Vegetable biology and breeding in the genomics era

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Vegetable crops provide a rich source of essential nutrients for humanity and represent critical economic values to global rural societies. However, genetic studies of vegetable crops have lagged behind major food crops, such as rice, wheat and maize, thereby limiting the application of molecular breeding. In the past decades, genome sequencing technologies have been increasingly applied in genetic studies and breeding of vegetables. In this review, we recapitulate recent progress on reference genome construction, population genomics and the exploitation of multi-omics datasets in vegetable crops. These advances have enabled an in-depth understanding of their domestication and evolution, and facilitated the genetic dissection of numerous agronomic traits, which jointly expedites the exploitation of state-of-the-art biotechnologies in vegetable breeding. We further provide perspectives of further directions for vegetable genomics and indicate how the ever-increasing omics data could accelerate genetic, biological studies and breeding in vegetable crops.

vegetable, genomics, multi-omics, gene discovery, molecular breeding

Introduction

Vegetable crops refer to plant species with an edible part, which are used almost exclusively for food and can be consumed raw or cooked, serving as the main source of multiple vitamins, minerals, and dietary fiber that are essential to the human diet. A total of 27 primary vegetable products, comprising artichoke, asparagus, bean, cabbage, carrot, cassava leaves, cauliflower, celery, chive, cucumber, eggplant, garlic, green corn, leek, lettuce, melon, mushroom, okra, onion, pea, pepper, pumpkin, radish, spinach, squash, tomato and watermelon are recognized by the Food and Agriculture Organization of the United Nations (FAO), with some 1.15 billion tons of overall production in 2020 (https://www.fao.org/faostat/zh/#data/QCL). Most vegetables are annuals and belong to the class Dicotyledoneae, with a few exceptions, such as species from the *Allium* genus; the families Solanaceae, Cucurbitaceae and Brassicaceae have the highest number of vegetable crops. Based on their edible tissues, they can further be classified into leaf, stem, fruit, flower, root, tuber, bulb, corm and podded vegetables.

Research on the biology and breeding of vegetable crops

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has long been hampered, owing largely to the lack of genome resources. Over the past twenty years, genomics technologies have rapidly advanced, which empowered the completion of reference genomes for increasing numbers of vegetables. Large-scale resequencing studies, in conjunction with transcriptome and metabolism analyses have also enhanced our understanding of the domestication history of vegetable crops, and the genetic basis for their various agronomic traits. In addition, the newly developed gene-editing technologies have also been exploited in several vegetable crops. This review summarizes the latest advances on high-quality reference genomes, population genomics, multi-omics, the genetic basis of domestication and important agronomic traits, and genome design of vegetable crops. This will provide a critical reference for modern biological research and breeding of vegetables. Furthermore, future directions and challenges of vegetable genomics, biology and breeding are also discussed.

Reference genomes

Sequencing and assembly of reference genomes for vegetable crop species have provided a foundation for not only comparative genomics analyses, but also genetics, functional research, and breeding. In 2009, the genome of cucumber (*Cucumis sativus*), the first for a vegetable crop, was generated by combining Illumina and Sanger sequencing technologies (Huang et al., 2009). The completion of this cucumber genome highlighted the feasibility of the cost-effective Illumina sequencing technology for assembling whole-genome sequences of various plants. Over the past few years, reference genomes have been released for more than ten Cucurbitaceae crops, such as cucumber, melon, watermelon, bottle gourd, wax gourd and pumpkin (Barrera-Redondo et al., 2019; Garcia-Mas et al., 2012; Guo et al., 2013; Montero-Pau et al., 2018; Sun et al., 2017; Urasaki et al., 2017; Wu et al., 2017), seven Brassicaceae species, including *Brassica rapa*, *B. oleracea* and *B. juncea* (Liu et al., 2014; Wang et al., 2011; Xie et al., 2019; Yang et al., 2016), and three Solanaceae species: tomato, pepper and eggplant (Barchi et al., 2019; Bolger et al., 2014; Hirakawa et al., 2014; Hosmani et al., 2019; Kim et al., 2017a; Kim et al., 2014; Li et al., 2019a; Liao et al., 2022; Qin et al., 2014; Razali et al., 2018; Schmidt et al., 2017; Stam et al., 2019; Takei et al., 2021; Tomato Genome Consortium, 2012; Wang et al., 2020b; Wei et al., 2020) (Figure 1 and Table 1).

Comparative evolutionary analyses of cucumber, melon and watermelon have provided insights into the origin of different basic chromosome numbers in these three evolutionarily close species: cucumber (n=7), melon (n=12) and watermelon (n=11). Furthermore, these three Cucurbitaceae species were found to have significantly contracted re-

pertoires of genes in the nucleotide-binding leucine-rich repeat (NLR) receptor type family, suggesting the existence of other possible mechanisms for confronting pathogen invasion (Garcia-Mas et al., 2012; Guo et al., 2013; Huang et al., 2009). *Solanum pennellii* is a wild species of cultivated tomato, endemic to South America. It possesses many important agronomic traits, including stress tolerance, disease resistance and plant morphology, which have been used as an important donor for introgression line construction in tomato breeding. The availability of its high-quality genome has paved the way for elucidating the genetic mechanisms underlying the favored traits introduced from this wild tomato species (Bolger et al., 2014).

The genomes of several vegetables from other botanical families, including carrot (*Daucus carota*) (Iorizzo et al., 2016), common bean (*Phaseolus vulgaris*) (Schmutz et al., 2014), coriander (*Coriandrum sativum*) (Song et al., 2019), cowpea (*Vigna unguiculata*) (Lonardi et al., 2019), "Jiaobai" (*Zizania latifolia*) (Guo et al., 2015), lettuce (*Lactuca sativa*) (Reyes-Chin-Wo et al., 2017), sacred lotus (*Nelumbo nucifera*) (Ming et al., 2013; Wang et al., 2013), spinach (*Spinacia oleracea*) (Xu et al., 2017), and sugar beet (*Beta vulgaris* ssp. *vulgaris*) (Dohm et al., 2014) have also been assembled (Table 1). The reference sequences and gene annotation could accelerate the mining of functional genes underlying agronomically important traits and expedite molecular breeding in many vegetable crops. For example, the root crop carrot plays an essential role in global food production and it is well known as a major vegetable source of provitamin carotenoids. Sequencing and assembly of a double-haploid carrot accession achieved a 421.5 Mb-genome containing 32,113 protein-coding genes. As the first sequenced species in the Apiaceae family, the carrot genome has enriched the understanding of species evolution in the euasterid II clade. This high-quality genome resource also enabled the identification of a candidate gene underlying carotenoid accumulation in the carrot taproot (Iorizzo et al., 2016).

Reference genome assemblies built using Illumina short reads are largely fragmentary, with several hundred to thousand kilobases of nucleotides remaining unresolved. With the recent technical advancements of long-read and long-range sequence information, newly emerged technologies, such as Pacific Biosciences (PacBio), Oxford Nanopore, 10X Genomics, Bionano optical genome mapping, and high-throughput chromosome conformation capture (Hi-C) are being used to improve the continuity and completeness of vegetable genomes. This information, at the early stage, was employed to fill gaps unresolved by short read-based contigs, or to connect contigs into scaffolds; e.g., in *Brassica juncea* (Yang et al., 2016), *Brassica rapa* (Cai et al., 2017; Li et al., 2020c), pepper (Hulse-Kemp et al., 2018), eggplant (Barchi et al., 2019), melon (Ruggieri et al., 2018) and wax gourd
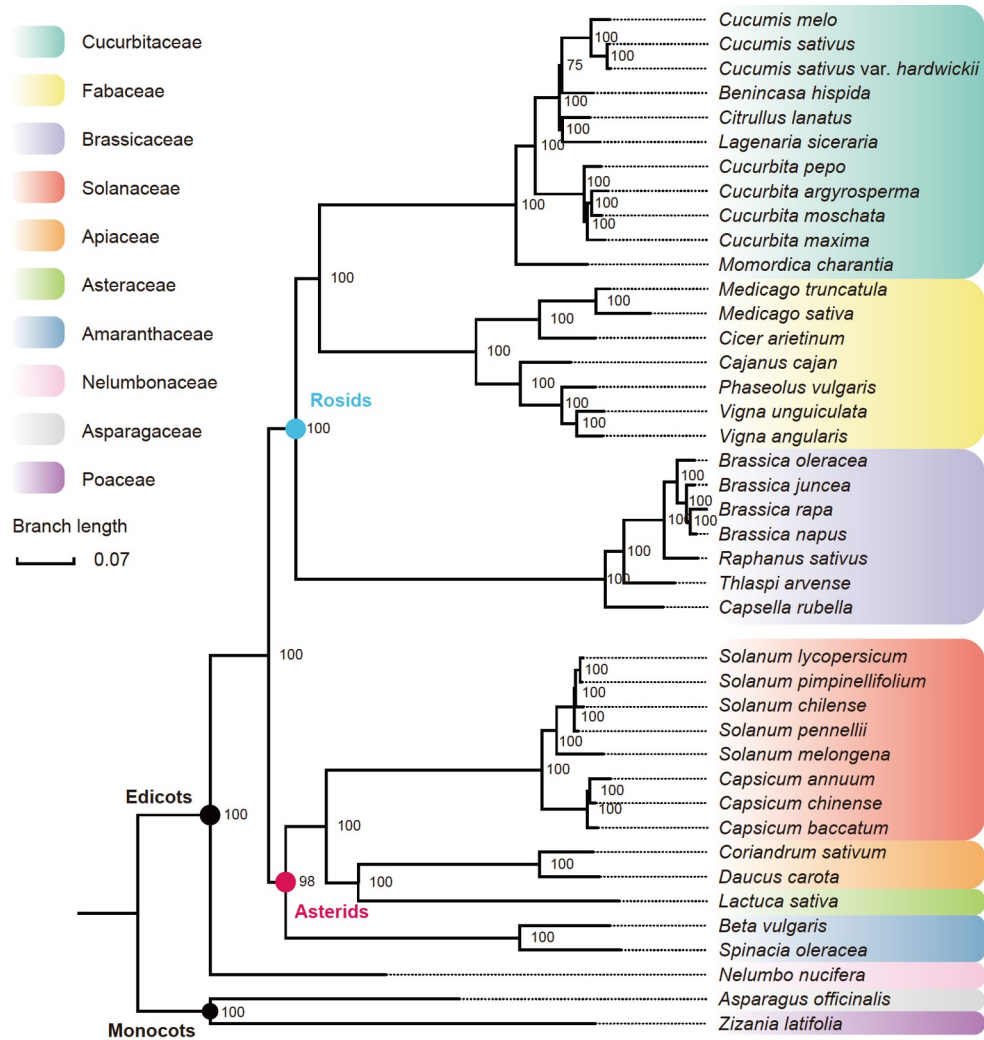
Figure 1 Phylogenetic relationships among the 41 released genomes of major vegetable species. Bootstrap support values are denoted beside the corresponding nodes. The tree was constructed based on amino acid sequence alignment of 289 single- or two-copy orthologous genes by the maximum likelihood approach implemented in RAxML (Stamatakis, 2014). Only genes from the A subgenome of *Brassica napus* were used.

