006; Feng et al., 2018).

Kyndt et al., 2015 reported the discovery of two horizontally transferred DNA (T-DNA) sequences from *Agrobacterium* spp., *Ib*T-DNA1 and/or *Ib*T-DNA2, that are integrated into the genomes of sweetpotato and some of its wild relatives (Kyndt et al., 2015; Quispe-Huamanquispe et al., 2019). These horizontally transferred DNA sequences were suggested to be natural genetic markers that are useful for identifying the origin of the cultivated sweetpotato and its relationship to its CWRs (Quispe-Huamanquispe et al., 2019). Yan et al. (2021) analyzed sweetpotato and representative wild tetraploid relatives that contain *Ib*T-DNA insertions from all relevant geographic locations. Their results suggest that *I. batatas* 4x consists of two lineages, the Ecuador lineage and the basal lineage. The Ecuador lineage is the sister group of cultivated sweetpotato, and the basal lineage is the probable tetraploid progenitor of sweetpotato, a conclusion supported by phylogenetics based on both homologous haplotypes and whole genome-wide variations. Based on morphological and phylogenetic analyses of

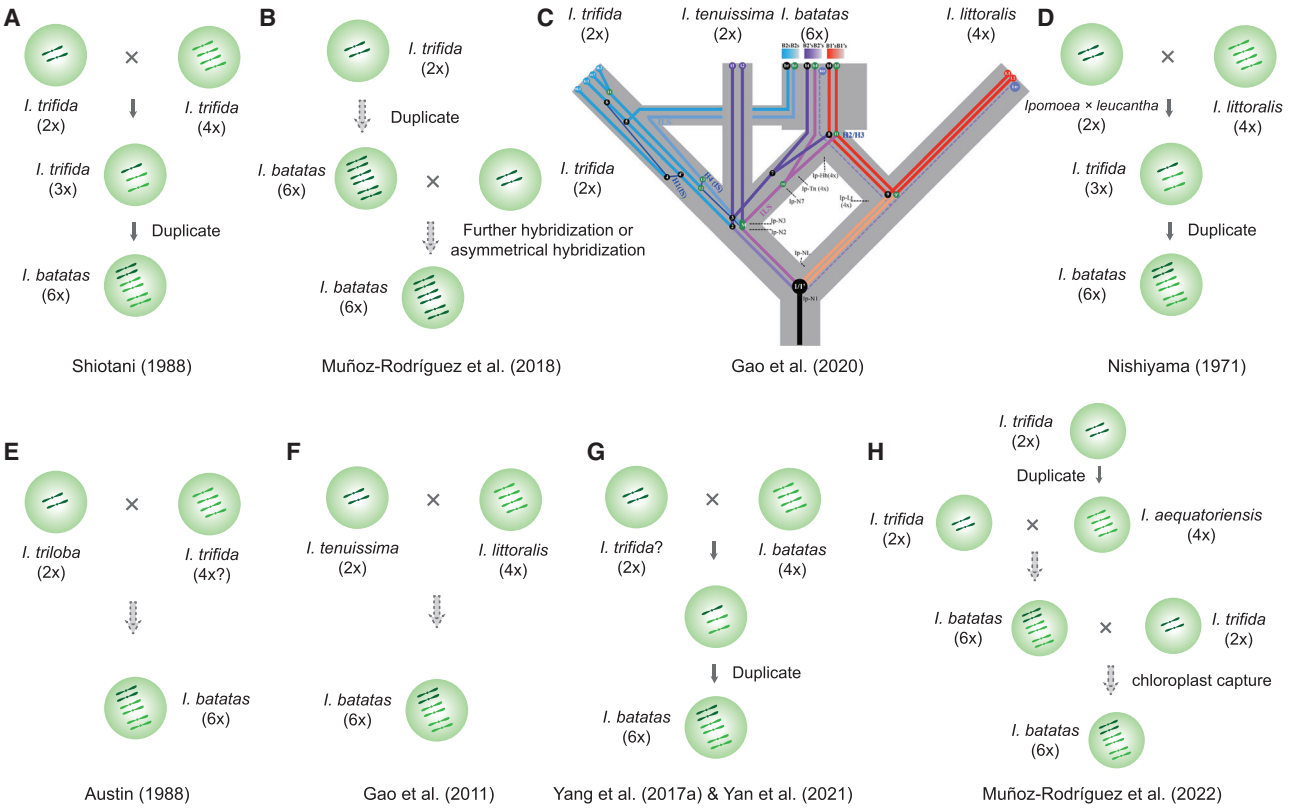

Figure 3. Hypotheses to describe the origin of cultivated sweetpotato

(A) The autopolyploid hypothesis suggests that *I. trifida* is the only progenitor of sweetpotato. Adapted from Shiotani (1988).

(B) Sweetpotato originated from *I. trifida*, and after the speciation of sweetpotato, a hybridization event occurred between sweetpotato and *I. trifida*. Adapted from Muñoz-Rodríguez et al. (2018).

(C) The species tree embodying the two hybridization networks demonstrates the segmental allopolyploid hypothesis. From Gao et al. (2020).

(D) The allopolyploid hypothesis of Nishiyama (1971): sweetpotato is derived from a triploid *I. trifida* that arose from hybridization of *Ipomoea* ×*leucantha* and *I. littoralis.*

(E) The allopolyploid hypothesis of Austin (1988): sweetpotato arose via hybridization between *I. trifida* and *I. triloba.*

(F) The allopolyploid hypothesis of Gao et al. (2011a, 2011b): sweetpotato arose via hybridization between *I. tenuissima* and *I. littoralis.*

(G) The allopolyploid hypothesis of Yang et al. (2017a) and Yan et al. (2021): sweetpotato is likely to be derived from a triploid that arose from a cross between *I. trifida* and *I. batatas* 4x.

(H) The allopolyploid hypothesis of Muñoz-Rodríguez et al. (2022): *I. aequatoriensis* arose from a whole-genome duplication in *I. trifida.* Sweetpotato (*I. batatas*) is likely to be derived from a cross between *I. trifida* and *I. aequatoriensis.* Subsequent introgression between *I. trifida* and sweetpotato resulted in chloroplast capture from *I. trifida.*

nuclear DNA and the chloroplast genome, Muñoz-Rodríguez et al. (2022) have described the Ecuador lineage of *I. batatas* 4x as a new species, *I. aequatoriensis*, and identified this lineage as the tetraploid progenitor of sweetpotato. In addition, they consider the other tetraploid lineage related to the basal lineage of Yan et al. (2021) as being a hybrid between sweetpotato and *I. trifida*. Therefore, the tetraploid progenitor of sweetpotato is still controversial. The key to confirming the tetraploid progenitor will be to establish an effective method or standard to distinguish the possible tetraploid progenitor and the hybrid offspring, and it is crucial to include data from real or simulated hybrids between sweetpotato and *I. trifida* in future studies.

The B_1 and B_2 subgenomes of sweetpotato retain a high degree of similarity (Magoon et al., 1970). Therefore, polysomic inheritance in sweetpotato (with some preferential pairing) resembles that of an autohexaploid (Ukoskit and Thompson, 1997; Kriegner et al., 2003; Cervantes-Flores et al., 2008a; Zhao et al., 2013a; Mollinari et al., 2020). Thus, sweetpotato has been treated as an autohexaploid during genetic map construction and genetic mapping (Mollinari et al., 2020; da Silva Pereira et al., 2020; Yamamoto et al., 2020; Chen et al., 2021).

Genetic diversity analysis of sweetpotato germplasm

Sweetpotato germplasm collections, such as those maintained by the International Potato Center (CIP) and the United States Department of Agriculture (USDA), can acquire and conserve an increasing number of *I. batatas* genotypes. In this effort, knowledge about the genetic diversity maintained in gene banks facilitates the most efficient use of resources and improves the general understanding of how the genetic relationships of sweetpotato crop genetic resources can be used in support of breeding and related activities (Buteler et al., 2002; Hu et al., 2003; Campos and Caligari, 2017). Traditionally, biochemical and morphological

Trait type	Trait	Population	Candidate loci	Markers	Method	Software	Reference
Yield	number of roots per plant (SS), weight of roots per plant (SZ), biomass in early stage (SZS)	1807 F_1 progenies derived from Yuzi7 × Xu18	4 QTLs (*IbEXP4A*) for SS; 2 QTLs for SZ; 1 QTL for SZS	1,670,312 SNPs (WGRS)	GWAS	OutcrossSeq	Chen et al. (2021)
	number of commercial roots per plant (NOCRs), number of noncommercial roots per plant (NONCs), total number of storage roots per plant (TNRs), commercial root yield (CYTHA), total root yield (RYTHA), foliage yield (FYTHA)	315 F_1 progenies derived from Beauregard × Tanzania	2 QTLs for NOCR; 4 QTLs for NONC; 4 QTLs for TNR; 1 QTL for CYTHA; 1 QTL for RYTHA; 1 QTL for FYTHA	30,684 SNPs (GBSpoly)	QTL	QTLpoly	Pereira et al. (2020)
	root yield	92 F_1 progenies derived from PSL × 90IDN-47	1 peak in 90IDN-47 and 2 peaks in PSL for yield	17,940 SNPs	GWAS	R Package rrBLUP 4.6	Okada et al. (2019)
	root yield	287 F_1 progenies derived from New Kawogo × Beauregard	12 QTLs	250 SSRs	GWAS	SAS 9.4	Yada et al. (2017)
	root yield	202 F_1 progenies derived from Xushu 18 × Xu 781	4 QTLs in Xushu 18 and 5 QTLs in Xu 781	Xushu 18: 1936 AFLPs and 141 SSRs; Xu 781: 1824 AFLPs and 130 SSRs	QTL	MapQTL 4.0	Li et al. (2014)
	top weight (TW), root weight (RW), root number (RN)	NT: 119 F_1 progenies derived from Nancy Hall (♀) × Tainung 27 (♂) TN: 112 F_1 progenies derived from Tainung 27 (♀) × Nancy Hall (♂)	1 QTL in population NT and 3 QTLs in population TN for TW; 2 QTLs in population NT and 1 QTL in population TN for RW; 1 QTL in population NT for RN	100 ISSRs	QTL	QTL Cartographer	Chang et al. (2009)
Root development	root thickness	*I. trifida* BC_1F_1 population	1 major QTL on chr06 (2.94–8.71 Mb)	SNPs (WGRS)	BSA	QTLseqr 0.7.5.2	Suematsu et al. (2021)
	continuous storage formation and bulking (CSRFAB), discontinuous storage root formation and bulking (DCSRFAB)	358 sweetpotato genotypes	13 SNPs and 13 candidate genes (*CSLD1*, *NHH*, *P-LNPHP*, *CmlP*, *HVA22*, *PLLSP*, *Amp-M1*, *KAKU4*, *P-RID*, *SAG*, *CLE-related*, *MAP3K-like*, and *NF-Y*) for CSRFAB; 5 SNPs and 5 candidate genes (*TRO-Z*, *DUF803*, *hypothetical*, *AGC-Kinase*, and *GBLD*) for DCSRFAB	33,068 SNPs (DArTseq)	GWAS	R package GAPIT 3.0	Bararyenya et al. (2020)

Table 2. Overview of trait association studies in sweetpotato.

(Continued on next page)

Trait type	Trait	Population	Candidate loci	Markers	Method	Software	Reference
Quality	amylase activity in the whole meal (amylase), dry-matter content (DMC), tuber surface smoothness (PC), root surface color (PS), root flesh color (RS)	1807 F_1 progenies derived from Yuzi7 × Xu18	1 QTL for amylase; 2 QTLs for DMC; 2 QTLs for PC; 1 QTL for PS; 1 QTL for RS	1,670,312 SNPs (WGRS)	GWAS	OutcrossSeq	Chen et al. (2021)
	anthocyanin content	94 F_1 progenies derived from Konaishin × Akemurasaki	1 major QTL (Myb-related gene)	15,430 and 15,403 Akemurasaki-specific and Konaishin-specific simplex SNPs (WGRS)	BSA	QTL-seq 1.4.4	Yamakawa et al. (2021)
	DMC, starch content (SC), β-carotene content (BC), flesh color (FC)	315 F_1 progenies derived from Beauregard × Tanzania	5 QTLs for DM; 2 QTLs for SC; 2 QTLs for BC (*phytoene synthase gene*, *15-cis-phytoene desaturase violaxanthin de-epoxidase* and *ORANGE*); 3 QTLs for FC (*phytoene synthase gene*, *15-cis-phytoene desaturase violaxanthin de-epoxidase* and *lycopene β-cyclase*)	30,684 SNPs (GBSpoly)	QTL	QTLpoly	Gemenet et al. (2020b)
	FC (related to anthocyanin content)	104 sweetpotato accessions with anthocyanin variation in root flesh	chr12: 17,809,090–23,930,961 (*IbMYB1-2*)	724,438 SNPs (88 transcriptomes/16 WGRS)	GWAS/ eQTL	EMMAX	Zhang et al. (2020a)
	anthocyanin content	94 F_1 progenies derived from Konaishin × Akemurasaki	Genes on LGs 2, 5, 10–15 (*IbF3H*, *IbDFR*, *IbMYB1*, *IbWD40*, *IbUF3GT*, *IbCHI*, *IbCHS*, *IbANS*, and *IbbHLH3*)	59,675 SNPs (ddRAD-Seq)	GWAS/ QTL	ngsAssocPoly/ MapQTL 6.0	Haque et al., (2020b)
	β-carotene content (BC), DMC, starch content (SC)	52 F_1 progenies derived from J-Red × Choshu	3 QTLs in J-Red and 2 QTLs in Choshu for BC; 2 QTLs in J-Red for DM; 2 QTLs in J-Red and 3 QTLs in Choshu for SC	J-Red: 5952 SNPs (ddRAD-Seq), 228 retrotransposon-based markers, and 161 SSRs; Choshu: 5640 SNPs (ddRAD-Seq), 192 retrotransposon-based markers, and 176 SSRs	GWAS/ QTL	TASSEL 5.2.49/ MapQTL 6.0	Haque et al., (2020a)