(Xie et al., 2019). Notably, the first allopolyploid vegetable genome of *Brassica juncea* was resolved by taking advantage of long reads (Yang et al., 2016). More recently, a number of vegetable genomes, such as cucumber (Li et al., 2019b), melon (Zhang et al., 2019), tomato (Hosmani et al., 2019), eggplant (Li et al., 2019a; Wei et al., 2020), *Brassica rapa* (Li et al., 2021; Li et al., 2020c; Zhang et al., 2018b), coriander (Song et al., 2019) and cowpea (Lonardi et al., 2019), have been *de novo* assembled using single-molecule long reads and anchored into chromosome scale using Hi-C information (Table 1). The continuity and completeness of these genome assemblies were significantly improved compared with assemblies previously built using short reads; e. g., the contig N50 for the cucumber genome increased from 37.9 kb in V2 to 8.9 Mb in V3, representing a staggering 235-fold improvement, and a large proportion of repetitive elements that were underrepresented in the previous assembly, such as transposons, were also assembled (Li et al.,

2019b).

The completion of vegetable crop reference genomes has enabled the characterization of whole-genome duplication (WGD), a major driving force in evolution providing additional genetic materials for gene divergence, sub-functionalization and neofunctionalization. WGD events were detected in all the reported genomes of the Brassicaceae and Solanaceae vegetables. The recent whole-genome triplication event, which occurred in Solanaceae species (71±19.4 million years ago (MYA)), may have contributed to the emergence of new functional loci controlling fruit traits, such as fruit fleshiness and color, through neofunctionalization after gene duplication (Qin et al., 2014; Tomato Genome Consortium, 2012). For Brassicaceae vegetables, the whole-genome triplication event was estimated to have occurred more recently, c. 5–9 MYA, and the extent of gene retention among the three resulting subgenomes varies greatly: one of the three subgenomes has retained a disproportionately large

Table 1 Genome resources for vegetable crops

Species/accession name	Family	Estimated genome size	Assembled length	Contig N50 size	Sequencing technology	Reference
Cucumis sativus var. *sativus* cv. 9930 v1	Cucurbitaceae	367 Mb (Flow cytometry) 350 Mb (K-mer)	243.5 Mb	19.8 kb	Sanger+Illumina	Huang et al., 2009
Cucumis sativus var. *sativus* cv. 9930 v2	Cucurbitaceae	367 Mb (Flow cytometry) 350 Mb (K-mer)	197 Mb	37.9 kb	Sanger+Illumina	Li et al., 2011
Cucumis sativus var. *sativus* cv. 9930 v3	Cucurbitaceae	367 Mb (Flow cytometry) 350 Mb (K-mer)	226.2 Mb	8.9 Mb	PacBio+10X Genomics +Hi-C	Li et al., 2019b
Cucumis sativus cv. Gy14	Cucurbitaceae	367 Mb	192.6 Mb	48.1 kb	454	Yang et al., 2012
Cucumis sativus cv. B10	Cucurbitaceae	367 Mb	193 Mb	23.3 kb	Sanger+454	Woycicki et al., 2011
Cucumis sativus var. *hardwickii* PI 183967	Cucurbitaceae	367 Mb	204.8 Mb	119 kb	Sanger+Illumina	Qi et al., 2013
Cucumis melo cv. DHL92 v3.5.1	Cucurbitaceae	450 Mb	361.4 Mb	18.2 kb	Sanger+454	Garcia-Mas et al., 2012
Cucumis melo cv. DHL92 v3.6.1	Cucurbitaceae	450 Mb	375.3 Mb	18.2 kb	Sanger+454+Optical mapping	Ruggieri et al., 2018
Citrullus lanatus subsp. *vulgaris* cv. 97103 v1	Cucurbitaceae	425 Mb	353.3 Mb	26.4 kb	Illumina	Guo et al., 2013
Citrullus lanatus subsp. *vulgaris* cv. 97103 v2	Cucurbitaceae	425 Mb	362.7 Mb	2.3 Mb	PacBio+Optical mapping +Hi-C	Guo et al., 2019b
Citrullus lanatus subsp. *vulgaris* cv. Charleston Gray	Cucurbitaceae	419.2 Mb	396.4 Mb	36.7 kb	Illumina	Wu et al., 2019
Cucurbita maxima var. *Rimu*	Cucurbitaceae	386.8 Mb	271.4 Mb	40.7 kb	Illumina	Sun et al., 2017
Cucurbita moschata var. *Rifu*	Cucurbitaceae	372.0 Mb	269.9 Mb	40.5 kb	Illumina	Sun et al., 2017
Cucurbita pepo subsp. *pepo* (Zucchini)	Cucurbitaceae	283 Mb	263.5 Mb	110.1 kb	Illumina	Montero-Pau et al., 2018
Lagenaria siceraria var. *USVL1VR-Ls*	Cucurbitaceae	334 Mb	313.4 Mb	28.3 kb	Illumina	Wu et al., 2017
Cucurbita argyrosperma subsp. *argyrosperma*	Cucurbitaceae	238 Mb	229 Mb	463.4 kb	Illumina+PacBio	Barrera-Redondo et al., 2019
Momordica charantia cv. OHB3-1	Cucurbitaceae	339 Mb	285.5 Mb	21.9 kb	Illumina	Urasaki et al., 2017
Momordica charantia cv. OHB3-1	Cucurbitaceae	339 Mb	303 Mb	9.9 Mb	PacBio	Matsumura et al., 2019
Benincasa hispida cv. B227	Cucurbitaceae	1.02 Gb	913 Mb	68.5 kb	Illumina+PacBio	Xie et al., 2019
Solanum lycopersicum Heinz 1706	Solanaceae	900 Mb	760 Mb	177 kb	Sanger+454	Tomato Genome Consortium, 2012
Solanum lycopersicum Heinz 1706 SL4.0	Solanaceae	900 Mb	782.5 Mb	5.5 Mb	PacBio+Hi-C+Optical mapping	Hosmani et al., 2019
Solanum pimpinellifolium LA1589	Solanaceae	900 Mb	739 Mb	5.1 kb	Illumina	Tomato Genome Consortium, 2012
Solanum pimpinellifolium LA0480	Solanaceae	900 Mb	811.3 Mb	27.4 kb	Illumina	Razali et al., 2018
Solanum pimpinellifolium LA2093	Solanaceae	923 Mb	807.6 Mb	10.9 Mb	Illumina+PacBio+Hi-C	Wang et al., 2020b
Solanum pennellii LA0716	Solanaceae	1.2 Gb	942.6 Mb	2.2 kb	Illumina	Bolger et al., 2014
Solanum pennellii LYC1722	Solanaceae	1.2 Gb	915 Mb	2.5 Mb	Nanopore	Schmidt et al., 2017
Solanum chilense LA3111	Solanaceae	1.2 Gb	914 Mb	9.8 kb	Illumina	Stam et al., 2019
Capsicum annuum cv. CM334	Solanaceae	3.48 Gb	3.06 Gb	30.0 kb	Illumina	Kim et al., 2014
Capsicum chinense PI159236	Solanaceae	3.14 Gb	2.95 Gb	27.9 kb	Illumina	Kim et al., 2014
Capsicum annuum cv. Zunla-1	Solanaceae	3.26 Gb	3.35 Gb	55.4 kb	Illumina	Qin et al., 2014
Capsicum annuum var. *glabriusculum* Chiltepin	Solanaceae	3.07 Gb	3.48 Gb	52.2 kb	Illumina	Qin et al., 2014

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Species/accession name	Family	Estimated genome size	Assembled length	Contig N50 size	Sequencing technology	Reference
Capsicum baccatum PBC81	Solanaceae	3.9 Gb	3.2 Gb	39 kb	Illumina	Kim et al., 2017a
Capsicum chinense PI159236	Solanaceae	3.2 Gb	3.0 Gb	50 kb	Illumina	Kim et al., 2017a
Capsicum annuum	Solanaceae	3.26 Gb	3.21Gb	1.72 Mb (scaffold)	10X Genomics	Hulse-Kemp et al., 2018
Solanum melongena cv. Nakate-Shinkuro	Solanaceae	1.13 Gb	844.1 Mb	14.3 kb	454+Illumina	Hirakawa et al., 2014
Solanum melongena cv. 67/3	Solanaceae	1.21 Gb (Flow cytometry) 1.04 Gb (K-mer)	1.47 Gb	16.7 kb	Illumina+Optical mapping	Barchi et al., 2019
Solanum melongena Guiqie1	Solanaceae	1.21 Gb	1.16 Gb	5.3 Mb	Illumina+Hi-C	Li et al., 2019a
Solanum melongena HQ-1315	Solanaceae	1.21 Gb	1.17 Gb	5.26 Mb	Illumina+Nanopore+10X Genomics+Hi-C	Wei et al., 2020
Brassica rapa ssp. *pekinensis* Chiifu-401-42 v1.5	Brassicaceae	485 Mb	283.8 Mb	46.3 kb	Illumina	Wang et al., 2011
Brassica rapa ssp. *pekinensis* Chiifu-401-42 v2.5	Brassicaceae	485 Mb	389.2 Mb	52.7 kb	PacBio+Illumina	Cai et al., 2017
Brassica rapa ssp. *pekinensis* Chiifu-401-42 v3.0	Brassicaceae	455 Mb	353.1 Mb	1.45 Mb	PacBio+Hi-C+Optical mapping	Zhang et al., 2018b
Brassica napus Darmor-bzh	Brassicaceae	1.13 Gb	840 Mb	38.9 kb	Sanger+454+Illumina	Chalhoub et al., 2014
Brassica oleracea var. *capitata* 02-12	Brassicaceae	630 Mb	539.9 Mb	26.8 kb	Sanger+454+Illumina	Liu et al., 2014
Brassica juncea var. *tumida* T84-66	Brassicaceae	922 Mb	955 Mb	61 kb	PacBio+Illumina+Optical mapping	Yang et al., 2016
Capsella bursa-pastoris	Brassicaceae	410 Mb	272.8 Mb	38 kb	Illumina	Kasianov et al., 2017
Capsella rubella Monte Gargano	Brassicaceae	219 Mb	134.8 Mb	24.6 kb	Sanger+454+Illumina	Slotte et al., 2013
Raphanus sativus Aokubi	Brassicaceae	528.6 Mb	402 Mb	46.3 kb	Sanger+Illumina	Kitashiba et al., 2014
Thlaspi arvense MN106	Brassicaceae	539 Mb	412.3 Mb	21.1 kb	PacBio+Illumina	Dorn et al., 2015
Vigna unguiculata Walp. IT97K-499-35	Fabaceae	560 Mb	519 Mb	10.9 Mb	PacBio+Optical mapping	Lonardi et al., 2019
Vigna angularis Jingnong 6	Fabaceae	542 Mb	466.7 Mb	38 kb	Illumina	Yang et al., 2015
Phaseolus vulgaris G19833	Fabaceae	587 Mb	473 Mb	39.5 kb	Sanger+454+Illumina	Schmutz et al., 2014
Cajanus cajan Asha	Fabaceae	833.1 Mb	605.8 Mb	21.9 kb	Sanger+Illumina	Varshney et al., 2012
Cicer arietinum var. kabuli	Fabaceae	738.1 Mb	544.7 Mb	23.5 kb	Sanger+Illumina	Varshney et al., 2013
Medicago sativa	Fabaceae	400–500 Mb	297.1 Mb	1.3 Mb (scaffold)	Sanger+454+Optical mapping	Young et al., 2011
Medicago truncatula A17	Fabaceae	465 Mb	430 Mb	204 kb	PacBio+Illumina+Optical mapping	Pecrix et al., 2018
Spinacia oleracea Sp75	Amaranthaceae	1 Gb	870 Mb	16.6 kb	Illumina	Xu et al., 2017
Beta vulgaris ssp. *vulgaris* KWS2320	Amaranthaceae	714–758 Mb	567 Mb	75.7 kb	Sanger+454+Illumina	Dohm et al., 2014
Lactuca sativa cv. Salinas	Asteraceae	2.7 Gb	2.38 Gb	36 kb	Illumina+Chicago	Reyes-Chin-Wo et al., 2017
Daucus carota subsp. *sativus* DH1	Apiaceae	473 Mb	421.5 Mb	31.2 kb	Sanger+Illumina	Iorizzo et al., 2016
Coriandrum sativum SJ01	Apiaceae	2.13 Gb	2.11 Gb	604.1 kb	PacBio+Illumina+10X Genomics+Hi-C	Song et al., 2019
Nelumbo nucifera China Antique	Nelumbonaceae	929 Mb	804 Mb	38.8 kb	454+Illumina	Ming et al., 2013
Nelumbo nucifera	Nelumbonaceae	879 Mb	792 Mb	39.3 kb	Illumina	Wang et al., 2013
Zizania latifolia HSD2	Poaceae	594 Mb	604.1 Mb	13.1 kb	Illumina	Guo et al., 2015
Asparagus officinalis DH00/086	Asparagaceae	1.3 Gb	1.16 Gb	21.2 kb	PacBio+Illumina+Optical mapping	Harkess et al., 2017
Moringa oleifera Lam.	Moringaceae	315 Mb	287.4 Mb	123 kb	Illumina	Tian et al., 2015