Table 2. *Continued*

(Continued on next page)

Trait type	Trait	Population	Candidate loci	Markers	Method	Software	Reference
	root skin color (RSC), internode length (LI)	F_1 progenies derived from Xushu18 × K123-11 (KX-F1); self-pollinated progenies of Xushu18 (X18-S1)	1 peak in KX-F1 and 1 peak in X18-S1 for RSC; 1 peak in KX-F1 and 1 peak in X18-S1 for LI	SNPs (ddRAD-Seq)	GWAS	ngsAssocPoly	Yamamoto et al. (2020)
	LI, root skin thickness (RST), main RSC (MRSC), secondary RSC (SRSC)	137 F_1 progenies derived from Yeseumi × Annobeny	3 QTLs for LI; 1 QTL for RST; 15 QTLs for MRSC; 2 QTLs for SRSC	210 SSRs	QTL	WinQTL Cartographer 2.5	Kim et al. (2017)
	BC, DMC, starch content (SC)	287 F_1 progenies derived from New Kawogo × Beauregard	8 QTLs for BC; 4 QTLs for DM; 6 QTLs for SC	250 SSRs	GWAS	SAS 9.4	Yada et al. (2017)
	Dry-matter and starch content (DMSC), BC, starch composition (SCP)	239 genotypes have various morphological types and geographical origins	32 QTLs for DMSC; 16 QTLs for BC; 17 QTLs for SC	887 SSRs	GWAS	TASSEL 5.0	Zhang et al., (2016)
	starch content	202 F_1 progenies derived from Xushu 18 × Xu 781	2 QTLs in Xushu 18 and 6 QTLs in Xu 781	Xushu 18: 1936 AFLPs and 141 SSRs; Xu 781: 1824 AFLPs and 130 SSRs	QTL	MapQTL 4.0	Yu et al., (2014)
	DMC	202 F_1 progenies derived from Xushu 18 × Xu 781	5 QTLs in Xushu 18 and 22 QTLs in Xu 781	Xushu 18: 1936 AFLPs and 141 SSRs; Xu 781: 1824 AFLPs and 130 SSRs	QTL	MapQTL 4.0	Zhao et al., (2013a)
	BC, DMC, starch content (SC)	240 F_1 progenies derived from Tanzania × Beauregard	3 positive QTLs and 1 negative QTL in Beauregard and 3 positive QTLs and 1 negative QTL in Tanzania for BC; 4 positive QTLs and 4 negative QTLs in Beauregard and 4 positive QTLs and 1 negative QTL in Tanzania for DM; 3 positive QTLs and 4 negative QTLs in Beauregard and 3 positive QTLs and 2 negative QTLs in Tanzania for SC	Beauregard: 726 AFLPs; Tanzania: 927 AFLPs	QTL	WinQTL Cartographer	Cervantes-Flores et al. (2011)

Table 2. ***Continued***

(Continued on next page)

Trait type	Trait	Population	Candidate loci	Markers	Method	Software	Reference
	BC	55 genotypes were selected from 73 F_1 genotypes developed from the maternal clones Beauregard, Excel, L94-96, L89-110, L86-33, and L96-117	17 markers were selected by discriminant analysis, and 9 markers were selected by logistic regression	259 AFLPs	DA/LRG	SAS	Mwamburi Mcharo and LaBonte (2010)
	RSC, FC, root shape (RS)	NT: 119 F_1 progenies derived from Nancy Hall (♀) × Tainung 27 (♂) TN: 112 F_1 progenies derived from Tainung 27 (♀) × Nancy Hall (♂)	3 QTLs in population NT and 3 QTLs in population TN for RSC; 4 QTLs in population NT and 2 QTLs in population TN for FC; 3 QTLs in population NT for RS	100 ISSRs	QTL	QTL Cartographer	Chang et al. (2009)
	basal branching number (FZS), diameter of the stem between the fifth and sixth expanded leaves (JC), length of the stem between the fifth and sixth expanded leaves (JJC), color of the stem between the fifth and sixth expanded leaves (JS), color of the leaf-petiole conjunction part of the sixth expanded leaf (MJS), length of petiole in the sixth expanded leaf (YBC), color of veins in the sixth expanded leaf (YMS), leaf shape of the sixth expanded leaf (YX)	1807 F_1 progenies derived from Yuzi7 × Xu18	2 QTLs for FZS; 4 QTLs for JC; 1 QTL for JJC; 1 QTL (*IbMYB1*) for JS; 1 QTL (*IbMYB1*) for MJS; 2 QTLs for YBC; 1 QTL (*IbMYB1*) for YMS; 2 QTLs (*IbFBW2*) for YX	1,670,312 SNPs (WGRS)	GWAS	OutcrossSeq	Chen et al. (2021)
Biotic resistance	root rot (caused by *Fusarium solani*)	300 F_1 progenies derived from Jizishu 1 × Longshu 9	6 QTLs in Jizishu 1 and 2 QTLs in Longshu 9	Jizishu 1: 484 SSRs; Longshu 9: 573 SSRs	QTL	MapQTL 5.0	Ma et al. (2020)
	weevil resistance (WS)	92 F_1 progenies derived from PSL × 90IDN-47	1 peak in 90IDN-47 and 1 peak in PSL for WS	17,940 SNPs (ddRAD-Seq)	GWAS	R Package rrBLUP 4.6	Okada et al. (2019)
	root-knot nematode resistance	113 F_1 progenies derived from J-Red × Choshu	3 QTLs in J-Red and 1 QTL in Choshu	J-Red: 5952 SNPs (ddRAD-Seq), 228 retrotransposon-based markers, and 161 SSRs; Choshu: 5640 SNPs (ddRAD-Seq), 192 retrotransposon-based markers, and 176 SSRs	GWAS/ QTL	TASSEL 5.0/ MapQTL 6.0	Sasai et al. (2019)

Table 2. ***Continued***

(Continued on next page)