fraction of genes. The asymmetrical gene retention, after WGD, offers important opportunities to further an understanding of the genetic basis of phytochemical and morphological variations (Liu et al., 2014; Wang et al., 2011). Cucurbit vegetables have also undergone a cucurbit-common tetraploidization (CCT), occurring c. 90–102 MYA, shortly after the core eudicot-common WGD event. This CCT was proposed to be an allotetraploidization of two diploid progenitor species (Huang et al., 2009; Sun et al., 2017; Wang et al., 2018).

Reference genomes have also enriched our understanding of chromosome evolution of vegetable crops. Comparative analyses of cucurbit species indicated that the genomes of wax gourd and melon are more conserved than those of other cucurbit vegetables, with the wax gourd genome representing the most ancestral karyotype. Further analyses suggested that all chromosomes, of extant cucurbit crops, were likely derived from 15 ancestral cucurbit chromosomes (Wu et al., 2017; Xie et al., 2019). In the *Cucumis* genus, five of the seven cucumber chromosomes arose from fusions of ten ancestral chromosomes (Huang et al., 2009; Yang et al., 2012). Among cucumber accessions, seven large inversions were only found in a proportion of wild accessions, providing a guide for properly selecting parental lines to construct segregating populations between wild and cultivated cucumbers (Li et al., 2022). These advances in reference genomes construction provide valuable resources and powerful platforms for vegetable breeding and biological studies.

Population genomics

Construction of reference genomes has enabled the resequencing of large diversity panels, empowering the characterization of genome-wide variation for several key vegetables, such as *Brassica* species, cucumber, lettuce, melon, pepper, spinach, tomato, watermelon, and wax gourd. These resources not only expand our knowledge of genetic diversity, but also provide additional insights into the genetic basis of domestication and determination of agronomic traits in these vegetable crops.

Cucurbitaceae crops have played a leading role in vegetable population genomics. In 2013, 115 accessions of cucumber, selected to represent the global variation of 3,341 lines, were used to generate a genomic variation map, which was the first vegetable resequenced at the whole-genome level (Qi et al., 2013). Global variation patterns in melon (Zhao et al., 2019a), watermelon (Guo et al., 2019b) and wax gourd (Xie et al., 2019) were subsequently explored by resequencing 1,175, 414 and 146 representative accessions, respectively. A total of 3.6 million variants were identified for cucumber (Qi et al., 2013; Zhang et al., 2015), 6.6 million for melon, 19.7 million for watermelon, and 18.4 million for

wax gourd. The greater numbers of variants for watermelon and wax gourd, compared with those in cucumber and melon, were likely derived from their wild accessions, especially for watermelon that contained 69 other species in the *Citrullus* genus.

Phylogenetic and population structure inference revealed that these four studied cucurbit crops underwent independent domestications, in Africa or India, and diversifying breeding selection across different areas across the globe (Guo et al., 2013; Guo et al., 2019b; Qi et al., 2013; Xie et al., 2019; Zhao et al., 2019a). Cucumber and wax gourd originated and were domesticated in India, and then spread to East Asia, Europe, North America, etc. At least three independent domestication events were detected in melon: one in Africa, and two in India, resulting in two cultivated subspecies, *melo* and *agrestis*. For watermelon, *Citrullus lanatus* and *C. mucosospermus* shared a common ancestor, and were domesticated for different purposes in Africa: such as fresh market and seed consumption.

During the domestication of these vegetable crops, some agronomic traits, such as expanded fruit size and loss of fruit bitterness, were convergently selected. One typical example is the *Bt* gene, encoding a basic helix-loop-helix (bHLH) transcription factor that regulates fruit bitterness, which displays a significant domestication signal in cucumber, melon and watermelon. These cucurbit crops underwent further extensive breeding selection, after their initial domestication, resulting in edible fruits with a variety of phenotypes. Numerous genomic regions/loci were identified to be associated with these domestication and diversification events; e.g., 112 regions containing 2,054 genes were identified to be within domestication sweeps in cucumber.

In the family Solanaceae, the genetic diversity and domestication of tomato and pepper have been studied by genome-wide resequencing. More than 600 tomato accessions were resequenced, and a total of 26.3 million single nucleotide polymorphisms (SNPs) were identified (Aflitos et al., 2014; Lin et al., 2014; Zhu et al., 2018). Based on the genetic variation of 360 tomato accessions (Lin et al., 2014), the red-fruited accessions were assigned into three groups: *S. pimpinellifolium* accessions (PIM), *S. lycopersicum* var. *cerasiforme* accessions (CER) and big-fruited *S. lycopersicum* accessions (BIG). PIM was proposed to be the progenitor of all cultivated tomatoes, and CER is evolutionarily intermediate between PIM and BIG. In the light of these results, Lin et al. (2014) proposed a two-step evolution for fruit mass, comprising two independent sets of quantitative trait loci (QTL) involved in domestication and improvement of modern cultivated tomatoes with big fruits. Moreover, in some modern processing tomato varieties, several large genomic fragments, on chromosomes 1, 6 and 9, were shown to be introgressed from wild species that contain disease or pest resistance genes, such as *Tm2^a*, *Mi-1* and *Ty-1*, possibly

leading to severe linkage drag. By sequencing an additional 66 tomato accessions, 239 significant associations for yield-related traits were identified (Ye et al., 2021).

Regarding pepper, over 400 accessions were resequenced, followed by construction of a pan-genome (Ou et al., 2018; Qin et al., 2014), which provided critical insights into genetic footprints of artificial selection. By comparing 18 cultivated and two semi-wild peppers, a total of 115 genomic regions were identified to be possibly affected by domestication, the 511 genes located within these regions may be responsible for the morphological and physiological differences between cultivated and wild peppers (Ou et al., 2018).

Brassica vegetables display highly diverse phenotypes, such as the leafy heads of Chinese cabbage (*Brassica rapa*) and cabbage (*B. oleracea*), and the enlarged roots of turnip (*B. rapa*) and kohlrabi (*B. oleracea*). All *Brassica* genomes have undergone a recent whole-genome triplication (WGT), which occurred some 9–15 MYA (Cheng et al., 2014). To explore the impact of WGT and the genetic basis of phenotypic variation, 199 *B. rapa* and 119 *B. oleracea* accessions were resequenced (Cheng et al., 2016), and their analysis suggested that this WGT event contributed largely to the diversification of leafy heads and enlarged roots, through convergent domestication. Among the subgenomes within *B. rapa* and *B. oleracea*, four loci, underlying leafy heads or enlarged roots, showed signals of parallel selection, whereas some loci were shared by the two species.

Valuable insights into the adaption of *Brassica* to different climates and environments were also provided at the population genomic level. By analyzing the genetic variations of 194 geographically diverse accessions from three *B. rapa* ecotypes (spring, summer and autumn), 23 loci under intensive selection putatively responsible for adapting to agro-environment were identified, and some underlying genes were dissected (Su et al., 2018). In addition, rapid genome-wide evolutionary shifts in allele frequencies were found to respond to a fluctuation in climate in *B. rapa* natural populations (Franks et al., 2016).

Lettuce is an important vegetable crop belonging to the *Lactuca* genus, in which 20 wild species have long been used in breeding programs. Analysis of RNA-seq data derived from 240 accessions, including 31 wild lettuces, revealed a single domestication event of cultivated lettuce (Zhang et al., 2017). To further elucidate the domestication history of lettuce and the genetic variants underlying favorable traits, 445 *Lactuca* accessions, covering 12 wild and one cultivated species, were resequenced, which led to the identification of more than 178 million variants. Phylogenetic analyses also resolved the taxonomic controversy among lettuce wild species and facilitated germplasm collection and utilization. Population demography implied that lettuce was first domesticated, as a seed crop, near the Caucasus, and was then developed as a leaf vegetable after introduction into South-ern Europe. Moreover, several genetic loci related to domestication and agronomic traits, such as disease resistance and flavonoid biosynthesis, were identified (Wei et al., 2021).

Spinach has a much smaller collection of genetic germplasms, compared with the other major vegetable crops. To explore the population structure, domestication and evolution of spinach, transcriptome sequencing of 120 cultivated and wild accessions was conducted (Xu et al., 2017). Based on the identified variants, the wild relative *Spinacia turkestanica* was considered to be the direct progenitor of cultivated spinach, and 93 domestication sweeps were identified, which were associated with important agronomic traits, such as flowering and leaf numbers. A recent study reported a genomic variation map, constructed by resequencing 305 cultivated and wild spinach accessions, which enhanced the understanding of population differentiation and genetic diversity of spinach. Genome-wide association signals were identified for 20 agronomic traits, providing rich resources for genome-guided breeding in spinach (Cai et al., 2021b).

Ample studies have indicated that a single reference genome, on which most existing population genomic studies of vegetable crops were based, cannot represent the full spectrum of genetic diversity within a given species (Liu and Tian, 2020). To overcome this limitation, multiple reference genomes, and pan-genomes, have been constructed for several vegetables. For tomato, genomes of two *S. pennellii* accessions (LA716 and LYC1722) (Bolger et al., 2014; Schmidt et al., 2017), *S. chilense* LA3111 (Stam et al., 2019) and *S. pimpinellifolium* (Razali et al., 2018; Takei et al., 2021; Wang et al., 2020b) were *de novo* assembled, and a pan-genome of 715 accessions was constructed by assembling the resequencing short reads, facilitating the identification of a rare non-reference allele that regulates tomato fruit flavor (Gao et al., 2019). The genomes of one wild and three cultivated cucumber accessions have been released (Huang et al., 2009; Li et al., 2019b; Li et al., 2011; Qi et al., 2013; Woycicki et al., 2011; Yang et al., 2012), followed by the development of a pan-genome, revealing a surprising amount of gene content absent in the reference genome (Li et al., 2022). The construction of pan-genomes for Chinese cabbage (Cai et al., 2021a) and *Raphanus* genus (Zhang et al., 2021e) also provided additional insights into the genome alteration during their domestication and breeding processes.

Most vegetable crops population genomics analyses were based on SNPs and small insertions/deletions (InDels). However, structural variants (SVs) are pervasive in plant genomes and are associated with several agronomically important traits (Alonge et al., 2020), which also play critical roles in crop domestication. The absence of SVs in population genomics hampers dissection of both the genetic basis of agronomic traits and domestication. The rapid advances in long-read sequencing technologies, along with improved

algorithms for SV detection, facilitate the emergence of graph-based pan-genomes, which embed non-reference sequences, representing highly divergent genomic regions, into a graph-like structure. Applications in cucumber (Li et al., 2022), Chinese cabbage (Cai et al., 2021a) and tomato (Zhou et al., 2022) have demonstrated its power on population-level genotyping of SVs and the importance of integrating SVs into association studies in these important vegetables. Construction of a tomato graph-based pan-genome, integrating genetic variants from 838 tomato accessions, yielded a 24% increase in the estimated heritability for 20,323 gene-expression and metabolite traits, demonstrating its power in quantitative genetics and genetic improvement in tomato (Zhou et al., 2022). Equipped with sequence diversity and marker-trait associations, vegetable breeders have entered a new age of unprecedented scales of omics data, offering ever-increasing opportunities to develop better varieties.

Multi-omics

In several vegetable crops, high-throughput sequencing technologies have enabled the generation of genetic variation maps across numerous accessions (variome), and large-scale gene expression atlases across different tissues, environmental conditions, and developmental stages (transcriptome). Metabolites of vegetable crops not only participate in plant growth and development but also serve as important sources of human nutrition and medicine (Zhu et al., 2018). The advancement in metabolite detection technologies (e.g., liquid chromatography-mass spectrometry (LC-MS) and gas chromatography-mass spectrometry (GC-MS)), and the corresponding mining tools, have also generated tremendous metabolic datasets (metabolome) at an unprecedented rate. Integrating and analyzing these multi-omics datasets are increasing at an exponential rate and have brought biological studies and breeding into the big data era, facilitating the identification of functional genes and characterization of given pathways in vegetable crops.

Among the vegetables, such multi-omics data have contributed mostly to tomato biological research and genetic breeding. Initial studies integrated metabolome and transcriptome data with a small number of genetic variants of a few accessions, such as different mutants and introgression lines, suggesting a correlation between the specific genes and metabolites (Alseekh et al., 2015; Osorio et al., 2011). The acquired metabolite data from 300 tomato accessions were analyzed, in combination with more than 10,000 SNPs and gene expression data, leading to the identification of 79 significant association signals for more than 30 metabolites (Bauchet et al., 2017). In addition, using some 400 tomato accessions, flavor-associated metabolites were quantified, together with the rated multiple sensory attributes from a consumer panel, which identified 28 metabolites as the largest contributors to flavor and consumer liking (Tieman et al., 2017). Based on these data, genome-wide association studies (GWAS), using genetic variants from whole-genome resequencing, identified genetic loci that affect most of the 28 target flavor metabolites. Of note is a population of between 399 and 610 diverse tomato accessions that was used to generate a large dataset, spanning variome, transcriptome, and metabolome (Zhu et al., 2018). Analysis of this dataset identified a total of 3,526 mGWAS signals, 2,566 *cis*-expression quantitative trait loci (eQTL), 93,587 *trans*-eQTL, and 232,934 expression-metabolite correlations. Such a multi-omics view of tomato metabolites provides insight into how breeding has altered the tomato metabolome, offering a solid foundation for further fruit quality improvement.

Through exploring genetic variants, gene expression profiles and accumulation patterns of cucurbitacin C in cucumber, an operon-like gene module, comprised of nine genes responsible for the biosynthesis of cucurbitacin C, and two regulator genes, *Bl* and *Bt*, were identified (Shang et al., 2014). *Bl* and *Bt* confer the bitterness trait by regulating the biosynthesis of cucurbitacin C in leaves and fruits, respectively. Furthermore, integration of comparative genomics data uncovered the biosynthetic gene sets and regulators for distinct bitterness compounds in melon (cucurbitacin B) and watermelon (cucurbitacin E) (Zhou et al., 2016).

Multi-omics-based methodologies have been and will continue to be applied to vegetable crops for biological research and breeding; e.g., watermelon (Umer et al., 2020). It is also important to stress that omics data sets are not limited to variome, transcriptome, and metabolome. With the rapid advance in epigenetics, proteomics and phenomics, more layers of large-scale datasets are being rapidly generated. To comprehensively analyze these multi-omics data, algorithms, tools and statistical models, such as those based on machine learning and deep learning (Liu et al., 2020), will need to be further improved.

Trait gene discovery

To date, several obstacles to vegetable production still need to be dismantled, including low agricultural productivity, reduced flavor and nutritional quality. Recent advancement of vegetable genomics has facilitated the identification of genes responsible for a wide range of valuable agronomic traits, such as yield, improved organ and product quality, as well as resistance to biological and abiotic stresses (Table 2).

Yield

A major aim of current vegetable breeding programs is to develop high-yielding varieties, and crop yield can be largely

impacted by plant architecture (Liu et al., 2021). In tomato, a strategy of trait-stacking of mutations in *SlER*, *SELF PRUNING 5G* (*SP5G*) and *SELF PRUNING* (*SP*) was employed to restructure vine-like tomato plants to give compact (Table 2), early yielding plants suitable for urban agriculture (Kwon et al., 2020). *SP* encodes a member of the CENTRORADIALIS, TERMINAL FLOWER1/SELF PRUNING (CETS) protein family and inhibits flowering by antagonizing the activity of another member of the protein family, SINGLE FLOWER TRUSS (SFT). They interact to regulate plant architecture and yield (Krieger et al., 2010; Park et al., 2014). *SP5G* is an important factor for photoperiod response, and its knockout elicits a quick burst of flower production, leading to early fruit yield (Soyk et al., 2017). In cucumber, the knockdown of *CsTFL1*, a key gene that regulates the indeterminate growth habit, resulted in determinate growth and formation of terminal flowers. In addition, *CsTFL1* competes with *CsFT* for interaction with *CsNOT2a-CsFDP* to inhibit determinate growth and terminal flower formation (Wen et al., 2019). *CsBRC1*, a member of the TEOSINTE BRANCHED1/CYCLOIDEA/PCF (TCP) family of genes, also suppresses the outgrowth of lateral buds, and its knockdown can reverse this inhibition (Shen et al., 2019).

The SALT network (*SAX*, *AP1*/*CAL*, *LFY*, and *TFL1* genes) determines cauliflower floral structure, which is critical for crop yield. Cauliflowers present an unusual organ arrangement with a multitude of spirals nested over a wide range of scales. A recent study showed that the steady state of the SALT network corresponds to the gene expression pattern in normal inflorescences meristem (Azpeitia et al., 2021).

The sex development of flowers determines fruit setting in cucurbit crops, which indirectly affects yield. In cucumber, four key genes (*CsACS2*, *CsACS11*, *CsACO2* and *ACS1G*), all of which encode important ethylene synthesis enzymes, control carpel development (Boualem et al., 2015) and female flower formation (Zhang et al., 2021b). In melon, the transcription factor gene *CmWIP1* facilitates the male flower formation in monoecious species by repressing *CmACS7* and carpel development (Martin et al., 2009).

The size, weight, and shape of fruits, during their development, are also important factors affecting crop yield. To date, only a few genetic loci for these traits have been successfully cloned. In tomato, mutations in *CLV3* result in an inability to signal inhibition of stem cell production, which has led to an increased fruit size during domestication (Xu et al., 2015). Studies on the genetic loci of *locule number* (*lc*), *fasciated* (*fas*), *Fasciated and branched* (*FAB*), and *Fasciated inflorescence* (*FIN*) revealed that fruit enlargement was due to the increase of ventricular number (Muños et al., 2011; Xu et al., 2015). In cucumber, a specific E3 ubiquitin ligase, SF1, can ubiquitinate and degrade both itself and the

substrate CsACS2 to finely control ethylene synthesis for regulating fruit elongation (Xin et al., 2019). Epigenetic regulation also plays a role in controlling fruit size. For example, *Histone Deacetylase Complex1* (*HDC1*) controls cucumber fruit cell proliferation through directly targeting of cytokinin (CK) and polyamine (PA) biosynthesis and metabolism (Zhang et al., 2020b). A fruit elongation suppressor gene, *CsFUL1*, encoding a MADS-box transcription factor, regulates the elongation and development of cucumber fruit by inhibiting expression of the cell expansion regulator, SUPERMAN, and the polar transport of auxin (Zhao et al., 2019b).

In addition, some vegetable crops have unique growth habits, which could be utilized for yield increase. For example, in Solanaceae crops, mutated *Pad-1*, an aminotransferase gene involved in auxin homeostasis, allows accumulation of auxin in the ovary, which then promotes parthenocarpy (Matsuo et al., 2020). A recent study showed that stigma-active oxygen species can regulate self-incompatibility in Chinese cabbage. Self-pollination stimulates stigma papillary cells to create reactive oxygen species, which inhibits expression of respiratory burst oxidase homologs and interferes with self-incompatibility (Zhang et al., 2021c). A reasonable exploitation of parthenocarpy and self-incompatibility has the potential to improve yield in these crops.

Quality

A common goal of vegetable breeding is to enhance their quality while also maintaining high yield. The quality of vegetable crops is the most important determinant of market competitiveness, which is mainly represented by flavor, color, and the content of aromatic and bioactive substances. However, during the domestication of most vegetable crops, the improvement of yield has usually been associated with the loss of genetic diversity and decline in flavor quality. Recently, high-quality reference genomes and variomes combined with GWAS analyses have greatly expedited the identification and utilization of genes underlying important quality traits (Table 2).