Trait type	Trait	Population	Candidate loci	Markers	Method	Software	Reference
	stem nematode resistance	196 F_1 progenies derived from Xushu 18 × Xu 781	4 markers displayed linkage to the *Rsn1* gene	200 SRAPs	BSA	Map Manager QTXb17	Zhao et al., (2013b)
	root-knot nematode resistance	92 F_1 progenies derived from Koganesengan × Hi-starch	9 AFLP markers that were present in resistant bulked DNAs and absent in the susceptible bulks; 1 QTL was mapped to the region around E33M53_090	360 AFLPs	BSA/ QTL	MapQTL 5.0	Nakayama et al. (2012)
	root-knot nematode resistance	240 F_1 progenies derived from Tanzania × Beauregard	7 QTLs in Tanzania and 2 QTLs in Beauregard	947 AFLPs	QTL	WinQTL Cartographer	Cervantes-Flores et al. (2008b)
	root-knot nematode resistance	48 F_1 genotypes developed in LSU and 55 F_1 progenies developed in CIP	5 and 4 AFLP markers that had a strong and significant association with respect to the resistance trait in the LSU and CIP populations	LSU population: 229 AFLPs; CIP population: 220 AFLPs	DA/LRG	SAS	Mcharo et al. (2005a)
	sweetpotato virus disease resistance (SPVD)	92 genotypes had mild or no symptoms of SPVD severity	4 were selected by discriminant analysis and logistic regression statistical methods	350 AFLPs	DA/LRG	SAS	Miano et al. (2008)
	sweetpotato chlorotic stunt virus resistance (SPCSV), sweetpotato feathery mottle virus resistance (SPFMV)	87 F_1 progenies derived from Tanzania × Wagabolige	7 QTLs for SPCSV; 4 QTLs for SPFMV	232 AFLPs and 37 RAPD markers	QTL/ DA/LRG	QGENE/SAS	Mcharo et al. (2005b)
	SPCSV, SPFMV, sweetpotato virus disease resistance (SPVD)	F_1 progenies derived from Tanzania × Wagabolige	9 QTLs for SPCSV; 4 QTLs for SPFMV; 7 QTLs for SPVD	Tanzania: 330 AFLPs; Wagabolige: 252 AFLPs	QTL	QGENE	Mwanga et al. (2002)

Table 2. ***Continued***

LSU, Louisiana State University; CIP, International Potato Center; QTL, quantitative trait locus; SNP, single-nucleotide polymorphism; AFLP, amplified fragment length polymorphism; GBS, genotyping by sequencing; ddRAD-Seq, Double-digest restriction-site associated DNA; SSR, simple sequence repeat; ISSR, inter-simple sequence repeat; WGRS, whole-genome re-sequencing; DArTseq, deamination adjacent to RNA modification targets; SRAP, sequence-related amplified polymorphism; RAPD, random amplified polymorphic DNA; GWAS, genome-wide association study; BSA, bulked segregant analysis; eQTL, expression quantitative trait locus; DA, discriminant analysis; LRG, logistic regression.

markers have been used to characterize sweetpotato diversity (Huamán et al., 1999). However, although morphological data (descriptors) provide useful information, their use has certain limitations, and biochemical markers often have low levels of polymorphism. In both instances, the expression of morphological traits and biochemical markers tends to be influenced by the plant growth stage(s) and various environmental factors (Nadeem et al., 2018).

Beginning in the 1990s, molecular markers based on allelic polymorphisms were developed, and they have been widely utilized to estimate genetic diversity in sweetpotato. Early studies of sweetpotato used a variety of markers, including restriction fragment length polymorphisms (RFLPs), random amplified polymorphic DNA (RAPD) (Jarret and Austin, 1994; Gichuki et al., 2003), amplified fragment length polymorphisms (AFLPs) (Zhang et al., 2000, 2004), inter-simple sequence repeats (ISSRs) (Li et al., 2008; Moulin et al., 2012), ESTs (Marian et al., 2018), and simple sequence repeats (SSRs) (Veasey et al., 2008; Som et al., 2014; Yang et al., 2015; Zawedde et al., 2015; Feng et al., 2018; Lee et al., 2019; Palumbo et al., 2019; Anglin et al., 2021). These markers have been used to characterize and define the accessions in sweetpotato germplasm collections and to examine population structure and gene pools of sweetpotato originating from Latin America, South America, Central America, Oceania, Asia, and Africa (Zhang et al., 2000; Gichuki et al., 2003; Li et al., 2008; Som et al., 2014).

Over the past decade, improvements in high-throughput DNA sequencing technology have enabled the identification of huge numbers of SNPs in the genomes of crop plants. The effectiveness of SNP analysis in detecting polymorphisms is much greater than that of other classes of molecular markers, and there are many ways to analyze genome-wide SNP data (Khlestkina and Salina, 2006). SNP markers have been adopted for certification of sweetpotato cultivars and breeding lines (Supplemental Table 3). Specific length amplified fragment sequencing (SLAF-seq) has been used to identify genome-wide SNPs in sweetpotato and to assess the population structure and genetic diversity of 197 sweetpotato accessions, most of which were from China (Su et al., 2017). Restriction site-associated DNA sequencing (RAD-seq) was also used to analyze the relationships among sweetpotato accessions and different ploidy forms of *I. trifida* (Feng et al., 2018), as well as the genetic relationships among 81 sweetpotato accessions (Feng et al., 2020). Wadl et al. (2018) used GBSpoly, an optimized GBS protocol for highly heterozygous and polyploid genomes, to determine the population structure and genetic diversity within a subset of the USDA sweetpotato collection. Wu et al. (2018) reported the first whole-genome re-sequencing (WGRS) study in sweetpotato and revisited the phylogeny and genetic diversity of the 16 sweetpotato cultivars in the Mwanga diversity panel (MDP). Using WGRS data, Yan et al. (2021) examined the relationships among the diploid and tetraploid wild relatives of sweetpotato and hexaploid sweetpotato cultivars based on consensus genome-wide variation analysis and an HPA pipeline.

Functional genomics and genetic mapping

Functional genomics studies are essential for marker-assisted breeding and crop improvement using genome editing (Monden and Tahara, 2017; Zhang et al., 2017). In sweetpotato, forward genetics approaches, such as QTL mapping, GWAS, and BSA, have been used to map economically important genes or genomic regions. The mapped genes include those affecting yield, root quality, biotic resistance, and various morphological traits (Table 2). Storage root yield is potentially the most important agronomic trait in sweetpotato. Thus, a number of independent studies have been conducted that focused on root yield and/or the number of storage roots per plant, and these studies identified many associated QTLs (Chang et al., 2009; Li et al., 2014; Yada et al., 2017; Okada et al., 2019; da Silva da Silva Pereira et al., 2020; Chen et al., 2021). The expansin gene *IbEXP4A* has been suggested as a candidate gene for determining the number of roots per plant (Chen et al., 2021). Storage root thickening is another important characteristic of interest to sweetpotato breeders. Suematsu et al. (2021) detected a major QTL (*qRT1*) on chromosome 6 (chr06) that regulates root thickness in *I. trifida*. The pattern of storage root formation and bulking is important when the crop is harvested. Commercial farming can require synchronized maturity or discontinuous storage root formation and bulking (DCSRFAB) at harvest. Multiple harvesting, which is predominantly practiced in sub-Saharan Africa, requires cultivars with continuous storage root formation and bulking (CSRFAB) to ensure availability of product over a longer growing season. Bararyenya et al. (2020) identified 12 and seven candidate genes that were annotated for CSRFAB and DCSRFAB, respectively.

Sweetpotatoes are used for a wide variety of purposes; therefore, the quality traits of sweetpotato are diverse. Dry-matter content and starch content are two related quality traits (Gemenet et al., 2020b), and both of them contribute to eating quality as well as to starch and ethanol production (Yamakawa, 1998; Kitahara et al., 2017). Many QTLs have been identified as being associated with these traits that include dry-matter content (Cervantes-Flores et al., 2011; Zhao et al., 2013a; Zhang et al., 2016; Yada et al., 2017; Gemenet et al., 2020b; Haque et al., 2020a; Chen et al., 2021), starch content (Cervantes-Flores et al., 2011; Yu et al., 2014; Zhang et al., 2016; Yada et al., 2017; Haque et al., 2020a; da Silva Pereira et al., 2020), starch composition (Zhang et al., 2016), and amylase activity (Chen et al., 2021). Sweetpotato is a significant source of vitamin A (β-carotene) and anthocyanins, and breeding for improved nutritional value has become increasingly important. Several genes or genomic regions responsible for β-carotene content (Mcharo and LaBonte, 2010; Cervantes-Flores et al., 2011; Zhang et al., 2016; Yada et al., 2017; Haque et al., 2020a; Gemenet et al., 2020b), anthocyanin content (Haque et al., 2020b; Yamakawa et al., 2021), and related root flesh color (Chang et al., 2009; Zhang et al., 2020a; Gemenet et al., 2020b; Chen et al., 2021) have been mapped. QTLs associated with additional sweetpotato root traits have been investigated. These include root skin smoothness (Chen et al., 2021), root skin thickness (Kim et al., 2017), root skin color (Chang et al., 2009; Kim et al., 2017; Yamamoto et al., 2020; Chen et al., 2021), and root shape (Chang et al., 2009). QTLs associated with vine traits have also been mapped, and these include top weight, internode length, stem diameter, stem color, leaf-petiole junction color, petiole length, vein color, and leaf shape (Chang et al., 2009; Kim et al., 2017; Yamamoto et al., 2020; Chen et al., 2021).

Software/pipeline	Purpose	Object	Reference	Link
HPA	genetic relationship detection between polyploids using homologous haplotypes	polyploid	Yan et al. (2021)	https://github.com/YanMengxiao/HPA
Ranbow	polyploid haplotype reconstruction	polyploid	Moeinzadeh et al. (2020)	https://github.com/moeinzadeh/Ranbow.git
Polyploid QTL-seq	polyploid QTL analysis by whole-genome resequencing (BSA-based)	autopolyploid	Yamakawa et al. (2021)	
Autopolyploid-Plant module of OutcrossSeq	GWAS in F_1 population with whole-genome low-coverage resequencing data	autopolyploid	Chen et al. (2021)	https://github.com/xhhuanglab/OutcrossSeq
ngsAssocPoly	GWAS with low-coverage NGS-based genotyping data	autopolyploid	Yamamoto et al. (2020)	https://github.com/yame-repos/ngsAssocPoly
MAPpoly	genetic map construction	autopolyploid	Mollinari et al. (2020)	https://github.com/mmollina/MAPpoly
QTLpoly	QTL mapping in F_1 population	autopolyploid	da Silva Pereira et al. (2020)	https://github.com/guilherme-pereira/qtlpoly
GBSapp	SNP calling, filtering, and allele dosage calling	polyploid	Wadl et al. (2018)	https://github.com/bodeolukolu/GBSapp

Table 3. Bioinformatics tools for genetic studies in sweetpotato.
HPA, haplotype-based phylogenetic analysis; QTL, quantitative trait locus; BSA, bulked segregant analysis; GWAS, genome-wide association study; NGS, next-generation sequencing; SNP, single-nucleotide polymorphism.

Sweetpotato can be affected by a number of fungal, bacterial, and virus or virus-like pathogens as well as nematodes and insect pests (Martin and Jones, 1986; Clark et al., 2013). Diseases and pest infestations can decrease the yield and quality of the sweetpotato crop (Jansson and Raman, 1991; Ma et al., 2020). Therefore, QTLs associated with resistances to economically important pests and diseases have been studied. These include resistance to sweetpotato weevil (Okada et al., 2019), root-knot nematode (Mcharo et al., 2005a; Cervantes-Flores et al., 2008b; Nakayama et al., 2012; Sasai et al., 2019), stem nematode (Zhao et al., 2013b), sweetpotato virus disease (Mwanga et al., 2002; Mcharo et al., 2005b; Miano et al., 2008), and root rot caused by the ascomycete fungus *Fusarium solani* (Ma et al., 2020).

New genetics tools for polyploid sweetpotato

Sweetpotato is a suitable model for studying the genetics of a complex polyploid crop species. In recent years, many bioinformatics tools and pipelines have been developed for sweetpotato (Table 3). Although these genetics tools were developed for sweetpotato, they can also be applied to other polyploid species. Haplotype phasing facilitates research on polyploid genetics, physiology, evolution, and crop breeding (Zhang et al., 2020b), and a number of related tools have been developed. For example, Ranbow, a tool for haplotype reconstruction of polyploid genomes from short-read sequencing data, has been used successfully to phase half of the hexaploid genome of sweetpotato (Yang et al., 2017a; Moeinzadeh et al., 2020). Recently, the HPA pipeline, which takes full advantage of the homologous variation in polyploids to disentangle complex relationships, was used to identify the closest tetraploid genotype related to sweetpotato (Yan et al., 2021). Bioinformatics programs have been developed for polyploid genetics and genetic mapping. These include tools for allele dosage estimation (GBSapp [Wadl et al., 2018] and ngsAssocPoly [Yamamoto et al., 2020]), genomic imputation (OutcrossSeq; Chen et al., 2021), genetic map construction (MAPpoly; Mollinari et al., 2020), QTL mapping (QTLpoly [da Silva Pereira et al., 2020] and polyploid QTL-seq [Yamakawa et al., 2021]), and GWAS using low-coverage resequencing data via ngsAssocPoly (Yamamoto et al., 2020) and OutcrossSeq (Chen et al., 2021). Using very low-coverage resequencing data (1.5×) from an F_1 population, OutcrossSeq successfully identified genomic regions associated with multiple agricultural traits (Chen et al., 2021).

PROGRESS IN SWEETPOTATO BREEDING

Traditional breeding

Traditional breeding approaches that involve hybridization of selected clones, visual evaluation of progeny, and subsequent rounds of selection have been widely applied to sweetpotato. These efforts have resulted in the generation of new cultivars with improved yield, nutrient content, pest resistance, and other quality factors. This process is labor intensive and often requires evaluation of extremely large progeny populations. Because of cross-incompatibility, multiple parents are usually employed in a polycross (Jones, 1965). This prevents the identification of superior parents (Quispe-Huamanquispe et al., 2019), although molecular markers may be used to assist with their identification (Martin, 1965; Hwang et al., 2002). Currently, 16 incompatibility groups have been identified in sweetpotato (Katayama et al., 2017). Additional issues of concern include poor flowering and sterility in some environments. Sweetpotato breeding faces more challenges than normally encountered in the breeding of other crop species (Martin, 1965).