The flavor of vegetables is largely dependent on their metabolites. Sugar content affects tomato fruit quality. *Brix9-2-5* is a key QTL that controls the amount of soluble solid in tomato fruits (Fridman et al., 2004). This gene encodes an apoplast sucrose invertase, Lin5, which breaks down sucrose into fructose and glucose. *SlSWEET7a* and *SlSWEET14* are located in the plasma membrane of tomato plants and mediate in the transport of fructose, glucose, and sucrose. Silencing of *SlSWEET7a* or *SlSWEET14* led to taller plants, bigger fruits and more sugar in mature fruits (Zhang et al., 2021d). Sugar content of ripe tomato fruits is also impacted by the number of plastids in green fruits (Nguyen et

Table 2   Important genes underlying agronomic traits of vegetable crops

Species	Trait	Locus name	Gene ID/GenBank accession	Annotation	Function	Reference
Tomato	Flowering time	*SP*	*Solyc06g074350*	A protein SELF-PRUNING	Inhibition of flowering signal	Park et al., 2014
		SFT	*Solyc03g063100*	A protein single flower truss	Translation of environmental cues and endogenous signals to initiate flowering	Krieger et al., 2010
		SP5G	*Solyc05g053850*	A protein SELF PRUNING 5G	Response to photoperiod	Soyk et al., 2017
	Fruit size	*Fw3.2*	*Solyc03g114940*	A cytochrome P450 protein SIK-LUH of the CYP78A subfamily	Enlargement of fruits by increasing the number of cells in the peel and septal tissue	Chakrabarti et al., 2013
		lc	*Solyc02g082670*	A homeodomain protein that regulates stem cell fate	Increase of ventricular number	Muños et al., 2011
		fas	*Solyc11g071810*	A YABBY-like transcription factor	Increase of ventricular number	Lippman and Tanksley, 2001
		FAB	*Solyc04g081590*	A receptor kinase CLV1 of CLV3	Increase of ventricular number	Xu et al., 2015
		FIN	*Solyc11g064850*	An arabinose transferase	Increase of ventricular number	Xu et al., 2015
	Fruit ripening	*NR*	*Solyc09g075440*	An ethylene receptor LE-ETR3	The ethylene signal transduction	Wilkinson et al., 1995
		GR	*Solyc01g104340*	An ethylene receptor interaction protein RTE1	The ethylene signal transduction	Barry and Giovannoni, 2006
		YFT1	*Solyc09g007870*	An important regulator of ethylene signaling pathway EIN2	The ethylene signal transduction	Gao et al., 2016
		ACS2	*Solyc01g095080*	A 1-aminocyclopropane-1-carboxy-late synthase	The ethylene signal transduction	Klee and Giovannoni, 2011
		ACS4	*Solyc05g050010*	A 1-aminocyclopropane-1-carboxy-late synthase	The ethylene signal transduction	Klee and Giovannoni, 2011
		ACO	*Solyc07g049530*	A 1-aminocyclopropane-1-carboxy-late oxidase	The ethylene signal transduction	Klee and Giovannoni, 2011
		EIL1	*Solyc06g073720*	An activate ethylene-responsive transcription factor	The ethylene signal transduction	Klee and Giovannoni, 2011
		rin	*Solyc05g012020*	A MADS-box transcription factor	The ethylene signal transduction	Vrebalov et al., 2002
		nor	*Solyc10g006880*	A NAC transcription factor	The ethylene signal transduction	Martel et al., 2011
		Cnr	*Solyc02g077920*	An SBP type transcription factor	The ethylene signal transduction	Manning et al., 2006
		SlERF.F12	Solyc02g077840	An ethylene response factor	Repress of transcription of ripening-related genes	Deng et al., 2022a
		SlLHP1b	*Solyc10g024470*	A tomato Polycomb Repressive Complex 1 (PRC1)-like protein	Inhibition of fruit ripening	Liang et al., 2020
	Fruit quality	*Brix9-2-5*	*Solyc09g010080*	An apoplast sucrose invertase Lin5	Control of the soluble solid content of tomato fruit	Fridman et al., 2004
		SlSWEET7a	*Solyc08g082770*	A plasma membrane-localized protein	Transport of fructose, glucose, and sucrose in tomato	Zhang et al., 2021d
		SlSWEET14	*Solyc03g097560*	A plasma membrane-localized protein	Transport of fructose, glucose, and sucrose in tomato	Zhang et al., 2021d
		SlALMT9	*Solyc06g072910 Solyc06g072920*	A transmembrane protein	Transport of malate in tomato	Ye et al., 2017
		GLK2	*Solyc10g008160*	A MYB transcription factor	Development of chloroplasts and reduction of pigment and sugar content in mature fruits	Powell et al., 2012
		UG	*Solyc01g100510*	A KNOX transcription factor	Development of chloroplasts and reduction of pigment and sugar content in mature fruits	Nadakuduti et al., 2014
		SlaN2-like	*Solyc10g086290*	A functional anthocyanin activator	Activation of anthocyanin biosynthesis	Sun et al., 2020a
		SlWRKY35	*Solyc02g021680*	A WRKY transcription factor	Positive regulation of carotenoid biosynthesis	Yuan et al., 2022
		WRKY32	*Solyc07g005650*	A WRKY transcription factor	Reduction of carotenoid accumulation	Zhao et al., 2021
		FLORAL4	*Solyc04g063350*	A 3-methyl-2-oxobutanoate dehydrogenase	Accumulation of phenylalanine-derived volatiles in tomato fruits	Tikunov et al., 2020
		Sl-LIP8	*Solyc09g091050*	A member of a novel class III lipase family	Synthesis of multiple short-chain fatty acid-derived volatile organic compounds in tomato fruits	Li et al., 2020b
		TomloxC	*Solyc01g006540*	A 13-lipoxygenase	Catalyzation of C5 volatile compounds in tomato fruits	Shen et al., 2014
		FIS1	*Solyc10g007570*	A Gibberellin2-oxidase	Regulation of fruit firmness	Li et al., 2020a

(*Continued*)

Species	Trait	Locus name	Gene ID/GenBank accession	Annotation	Function	Reference
Tomato	Disease resistance	*Ph-2*	*Solyc10g085460*	A CC-NB-ARC type resistance gene	Resistance to late blight disease	Zhi et al., 2020
		Ph-3	*Solyc09g092280, Solyc09g092290, Solyc09g092300* and *Solyc09g092310*	A CC-NB-ARC type resistance gene	Resistance to late blight disease	Zhang et al., 2014
		I	*Solyc11g011180*	A leucine-rich repeat receptor-like gene (*LRR-RLP*)	Resistance to fusarium wilt	Catanzariti et al., 2017
		I-3	*Solyc07g055640*	An S-receptor-like kinase (*SRLK*) gene	Resistance to fusarium wilt	Catanzariti et al., 2015
		I-7	*Solyc08g077740*	A leucine-rich repeat receptor-like gene (*LRR-RLP*)	Resistance to fusarium wilt	Gonzalez-Cendales et al., 2016
		Ve1	*Solyc09g005090*	A leucine-rich repeat receptor-like gene (*LRR-RLP*)	Resistance to verticillium wilt	de Jonge et al., 2012
		Ve2	*Solyc09g005080*	A leucine-rich repeat receptor-like gene (*LRR-RLP*)	Resistance to verticillium wilt	Nazar et al., 2018
		Ty-1/Ty-3	*Solyc06g051170, Solyc06g051180,* and *Solyc06g051190*	An RNA-dependent RNA polymerase	Resistance to *Tomato yellow leaf curl virus*	Verlaan et al., 2013
		Ty-2	*Solyc11g069620*	An NBS-LRR type resistance gene	Resistance to *Tomato yellow leaf curl virus*	Yamaguchi et al., 2018
		Ty-5	*Solyc04g009810*	A messenger RNA surveillance factor Pelota	Resistance to *Tomato yellow leaf curl virus*	Lapidot et al., 2015
		CslG2	*Solyc07g043390*	A cellulose synthase-like protein	Resistance to *Tomato yellow leaf curl virus*	Choe et al., 2021
		MYC2	*Solyc08g076930*	A core transcription factor of the jasmonic acid signaling pathway	Response to wounding and pathogen infection	Du et al., 2017
Pepper	Fruit quality	*MYB31*	LOC107878306	A MYB31 transcription factor	Capsaicin synthesis	Zhu et al., 2019
		ZEP	MW713794.1	A zeaxanthin epoxidase	Pepper fruit color	Lee et al., 2021
		PSY1	LOC107868281	A phytoene synthase	Pepper fruit color	Kim et al., 2010
		PSY2	LOC107859651	A phytoene synthase	Pepper fruit color	Jang et al., 2020
		CCS	LOC107875664	A capsanthin-capsorubin synthase	Pepper fruit color	Lefebvre et al., 1998
		PRR2	*Capana01g000809*	A pseudo-response regulator	Pepper fruit color	Jeong et al., 2020
		CcLOL1	*CA00g77830*	A zinc-finger transcription factor	Immature pepper fruit color	Borovsky et al., 2019
	Disease resistance	*CaMlo1*	AAX31277	A *Mildew Locus O* (*MLO*)-like gene	Resistance to powdery mildew	Zheng et al., 2013
		CaMlo2	JN896629	A *Mildew Locus O* (*MLO*)-like gene	Resistance to powdery mildew	Zheng et al., 2013
		CaRGA2	Gu116570	An NBS-LRR type resistance gene	Resistance to *Phytophthora* root rot	Zhang et al., 2013
		CaDMR1	NA	A homoserine kinase gene	Resistance to *Phytophthora* root rot	Rehrig et al., 2014
		CaPhyto	*Capana05g000764* and *Capana05g000769*	A serine/threonine-protein kinase gene/A CC-NB-ARC type resistance gene	Resistance to *Phytophthora* root rot	Wang et al., 2016
		CaHDZ27	NA	A homeodomain-leucine zipper class I (HD-Zip I) transcription factor gene	Resistance to bacterial wilt	Mou et al., 2017
		CA02g19570	*CA02g19570*	A TIR-NB-LRR type resistance gene	Resistance to *Cucumber mosaic virus*	Guo et al., 2017
		CaWRKYb	AY743433	A WRKY transcription factor gene	Resistance to *Tobacco mosaic virus*	Lim et al., 2011
		Pvr4	*CaNBARC322*	A CC-NB-ARC type resistance gene	Resistance to *Potyviruses*	Kim et al., 2017b
		Tsw	*CcNBARC575*	A CC-NB-ARC type resistance gene	Resistance to *Tomato spotted wilt virus*	Kim et al., 2017b
		CaRKNR	ACI43068	An NBS-LRR type resistance gene	Resistance to root-knot nematodes	Mao et al., 2015
Eggplants	Parthenocarpy	*Pad-1*	LC500834	An aminotransferase	Auxin homeostasis	Matsuo et al., 2020

(*Continued*)