In a polycross breeding strategy, 20–30 or more parental lines are selected and used to produce 10,000–100,000 true seeds. These seeds provide the progeny that are subsequently used for gene pool separation and selection. In a typical polycross nursery, the male parent of the selected progeny is often unknown. In the past century, polycross strategies have been successfully used in sweetpotato breeding programs at Louisiana State University (LSU), the Xuzhou Sweetpotato Research Center in China, and the National Crops Resources Research Institute (NaCRRI) in Kampala, Uganda. The leading sweetpotato cultivar 'Beauregard' was developed using polycross selection and was released by LSU (Rolston et al., 1987). Between 1999 and 2003, 22 sweetpotato cultivars were released by the NaCRRI. These were also developed using a polycross selection process that included 24 parents (Mwanga et al., 2016).

To increase the chances of detecting/selecting desirable minor and recessive genes, polycrossing in combination with recurrent selection has become a popular breeding approach. In this method, a polycross population is generated by controlled crossing, and the progeny with desirable traits are selected for use as parents in a second round of polycrossing. The white-fleshed boniato-type cultivar 'Arapey' was developed by the Instituto Nacional de Investigación Agropecuaria in Uruguay using a polycross-recurrent selection approach (Lebot, 2010). To further increase breeding efficiency, an ABS can be used in sweetpotato. An ABS approach involves a multi-location field evaluation in the initial generation instead of multiple evaluations over a period of years in a single selection environment (Grüneberg et al., 2015).

CWRs often express higher levels of biotic and abiotic stress resistance than cultivated species or their commercial cultivars. Successful hybrid crosses between *I. batatas* and one or more of its wild relatives have been reported. This approach has been proposed as a means to integrate stress tolerance traits into commercial cultivars. Several sweetpotato cultivars that were derived from hybridization between *I. batatas* and *I. trifida* have been reported (Nishiyama, 1971; Shiotani and Kawase, 1987).

As an alternative to conventional hybridization that could overcome cross incompatibility and ploidy differences, somatic hybridization involving fusion of protoplasts of two species has been explored. A storage-root-producing hybrid was generated via somatic hybridization between the sweetpotato cultivar 'Kokei 14' and *I. triloba* (Yang et al., 2009). Although interspecific hybridization and somatic hybridization may ultimately prove useful in efforts to improve the crop, plant regeneration is still a bottleneck in the production of new cultivars.

Mutation breeding strategies have been used to improve the sweetpotato crop. Shoot apices from irradiated plants of the cultivar 'Kokei 14' were cultured to form embryogenic callus cultures. Regenerated plants exhibited higher yields and altered storage root flesh color compared with the controls (Wang et al., 2007). Shin et al. (2011) regenerated plants from irradiated stem segments that varied with respect to storage root size, shape, and yield.

Not all sweetpotato clones flower readily, profusely, or in synchrony. Various approaches have been used to promote flowering and enable hybridization to occur. An approach used successfully in some breeding programs is the utilization of a flower-inducing rootstock (Lam et al., 1959) such as *Ipomoea carnea* (Dukes et al., 2019). Other approaches to promote flowering include the use of growth regulators such as 2,4-dichlorophenoxyacetic acid (2,4-D), gibberellic acid (GA_3), and 1-naphthaleneacetic acid (NAA) and the adjustment of photoperiod and/or temperature (Lam et al., 1959; Mubayiwa et al., 2016).

Molecular breeding

Molecular breeding offers the promise of a more rapid and efficient means of crop improvement and production of novel cultivars. In general, molecular breeding approaches can be classified into two types: (1) molecular marker-assisted breeding and (2) genome-modified breeding.

As described under "Functional genomics and genetic mapping," molecular markers such as SSRs, RFLPs, AFLPs, and SNPs have been used in QTL mapping and GWAS analyses in sweetpotato. Gemenet et al. (2020c) developed 30 reliable SNP markers for quality assurance and control in a genomics-assisted breeding program. These markers were selected based on population structure and genetic distance. Six trait-specific markers were also selected for quality control. However, because of the complex hexaploid nature of the sweetpotato genome, successful application of marker-assisted selection (MAS) and GS has been limited (Grüneberg et al., 2009).

Genome-modified breeding (including breeding that involves transgenes and genome editing) relies on the technical feasibility of successful plant genetic transformation. *Agrobacterium tumefaciens*-mediated transformation of sweetpotato using embryogenic suspension cultures provides a powerful platform for genome-modified breeding in this crop (Gama et al., 1996; Yang et al., 2011). Transgenic sweetpotatoes have been generated that possess weevil resistance (expressing cowpea trypsin inhibitor), virus resistance (expressing the coat protein gene of sweetpotato feathery mottle virus), herbicide resistance (expressing the herbicide resistance *bar* gene), and stress tolerance (expressing the *Low Osmotic Stress five* gene) (Newell et al., 1995; Okada et al., 2001; Otani et al., 2003; Gao et al., 2011b). Transgenic sweetpotato plants have also been developed by endogenous gene overexpression or RNA interference (RNAi). Changes in the expression of the starch synthase I (*SSI*), starch branching enzyme II (*SBEII*), and granule-bound starch synthase I (*GBSSI*) genes have been shown to improve starch content (Otani et al., 2007; Zhou et al., 2015; Wang et al., 2017).

CRISPR-Cas9 gene editing technology, which allows precisely targeted genome modifications, has been used successfully to edit two starch biosynthetic pathway genes (*GBSSI* and *SBEII*) in sweetpotato. In *GBSSI* knockout plants, the amylose content was reduced, and in *SBEII* knockout plants, the amylose content was increased (Wang et al., 2019; Lyu et al., 2021).

Current challenges and future perspectives

The long-term efforts of breeders and plant scientists have resulted in the production and distribution of many high-quality sweetpotato cultivars. However, compared with other important

crops, sweetpotato breeding has lagged behind because of its complex polyploid genome. With the recent explosive growth in genome sequencing and editing technologies, a combination of state-of-the-art techniques and molecular breeding strategies (Figure 4) will greatly facilitate genetic improvement of sweetpotato for sustainable global production.

Haplotype-phased genomes and pan-genomes

When assembling reference genomes, homoeologous chromosomes (chromosomes that are partially homologous because of a common ancestry) are sometimes collapsed together, and the resulting assembly is considered a "mosaic" reference. This type of assembly can result in false variants, imprecise gene annotation, and misleading biological interpretations (Korlach et al., 2017; Koren et al., 2018). Sweetpotato, as a highly heterozygous hexaploid, requires a haplotype-phased assembly to understand the molecular basis of trait variability and polyploid evolution. A haplotype-phased assembly captures all allelic variants and can be used to examine allele-specific expression. It reveals the functionally important haplotypes that are critical for the fixation of desirable traits (Zhang et al., 2020b). Although the current sweetpotato reference genome is half phased (Yang et al., 2017a), the haplotypes are too fragmented to infer biological functions. Therefore, alternate technologies, such as Hi-C and/or single-cell sequencing of gamete genomes, are required to achieve a fully haplotype-phased assembly of the sweetpotato genome.

A single reference genome cannot adequately represent the full range of genetic diversity of sweetpotato. Therefore, a pan-genome approach is required to investigate the entire gene repertoire of the crop (Golicz et al., 2016; Tao et al., 2019). The pan-genome enables the identification of genetic variants, particularly larger structural variations (SVs) such as presence/absence variants (PAVs) and copy number variants (CNVs), which play important roles in the genetic determination of agronomic traits (Lu et al., 2015; Zhao et al., 2018; Lye and Purugganan, 2019).

Phenotyping

In addition to genotypic information, phenotypic data are also critical for genetic advancement in a breeding program (Araus and Cairns, 2014). To deal with the large number of progeny plants in a breeding population, breeding programs can benefit greatly from automated high-throughput phenotyping technologies. Phenomics aims to analyze the relationship between genes and agronomic/horticultural traits in support of precision breeding (Zhao et al., 2019). High-throughput plant phenotyping platforms that use red green blue (RGB) imaging (https://www.qubitphenomics.com/rgb-structural-imaging/), chlorophyll fluorescence imaging, hyperspectral imaging, thermal imaging, and lidar, have been widely used to improve the efficiency and accuracy of phenotypic data collection (Zhao et al., 2019). In field environments, ground-based field phenotyping and unmanned aerial vehicles (UAVs) have been used. For example, the Eidgenössische Technische Hochschule Zürich field phenotyping platform, which contains a digital single-lens reflex (DSLR) camera, laser scanner, and thermal camera, was used to monitor canopy cover, canopy height, and other traits in winter wheat, maize, and soybean (Kirchgessner et al., 2017). A fixed-wing UAV was used for weed detection, estimation of net photosynthesis, and stress detection in maize, peach, and citrus plantings (Yang et al., 2017b).

Sweetpotato is a highly polymorphic crop with numerous genetically complex morphological traits (Jackson et al., 2018). With the help of RGB imaging, colorimetry, and other technologies, high-quality morphological characterization data can be obtained. Such data can be useful in identifying target traits (superior progeny) with greater accuracy. Despite their many advantages, automated, multifunctional, and high-throughput phenotyping technologies have yet to be widely applied to sweetpotato. Currently, phenotyping technologies typically focus on the aerial parts of plants. Information on the development of underground parts (such as storage roots) is important in sweetpotato. However, obtaining high-throughput phenotypic data of storage root development during the growing period clearly poses a significant challenge. UAV-based hyperspectral imagery and machine learning have been used to predict end-of-season tuber yield and tuber set in potatoes (Sun et al., 2020).

Other novel and emerging technologies have also found some applications in sweetpotatoes, including evaluation of harvested storage roots for size, shape, interior and exterior color, and insect damage. Villordon and Carroll (2002) used digital imaging to assess herbicide damage in sweetpotato storage roots. Villordon et al. (2020) used three-dimensional (3D) imaging technology to assess the surface area and volume of sweetpotato storage roots because these characteristics relate to post-harvest product recovery. Dangles and Heider (2015) evaluated high-resolution, UAV-acquired thermal infrared images for the detection of heat-tolerant varieties of sweetpotato. Other technologies, such as artificial intelligence (AI) (Vásquez-Villalobos et al., 2018) and machine learning (ML) (Villordon et al., 2010), are finding applications in the culture and processing of sweetpotato crops.

MAS and GS

MAS breeding programs use DNA-based markers that are known to be linked to desirable genes and/or favorable traits. Utilization of MAS has facilitated and accelerated the breeding of sweetpotato (Zhang et al., 2016). Several strategies, including identification of QTLs and association mapping, have been used to identify the linked markers (Table 2), and DNA marker loci linked to root quality and biotic resistance genes have been reported (Nakayama et al., 2012; Zhao et al., 2013b; Zhang et al., 2016; Sasai et al., 2019). However, to our knowledge, DNA markers have not yet been used in an MAS program with sweetpotato (Yada et al., 2017; Haque et al., 2020a). MAS is used mainly for selection of traits controlled by genes with relatively large effects. Therefore, this approach is not suitable for use with complex traits, such as yield, that are controlled by many genes or QTLs with relatively small individual effects (Xu et al., 2020).

GS utilizes genome-wide DNA markers, and it was developed for complex traits, such as yield, that are affected by a large number of genes, each of which typically has a small effect (Hickey et al., 2019; Xu et al., 2020). GS offers several advantages compared with traditional MAS. GS targets multiple traits simultaneously without the need to identify the QTLs related to the target traits