Species	Trait	Locus name	Gene ID/GenBank accession	Annotation	Function	Reference
Cucumber	Sex determination	CsACS11	Csa2G353460	A 1-aminocyclopropane-1-carboxylic acid synthetase	Carpel development	Boualem et al., 2015
		CsACS2	Csa1G580750	A 1-aminocyclopropane-1-carboxylic acid oxidase	Carpel development	Boualem et al., 2015
		ACS1G	Csa6G496970	A 1-aminocyclopropane-1-carboxylic acid synthetase	Carpel development	Zhang et al., 2021b
	Fruit elongation	SF1	Csa2G174140	A specific E3 ubiquitin ligase	Cell division and fruit elongation	Xin et al., 2019
		HDC1	Csa2G337260	A subunit of the conserved histone deacetylase complex	Coordinating phytohormones to control the rapid division of fruit cells	Zhang et al., 2020b
		CsFUL1	Csa1G039910	A MADS-box transcription factor	Elongation and development of fruits	Zhao et al., 2019b
	Fruit quality	Bi	Csa6G088690	A cucurbitadienol synthase	Cucurbitacin C synthesis	Shang et al., 2014
		Bl	Csa5G156220	A putative basic helix-loop-helix (bHLH) transcription factor	Cucurbitacin C synthesis	Shang et al., 2014
		Bt	Csa5G157230	A bHLH36 transcription factor	Cucurbitacin C synthesis	Shang et al., 2014
		Cs160	Csa6G088160	A C25 hydroxylase	Cucurbitacin C synthesis	Shang et al., 2014
		Cs170	Csa6G088170	A cytochrome P450 enzyme	Cucurbitacin C synthesis	Shang et al., 2014
		Cs180	Csa6G088180	A cytochrome P450 enzyme	Cucurbitacin C synthesis	Shang et al., 2014
		Cs710	Csa6G088710	A cytochrome P450 enzyme	Cucurbitacin C synthesis	Shang et al., 2014
		Cs490	Csa3G698490	A cytochrome P450 enzyme	Cucurbitacin C synthesis	Shang et al., 2014
		Cs540	Csa3G903540	A C19 hydroxylase	Cucurbitacin C synthesis	Shang et al., 2014
		Cs550	Csa3G903550	A cytochrome P450 enzyme	Cucurbitacin C synthesis	Shang et al., 2014
		Cs890	Csa1G044890	A C11 carboxylase+C20 hydroxylase	Cucurbitacin C synthesis	Shang et al., 2014
		CsACT	Csa6G088700	An acyltransferase (ACT)	Cucurbitacin C synthesis	Shang et al., 2014
	Plant architecture	CsTFL1	Csa6G452100	A homolog of the *Arabidopsis TFL1*	Regulation of the unlimited growth in cucumber	Wen et al., 2019
		CsBRC1	Csa1G020890	A TCP transcription factor	Inhibition of local shoot branching	Shen et al., 2019
		CsTEN	Csa5G644520	A conserved TCP transcription factor	Tendril development	Wang et al., 2015
	Disease resistance	CsMLO1	Csa5G623470	A *Mildew Locus O* (*MLO*)-like gene	Resistance to powdery mildew	Nie et al., 2015a; Nie et al., 2015b
		Csa5G622830	Csa5G622830	A GATA transcription factor	Resistance to powdery mildew	Zhang et al., 2018a
		CsGy5G015660	CsGy5G015660	A putative leucine-rich repeat receptor-like serine/threonine-protein kinase	Resistance to powdery mildew	Zhang et al., 2021a
		CsSGR	Csa5G156180	A magnesium dechelatase	Resistance to downy mildew	Wang et al., 2019
		CsLRK10L2	Csa4G410850	A receptor-like kinase	Resistance to downy mildew	Berg et al., 2020
		cca-3	Csa6G375730	A CC-NB-ARC type resistance gene	Resistance to target leaf spot	Wen et al., 2015
		zym	Csa6G152960	A vacuolar protein sorting-associated protein 4-like (VPS4-like) protein	Resistance to *Zucchini yellow mosaic virus*	Amano et al., 2013
Watermelon	Fruit quality	ClAGA2	Cla97C04G070460	An alkaline α-galactosidase	Rapid hydrolyzation of rfos	Ren et al., 2021
		ClVST1	Cla97C02G031010	A sugar transporter protein	Unloading of sugar in the phloem of fruits through changes in membrane location	Ren et al., 2020b
		ClSWEET3	Cla97C01G000640	A sugar transporter protein	Transport of plasma membrane sugars	Ren et al., 2021
		ClTST2	Cla97C02G036390	A vacuolar membrane sugar transporter	Transport of plasma membrane sugars	Ren et al., 2021
	Disease resistance	Cla001017	Cla001017	A CC-NB-ARC type resistance gene	Resistance to anthracnose	Jang et al., 2019
		Cla001017	Cla001017	A CC-NB-ARC type resistance gene	Resistance to gummy stem blight	Ren et al., 2020a
		Cla001019	Cla001019	A pathogenesis-related gene	Resistance to gummy stem blight	Ren et al., 2020a

(*Continued*)

Species	Trait	Locus name	Gene ID/GenBank accession	Annotation	Function	Reference
Melon	Sex determination	*CmACS11*	*MELO3C010779*	A 1-aminocyclopropane-1-carboxylic acid synthetase	Carpel development	Boualem et al., 2008
		CmACS7	*MELO3C015444*	A 1-aminocyclopropane-1-carboxylic acid oxidase	Carpel development	Boualem et al., 2008
		CmWIP1	GQ870274	A WIP1 transcription factor	Carpel development	Martin et al., 2009
	Fruit quality	*CmOr*	*MELO3C005449*	A DnaJ cysteine-rich domain-containing protein	Regulation of plastid development	Galpaz et al., 2018
		CmPPR1	*Melo3C003069*	A member of the pentaphosphate peptide protein	Involved in the RNA processing and the accumulation of carotenoids and chlorophyll pigments in plastid	Galpaz et al., 2018
		CmAAT1	*MELO3C024771*	An alcohol acyl-transferase	Production of melon aromatic gas	Galpaz et al., 2018
	Disease resistance	*CmPMR1*	*MELO3C002441*	A natriuretic peptide receptor (NPR) like protein	Resistance to powdery mildew in leaves	Cui et al., 2022
		CmPMRrs	*MELO3C012438*	A *Mildew Locus O* (*MLO*)-like gene	Resistance to powdery mildew in stems	Cui et al., 2022
		MePhyto	*MELO3C002430*	A wall-associated receptor kinase gene	Resistance to *Phytophthora* root rot	Wang et al., 2020a
		Fom-2	LOC103498352	An NBS-LRR type resistance gene	Resistance to fusarium wilt	Oumouloud et al., 2012
		Fom-1	LOC103498649	A TIR-NB-LRR type resistance gene	Resistance to fusarium wilt	Brotman et al., 2013
		Prv	LOC103498647	A TIR-NB-LRR type resistance gene	Resistance to *Papaya ringspot virus*	Brotman et al., 2013
		cmv1	*MELO3C004831* and *MELO3C004827*	A vacuolar protein sorting-associated protein 4-like (VPS4-like) gene	Resistance to *Cucumber mosaic virus*	Giner et al., 2017
		Vat	*MELOC004317*	A CC-NB-ARC type resistance gene	Resistance to aphids and whiteflies	Boissot et al., 2010
Chinese Cabbage	Self-inflicted incompatibility	*BrRbohs*	*Bra037520, Bra020724, Bra027764, Bra033151, Bra009266, Bra011911, Bra031658, Bra029194, Bra013862, Bra031070, Bra025721, Bra019191* and *Bra019189*	Homologs of respiratory burst oxidases	Interfere with self-incompatibility	Zhang et al., 2021c
	Disease resistance	*sBrDM8*	*Bra016457*	A serine/threonine kinase gene	Resistance to downy mildew	Yu et al., 2016
		CRa	LOC103861267	A TIR-NB-LRR type resistance gene	Resistance to clubroot disease	Ueno et al., 2012
		Crr1a	NA	A TIR-NB-LRR type resistance gene	Resistance to clubroot disease	Hatakeyama et al., 2013
		CRb	*Bra019410* and *Bra019413*	A TIR-NB-LRR type resistance gene	Resistance to clubroot disease	Hatakeyama et al., 2017
		retr02	*Bra035393*	A eukaryotic initiation factor 4E (eif4E)	Resistance to *Turnip mosaic virus*	Qian et al., 2013
		TuRB07	*Bra018863*	A CC-NB-ARC type resistance gene	Resistance to *Turnip mosaic virus*	Jin et al., 2014
		BrCRT2	*Bra018575*	A calreticulin family gene	Resistance to tipburn	Su et al., 2019
Cauliflower	Disease resistance	*FOC1*	*Bol037156*	A TIR-NB-LRR type resistance gene	Resistance to fusarium wilt	Lv et al., 2014
		FocBo1	*Bol037163*	A TIR-NB-LRR type resistance gene	Resistance to fusarium wilt	Shimizu et al., 2015
Brassica juncea	Disease resistance	*retr03*	*BjuA006209*	A eukaryotic initiation factor 2Bβ (eif2Bβ)	Resistance to *Turnip mosaic virus*	Shopan et al., 2017
Spinach	Disease resistance	*Spo12784*	*Spo12784*	An NBS-LRR type resistance gene	Resistance to downy mildew	Bhattarai et al., 2020
		Spo12903	*Spo12903*	A CC-NB-ARC type resistance gene	Resistance to downy mildew	Bhattarai et al., 2020
Carrot	Fruit quality	*DcMYB7*	MK572814–MK572817	A MYB113-like transcription factor	Anthocyanin biosynthesis	Xu et al., 2019
		DcMYB113	LOC108212072	A R2R3-MYB transcription factor	Anthocyanin biosynthesis	Xu et al., 2020
		CYP97A3	JQ655297	An α-carotene synthase	α-carotene synthesis	Arango et al., 2014

al., 2014). Recent studies revealed that two important genes, *Golden 2-like 2* (*GLK2*) and *uniform gray-green* (*UG*), encoding a MYB and a KNOX transcription factor, respectively, are involved in the formation of green shoulder in tomato fruits. Loss of functions of these two genes affect the development of chloroplasts and thus reduce the pigment and

sugar content in mature tomato fruits (Nadakuduti et al., 2014; Powell et al., 2012). In addition, the acidity level also affects the flavor of tomato fruits. Recent research suggested that malate metabolism can affect the sourness of tomato, in which, *TFM6*, that encodes the Al-ACTIVATED MALATE TRANSPORTER9 (SlALMT9), was shown to be the major QTL responsible for variation in fruit malate accumulation (Ye et al., 2017).

In pepper, capsaicin content is the most important quality trait. Functional genomics research revealed that MYB31, a transcription factor that is specifically expressed in capsicum placenta, and *PUN1*, a gene encoding a capsicum acyl-transferase, play important roles in capsaicin synthesis (Kim et al., 2014; Stewart et al., 2005; Zhu et al., 2019).

Watermelon and melon are cucurbit crops bearing sweet and tasty fruits. How their fruits became sweeter during domestication has been revealed by functional genomic studies (Guo et al., 2019b; Zhao et al., 2019a). In watermelon, a novel sugar transporter, ClVST1, regulates the unloading of sugar from the phloem (Ren et al., 2020b). Another gene, *ClAGA2*, which encodes an alkaline α-galactosidas and specifically expresses in the vascular bundles in the developing fruit, functions in hydrolysis of RFOs into sucrose (Ren et al., 2021). Two transporters, ClSWEET3 and ClTST2, coordinately mediate the transport of sucrose across the cellular plasma membrane and tonoplast for storage in the vacuole (Ren et al., 2021).

Certain metabolites can impair vegetable crop quality (Tomás-Barberán and Espín, 2001). These degrading metabolites can also help reduce or eliminate associated metabolites, improving vegetable crop quality. Steroidal glycoalkaloids (SGAs) are poisonous nitrogenous secondary metabolites with a bitter taste found in Solanaceae species, and several genes that participate in their biosynthesis have been isolated. The *GLYCOALKALOID METABOLISM1* (*GAME1*) gene encodes a galactosyltransferase that glycosylates lycopene (Itkin et al., 2011). *GAME4* encodes a cytochrome P450 protein involved in SGA synthesis; inhibiting GAME4 decreases SGAs in potato tubers and tomato fruits (Itkin et al., 2013). GAME9 regulates upstream mevalonate pathway genes to modulate SGA synthesis. Overexpression of *GAME9* promotes SGA in tomato and potato (Cárdenas et al., 2016). The bitterness of cucurbit fruits is mainly derived from cucurbitacin B (melon), cucurbitacin C (cucumber) and cucurbitacin E (watermelon); the *Bi* (*bitterness*) gene and its homologs are key in cucurbitacin synthesis. In cucumber, *Bi* is specifically regulated by two transcription factors, Bl (bitter leaf) and Bt (bitter fruit) in leaves and fruits, respectively (Shang et al., 2014; Zhou et al., 2016).

The organ color is an important commercial-quality feature. Indigo Rose, a purple tomato cultivar containing anthocyanins, contains a *SlAN2-like* gene, which plays a

crucial regulatory role in the stimulation of anthocyanin biosynthesis (Sun et al., 2020a). In pepper, *CcLOL1* affects chloroplast development and immature pepper fruit color (Borovsky et al., 2019). Anthocyanin synthesis in purple carrots is mainly regulated by *DcMYB7*. Knockout of *DcMYB7* in carrot "Deep purple" produces yellow meaty roots (Xu et al., 2019). Another MYB transcription factor DcMYB113 is selectively expressed in the roots of "Purple haze", a carrot cultivar with purple roots and nonpurple petioles (Xu et al., 2020). In addition, a chlorophyll synthase-encoding gene *PSY* and a carotene hydroxylase-encoding gene *CYP97A3*, determine carrot carotenoid production and also the orange color of carrot (Arango et al., 2014).

The odor of vegetable crops is primarily produced by volatile organic compounds. In tomato, C5 volatile compounds, derived from fatty acids, are the most important contributor to consumer liking of fresh tomatoes and they are partially catalyzed by a 13-lipoxygenase (LOX), TomloxC (Shen et al., 2014). A tomato pan-genome study uncovered that *TomLoxC* plays a role in apocarotenoid biosynthesis and enhance fruit flavor (Gao et al., 2019). One of the clear substances produced after mechanical crushing of cucumber are alcoholic aldehydes, primarily (E,Z)-2,6-nonadienal, giving cucumber fruits a clean and fresh flavor. Their biosynthesis is thought to be generated from fatty acids following a series of reactions such as degradation and oxidation under the catalyzation of lipoxygenase (Shan et al., 2020).

Resistance

To face impaired production and quality, owing to pathogen invasions, vegetable breeding strategies have historically prioritized pest and disease management. Major vegetable diseases include downy mildew, powdery mildew (PM), late blight, clubroot, target leaf spot, anthracnose, fusarium wilt, verticillium wilt, Phytophthora root rot, root-knot nematodes and various viruses, such as Cucumber mosaic virus (CMV), Zucchini yellow mosaic virus (ZYMV), Tomato yellow leaf curl virus (TYLCV), Turnip mosaic virus (TuMV), and Papaya ringspot virus. Since the rapid development of genomic resources, over 50 genes providing disease or pest resistance in key vegetables have been cloned. Most of these genes encode NLRs and repeat receptor-like proteins (RLPs), which are essential components for plant immune signaling. These advances provide useful assistance for breeding varieties with enhanced resistance (Table 2).

Most tomato disease resistance genes are derived from wild tomato relatives. These include the anti-bacterial/fungal disease genes, *Prf*, *I-2*, and *Ph-3*, the antiviral disease genes, *Tm-2²*, and *Sw-5*, and the nematode resistance genes, *Mi-1*, and *Hero*, all of which belong to typical NLR disease re-

sistance genes (Kourelis and van der Hoorn, 2018). Specially, the *CslG2* gene, which encodes a cellulose synthase-like protein, can significantly reduce the severity of TYLCV symptoms and increase the disease resistance and yield of TYLCV-infected tomatoes (Choe et al., 2021). Regulating the expression of *MYC2*, encoding a core transcription factor of the jasmonic acid signaling pathway that is closely related to disease resistance and insect resistance, achieved an effective defense against biological stress (Du et al., 2017). Tipburn in Chinese cabbage is caused by calcium deficiency. In the susceptible parent, a candidate gene *BrCRT2* was cloned, which encoded protein with 17 amino acid deletions in its key structural domain. Further studies proved that the deletion of these 17 amino acids leads to decrease of the protein's calcium ion binding capacity, thereby reducing the ability of plants to cope with calcium deficiency stress, and ultimately results in the occurrence of tipburn (Su et al., 2019). Polyacetylenic lipids are a type of resistance compound found in many Apiaceae species. Studies in carrot discovered the involvement of 24 fatty acid desaturase 2 (FAD2)-type enzymes required for Polyacetylenic lipid biosynthesis, and functionally validated six key candidate genes (Busta et al., 2018).

Late blight caused by *Phytophthora infestans* remains one of the most devastating diseases in potato and tomato. Recent research explored the diversity of resistance genes in wild Solanaceae species closely related to potato and tomato, and found that *Solanum americanum*, a wild nightshade species, is a promising source of new resistance genes to late blight. *Rpi-amr3* was the first late blight resistance gene cloned from *S. americanum*, displaying a high level of late blight resistance when transferred to cultivated potatoes (Witek et al., 2016). Recently, Witek et al. (2021) cloned the late blight resistance gene *Rpi-amr1* from diploid *S. americanum*, which encodes a resistance protein with NB (nucleotide binding)-CC (coiled-coil) domains. The functional alleles show extensive allelic variation and confer strong resistance to all 19 tested diverse *P. infestans* isolates, and it is the only known strong late blight resistance gene that has not been overcome (Witek et al., 2021). Appropriate harnessing of the late blight resistance from wild *Solanum* species present great potential to accelerate resistance breeding in tomato and other Solanaceae vegetable crops.

In conclusion, the development of vegetable reference genomes and population genomics has facilitated the identification of several genes underlying agronomically significant traits, such as yield, quality, and disease and stress resistance. These discoveries pave the way for an understanding of the genetic basis of specific phenotypes or pathways and present a valuable gene or allele repertoire that can be used in breeding programs to generate elite varieties, using cutting-edge technologies such as genome editing and genome design.

Genome design in vegetable breeding

Conventional breeding has contributed greatly to the development of elite vegetable varieties. With the current availability of tremendous genomic resources for vegetable crops, the efficiency of genetic improvement can now be accelerated. In the future, selection of natural alleles from germplasms, creation of novel genes/alleles by genetic modification, and re-domestication of wild accessions will be major avenues for the genome design of vegetable crops, in this genomics era.

Natural alleles

Marker-assisted selection (MAS) has become an essential breeding strategy to introduce desirable traits into vegetables (Figure 2A). In the past decades, development of molecular markers was laborious and cost-ineffective, due to the lack of genome information. The release of vast omics datasets has significantly contributed to the development of a large array of simple sequence repeat (SSR), InDel and SNP markers in major vegetable crops. For example, some 1,000 highly polymorphic SSRs in cucumber were developed, based on the reference genome sequences, seven times more efficiency than the previous methods (Ren et al., 2009). A large number of InDel markers in several vegetables, such as Chinese cabbage, tomato and pepper, were also developed and applied in practical breeding (Chen et al., 2021; Guo et al., 2019a; Liu et al., 2013; Yang et al., 2014). Due to the nature of ubiquity, high polymorphism and high throughput, SNP has become the most widely used type of markers and have been explored at the population level in numerous vegetable crops, as described above. Selection of an appropriate platform is critical in the context of various markers and samples. Given the moderate number of markers and samples, the Kompetitive Allele-Specific PCR (KASP) platform is currently dominant. For the combination of a high number of samples and low number of markers, Douglas has its advantages. In addition, markers based on significantly associated or causal SVs for agronomic traits should also be developed, given their important roles in regulation of many plant phenotypes.

Genetic modification

Mutagenesis methods, such as ethyl methanesulfonate (EMS), fast neutron, and T-DNA insertion, have generated a large number of mutants with a variety of agronomic traits for vegetables (Figure 2B). With an increasing number of dissected genes, recently, targeted gene modification technologies, such as the clustered regularly interspaced short palindromic repeats (CRISPR)-CRISPR-associated protein 9 (Cas9) CRISPR-Cas9-based gene editing (Jiang and Doud-
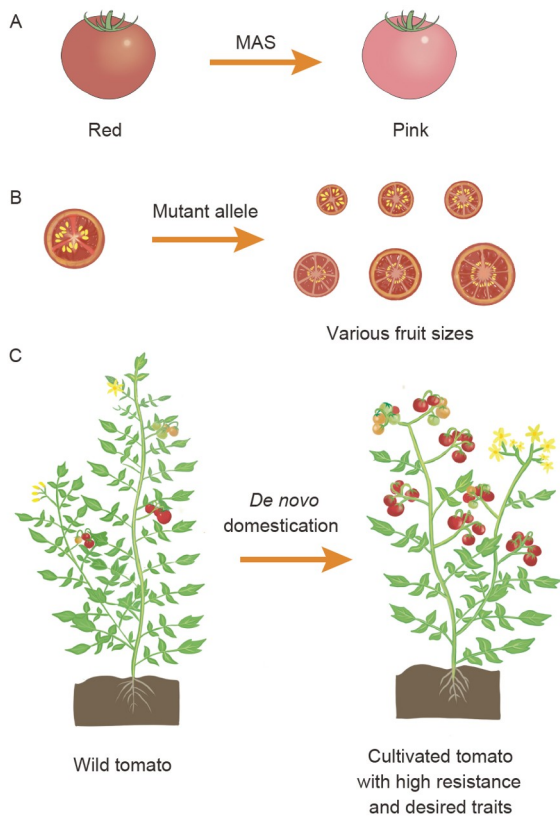
Figure 2   State-of-the-art biotechnologies for vegetable breeding. A, Application of MAS for breeding of pink-fruited tomato varieties. B, Generation of tomatoes with different fruit sizes by screening mutant alleles. C, Breeding of tomato varieties by exploiting *de novo* domestication of wild species.

na, 2017), have begun to be used to modify agronomic traits in vegetables. Tomato has a stable genetic transgenic system, and thus was used as an ideal model for improvement using CRISPR technology. For breeding, double haploid lines are crucial for the development of elite inbred lines, and in tomato, the maternal haploids were induced by editing the orthologous *DMP* gene (Zhong et al., 2022). The tomato plants with albino phenotype, abnormal fruit ripening, rapid flowering, balanced branching, parthenocarpic and pink fruit were generated by modifying *PDS*, *ORRM4*, *SP5G*, *MADS-box*, *AA9* and *MYB12* genes, respectively (Komatsu et al., 2020; Ueta et al., 2017; Yang et al., 2017; Zhu et al., 2018). In cucurbit crops, *WIP* was knocked out to obtain cucumber and watermelon plants which generate nearly all female flowers (Hu et al., 2017; Zhang et al., 2020a), and the editing of tolerance-related genes resulted in herbicide-tolerant watermelon (Tian et al., 2018; Tian et al., 2017) and salinity-tolerant pumpkin (Huang et al., 2019). For other vegetables, a few gene-edited plants have also been generated, such as yellow carrot and albino cabbage (Ma et al., 2019). Moreover, engineering promoter sequences of key tomato genes, such as *CLV3* and *WOX*, produced a series of *cis*-regulatory alleles with a range of quantitative traits (Hendelman et al.,

2021; Wang et al., 2021), some of which can be precisely selected during breeding.