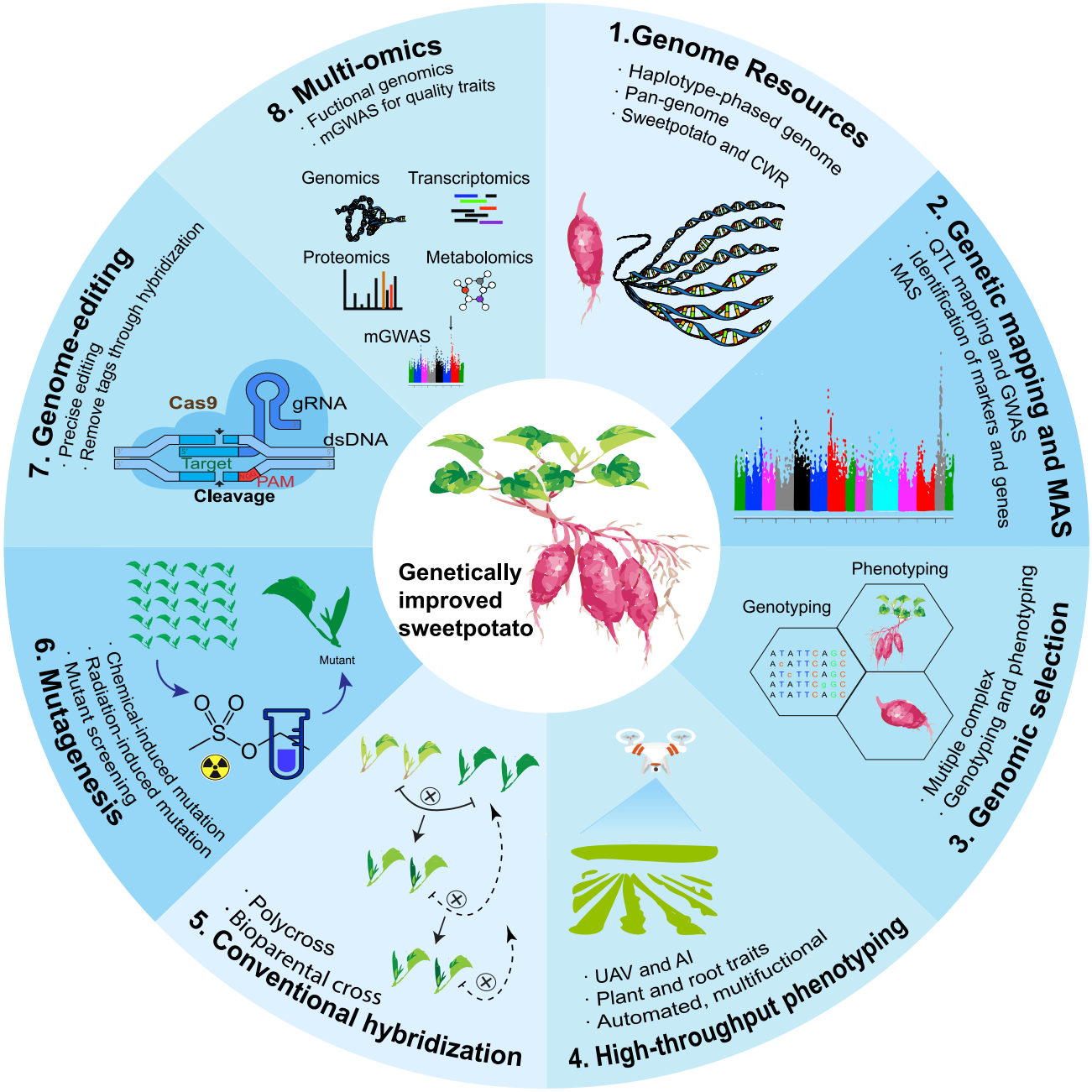

Figure 4. Strategies for sweetpotato genetics and breeding in the future

(1) Genome resources. Haplotype-phased genomes and pan-genome sequencing provide basic information for genetics and breeding. CWR, crop wild relative.

(2) Genetic mapping and marker-assisted selection (MAS). Genetic mapping enables association of specific genes, SNPs, or markers with agricultural traits and facilitates MAS. QTL, quantitative trait locus; GWAS, genome-wide association study; SNP, single-nucleotide polymorphism.

(3) Genomic selection (GS). GS targets multiple complex traits simultaneously and accelerates breeding in sweetpotato.

(4) High-throughput phenotyping. Automatic and high-throughput phenotyping technologies make it possible to handle a large number of progeny in breeding programs. UAV, unmanned aerial vehicle; AI, artificial intelligence.

(5) Conventional hybridization. Hybridization of selected clones, visual evaluation of progeny, and subsequent selection.

(6) Mutagenesis. Creating random mutations in the genome using chemical or radiation treatment with subsequent selection of plants with desirable traits.

(7) Genome editing. Precise editing of the target site using CRISPR-Cas9-based tools. The transgene cassette is removed by chromosomal segregation after self-pollination or outcrossing in subsequent generations.

(8) Multi-omics. An efficient means to identify the genes and gene networks involved in controlling a target trait. mGWAS, metabolite genome-wide association study.

and without the need for phenotyping during the later stages of breeding (Nakaya and Isobe, 2012; Hickey et al., 2019). Gemenet et al. (2020a) evaluated the sequencing depth, genotype quality, and predictive models required for accurate GS applications in sweetpotato. This was the first attempt to apply GS to sweetpotato. It is anticipated that sweetpotato breeding programs will routinely employ MAS and GS in the future.

Integration of multi-omics approaches in functional genomics studies

In the "omics" era of the life sciences, data are being generated at an unprecedented rate. These data represent layers of information that reflect various types of biological systems, including, but not limited to, the genome, transcriptome, epigenome, proteome, and metabolome (Li and Chen, 2014; Li and Yan, 2020). A multi-omics approach has already been shown to be an efficient means of characterizing complex biological systems, such as determining the genes and the gene networks involved in controlling a target trait (Li and Yan, 2020; Wu et al., 2021). This capability will support future breeding activities for the improvement of sweetpotato. To date, multi-omics studies in sweetpotato are limited. In two recent studies, integration of transcriptomic and metabolomic data facilitated the identification of genes and metabolites involved in anthocyanin accumulation and the mechanism of saccharification in tuberous roots of sweetpotato (He et al., 2020; Li et al., 2021a). Genome-wide analysis of expression QTLs (eQTLs) has also been applied to sweetpotato and was used to reveal the regulatory architecture of gene expression variation (Zhang et al., 2020a; Chen et al., 2021).

Metabolite GWAS (mGWAS) and the integration of metabolomics and transcriptomics are powerful tools for exploring the genetic and biochemical basis of plant metabolism (Alseekh et al., 2015; Fang and Luo, 2019). These combined approaches have been applied to the study of metabolite-related quality traits in many crops, including maize, rice, wheat, and tomato (Chen et al., 2014, 2020; Wen et al., 2014; Zhu et al., 2018). In sweetpotato, many important quality traits are also related to plant metabolites, including sugar, starch, anthocyanin, β-carotene, and proteins in storage roots and the content of vitamins, flavonoids, and phenolic compounds in leaves (Padmaja, 2009; Johnson and Pace, 2010). Identification of the genetic determinants of metabolite production has an important role in the improvement of sweetpotato. Integration of metabolomics, genomics, and transcriptomics data, such as mGWAS, provides a means to determine the mechanisms that regulate metabolites in sweetpotato.

Genome editing for crop improvement

Reports of CRISPR-Cas9-based genome editing first appeared in 2013 (Cong et al., 2013; Feng et al., 2013; Mao et al., 2013). Since then, genome editing technologies have proven to be powerful and efficient tools for the improvement of many crop species. At present, genome editing has been widely used to introduce/modify agronomically important traits, such as increased yield, improved nutritional quality, and resistance to biotic and abiotic stresses, in multiple crops, including rice, wheat, maize, tomato, and potato (Lu et al., 2017; Soyk et al., 2017; Tang et al., 2017; D'Ambrosio et al., 2018; Ye et al., 2018; Miao et al., 2019; Zhang et al., 2019; Zhong et al., 2019; Butt et al., 2020; Zhang et al., 2020c; Li et al., 2021b; Zhan et al., 2021). CRISPR-Cas-based genome editing has been extended to targeted mutagenesis, base editing, and precisely targeted gene/allele replacement or tagging in plants. mportantly, using CRISPR-Cas9 technology, transgenes present in the genomes of genome-edited plants can be removed by chromosomal segregation via a simple self-pollination or hybridization step. Gene editing technologies continue to be developed and utilized (Mao et al., 2013; Lu and Zhu, 2017; Lu et al., 2020).

CRISPR-Cas9 gene editing technology has been successfully applied to sweetpotato (Wang et al., 2019) to generate plants with improved starch content, demonstrating the feasibility of using this technology to improve root quality traits. As functional genomics and genetic studies continue to identify an increasing number of sweetpotato genes controlling agronomically important traits, those genes will become potential targets for genome editing.

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at *Plant Communications Online*.

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AUTHOR CONTRIBUTIONS

M.Y., H.N., Y.W., X.W., and J.Z. wrote and edited the manuscript. M.Y. and H.N. designed the figures. M.Y., Y.W., and X.W. drew the original version of the figures. R.J. wrote and revised the manuscript. J.Y. and H.W. designed and revised the manuscript.

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