De novo domestication

Domestication and breeding have produced a number of elite crop varieties for human preference, via selection; however, an unexpected amount of genetic diversity, quality traits and disease and pest resistance were simultaneously lost. With a deeper understanding of the genetic basis of crop domestication, *de novo* domestication was proposed, by targeted manipulation of several fundamental domesticated genes, to develop crops with both the stress resistance and nutritional quality of wild materials and favorable domestication traits (Yu and Li, 2022; Yu et al., 2021). The multiplex CRISPR-Cas9 strategy was used to introduce genes related to day-length sensitivity (*SP5G*), shoot architecture (*SP*), flower and fruit production (*CLV3* and *WUS*), and nutrient content (*GGP1*) to wild tomato *S. pimpinellifolium* (Figure 2C). These efforts achieved tomato progeny with domesticated phenotypes while retaining disease resistance and stress tolerance (Li et al., 2018). In another report, simultaneous editing of six genes in *S. pimpinellifolium* resulted in *de novo* domesticated tomato plants with the modification of fruit number, size and shape, nutrient content and plant architecture. In these edited plants, fruit lycopene content was improved by 5-fold compared with the widely cultivated varieties (Zsögön et al., 2018). With the advancement of gene-editing technologies and a deeper understanding of the genomic basis of domestication in more vegetables, the knowledge-driven re-domestication of wild plants will be proven to be a reliable and efficient tool for their genetic improvement.

Perspectives

The rapid advancement of cost-effective and high-throughput sequencing technologies has contributed to the exponential growth of genomic data for vegetables, enriching an understanding of the genetic basis of domestication and agronomic traits. In the future, increasing numbers of omics datasets will be integrated to dissect functional genes, at an unprecedented rate, and more elite varieties with consumer preferred traits and enhanced resistance will be developed using targeted gene editing. Moreover, to effectively explore the copious omics data, global collaboration should be proposed to generate, organize, curate and share related information and resources.

Where next for assembling vegetable reference genomes?

Although reference genomes for many vegetable crops have

been established, with some having high-quality chromosome-scale assemblies, other vegetable crops, of great economic value, still lack genomics databases. For example, the genus *Allium* (the family Amaryllidaceae) contains several widely cultivated species, such as bulb onion (*Allium cepa*), garlic (*A. sativum*), bunching onion (*A. fistulosum*) and Chinese chives (*A. tuberosum*). All *Allium* species have a particularly large genome size of approx. 16.0 Gb, with a large array of copies of repetitive elements, which greatly hampers the deciphering of their genomes. Currently, only draft genome assemblies for garlic and onion have been generated, with relatively low continuity and completeness (Finkers et al., 2021; Sun et al., 2020b). Given the economic and nutritional importance of these *Allium* crops, the future development of chromosome-scale and high-quality reference genomes is of great importance for breeding purposes.

Most constructed reference genomes for vegetable crops have covered their major cultivated forms and closely related progenitor species. Importantly, crop wild relatives contain genetic diversity likely absent in their domesticated counterparts, some of which may underlie favored traits, such as disease resistance, stress tolerance, flavor quality and variations in plant architecture. Unfortunately, genome resources, especially for high-quality reference genomes, are still relatively lacking for these vegetable wild species. Thus, a concerted effort will be needed to construct reference genomes for these vegetable wild species, as this will facilitate the discovery of wild-type genes or alleles that could be exploited for improvement of modern cultivars.

For most vegetable crops, haplotype-resolved, gap-free and telomere-to-telomere (T2T) genome assemblies, using state-of-the-art sequencing technologies and assembly algorithms, would be an ultimate goal for assembling reference genomes, as this would allow the discovery of hidden sequences associated with genomic architecture and functional attributes. A recent study constructed a gap-free and T2T reference genome for a watermelon inbred line "G42", rescuing 173 protein-coding genes previously inaccessible owing to assembly gaps in the 97103 v2 watermelon reference genome (Deng et al., 2022b). As the first T2T reference genome for Cucurbitaceae species, and also for vegetable crops, this will surely motivate a broad range of efforts to build the next-generation reference genomes for more vegetable plants.

The next-generation population genomics

Pan-genomics have been proven to be superior in characterizing certain categories of genetic variants, e.g., SVs, and are similarly useful in discovering genes or variants underlying agronomically important traits (Della Coletta et al., 2021; Zhou et al., 2022). Existing pan-genome studies in

vegetable crops are mainly focused on cultivated species and their closely related progenitors; however, wild species possess unharnessed beneficial genes and alleles, some of which have been lost during domestication. Therefore, genetic diversity of these wild species has been underrepresented in most constructed vegetable pan-genomes. To gain a deeper understanding of biodiversity, within both wild and cultivated vegetable species, we thus anticipate the development of reference genomes of more distantly-related wild species of vegetable crops, which will ultimately empower the construction of super-pangenomes (Khan et al., 2020); i.e., the collection of biodiversity from different species for a botanical genus. These efforts have the potential to further accelerate vegetable crop improvement by exploiting wild relatives. However, some wild species for certain vegetable crops display high degrees of inconsistency compared with their cultivated counterparts, impeding the application of conventional sequence mapping and variant calling methods. This, therefore, calls for the development of dedicated pipelines or algorithms tailoring for these analyses.

Conventional population genomics studies rely on single reference-based short-read mapping, and further analyses are mostly conducted using small variants, such as SNPs. Despite their achievement on providing insights into crop domestication, divergence and evolution history, the information of variants that are difficult to be accessed by short read sequencing, including large InDels, inversions and duplications, are inevitably lost. Given that increasing numbers of studies have indicated the importance of these variants (Alonge et al., 2020; Della Coletta et al., 2021; Gao et al., 2019; Li et al., 2022; Zhou et al., 2022), we envision a cognitive shift from conventional population genomics to the development and characterization of graph-based pan-genomes, using representative high-quality genome assemblies, coupled with low-coverage short-read sequencing data for large panels of accessions. This will greatly facilitate the identification and characterization of those abovementioned types of variants. However, this shift will require the implementation of new algorithms to accommodate large-scale comparative genomics results, and next-generation genomic databases capable of hosting, processing, and visualizing these enormous datasets. These approaches will empower the identification of more loci, or alleles, underlying agronomic traits, as well as offering additional insights into vegetable domestication and divergence.

Gene discovery in the vegetable genomics era

The availability of increasing omics resources for vegetable crops has promoted the application of several strategies to accelerate trait gene isolation, a promising one of which is constructing a mutant library. To date, mutant populations, derived from EMS or fast-neutron mutagenesis, have been

reported in various vegetables, such as carrot (Wu et al., 2020), Chinese cabbage (Lu et al., 2014), cucumber (Chen et al., 2018), melon (Galpaz et al., 2013), tomato (Menda et al., 2004) and watermelon (Deng et al., 2022b). A series of follow-up analytic pipelines, derived from MutMap (Abe et al., 2012; Fekih et al., 2013; Takagi et al., 2013), have been devised to facilitate candidate gene isolation. These approaches achieve rapid gene mapping by reducing the number or crosses and are particularly useful when the target gene contributes to minor phenotypic effects (Abe et al., 2012). As genome sequencing is becoming routine for increasing species, we predict that mutant library development, coupled with MutMap-based gene cloning, will emerge as the system of choice for more vegetable species.

The recent explosion of omics datasets, for major vegetable crops, also has the potential to facilitate trait gene discovery. Comparative genomics would be an ideal approach to help identify genes underlying agronomic traits. One example is the rapid cloning of *CsaBCH1*, a gene that encodes a β-carotene hydroxylase and confers orange colored fruit endocarp in cucumber (Qi et al., 2013). This was achieved by searching missense SNPs displaying the strongest population divergence (fixation index=1) between 19 Xishuangbanna cucumbers with orange fruits and the 96 remaining cucumber accessions, which markedly narrowed the number of SNPs from 3,305,010 to 43. Among these SNPs, only one was localized in the coding region of *CsaBCH1* within the genetic mapping interval of *ore*, which was reported to be responsible for the orange fruit endocarp in cucumber. Further experiments revealed that *CsaBCH1* defines *ore* and is causative for this trait in Xishuangbanna cucumbers. Another example is the identification of Identity of Tuber 1 (IT1), a TCP transcription factor that is key to potato tuberization. This gene was discovered by intersecting genes carrying potato-specific conserved non-coding sequences, genes predominantly expressed in stolons or tubers, and genes conserved in wild and cultivated potatoes (Tang et al., 2022). We suggest that more efforts on omics-guided research should be made for accelerating trait gene mining.

Subsequent to the determination of candidate genes, genetic transformation and gene editing are two straightforward methods to validate their functions; however, the majority of vegetable crops lack efficient transformation systems, thereby hampering the progress of genetic and biological studies. Previous studies have reported that expression of fused GROWTH-REGULATING FACTOR4 (GRF4) and GRF-INTERACTING FACTOR1 (GIF1), two transcription factors highly conserved in angiosperms that regulate plant growth, can significantly increase regeneration efficiency in wheat, citrus and watermelon, suggestive of a general approach for a broad range of eudicots (Debernardi et al., 2020; Feng et al., 2021). This strategy can also be combined with CRISPR-Cas9 to generate efficient gene editing plants. Hence, we envision the development of stable systems for genetic transformation in more vegetable crops that are recalcitrant to the conventional *Agrobacterium tumefaciens*-mediated transformation. This may motivate high-efficiency and precise gene editing, via the CRISPR-Cas9 system, which will significantly expedite the examination of gene functions and elucidation of underlying mechanisms in vegetable crops.

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