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Genome sequences of horticultural plants: past, present, and future

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Abstract

Horticultural plants play various and critical roles for humans by providing fruits, vegetables, materials for beverages, and herbal medicines and by acting as ornamentals. They have also shaped human art, culture, and environments and thereby have influenced the lifestyles of humans. With the advent of sequencing technologies, there has been a dramatic increase in the number of sequenced genomes of horticultural plant species in the past decade. The genomes of horticultural plants are highly diverse and complex, often with a high degree of heterozygosity and a high ploidy due to their long and complex history of evolution and domestication. Here we summarize the advances in the genome sequencing of horticultural plants, the reconstruction of pan-genomes, and the development of horticultural genome databases. We also discuss past, present, and future studies related to genome sequencing, data storage, data quality, data sharing, and data visualization to provide practical guidance for genomic studies of horticultural plants. Finally, we propose a horticultural plant genome project as well as the roadmap and technical details toward three goals of the project.

Introduction

Horticultural plants mostly comprise vegetable-producing, fruit-bearing, ornamental, and beverage-producing plants and herbal medicinal plants. These plants have played important economic and social roles in the human lives and health by providing basic food needs, beautifying urban and rural landscapes, and improving personal esthetics. For example, the Food and Agriculture Organization of the United Nations reported that, while worldwide cereal food together is valued at 125 points (normalized value), vegetables and fruits together are valued at 137 points (http://faostat.fao.org). Horticultural plants also contribute to ecological balance by improving our biological environment by providing oxygen and balancing urban temperatures.

Horticultural plants are distributed among a wide variety of taxonomic plant spectra, which include a large number of flowering plants and a few early-divergent land plants. The sizes of their genomes vary greatly. For example, the vegetable garlic (*Allium sativum*) has a diploid genome ($2n = 16$) with an estimated genome size of >30 Gb[1], and onion (*Allium cepa*) has a similar genome size[2]. In addition, most horticultural plants are domesticated, and their genome sequences have experienced strong artificial selection. For example, grape was found to have been cultivated (via viticulture) for >6000 years[3]; citrus, >4000 years[4]. In addition, some horticultural plants are intermediates of domesticated and wild plants, such as medicinal plants including ginseng (*Panax ginseng*), noto ginseng (*Panax notoginseng*), and Artemisia (*Artemisia annua*). Many domesticated horticultural plants have high levels of genetic diversity and heterozygosity, such as sunflower (10% of bases differ between homologous chromosomes)[5], grape (7%)[6], and potato (4.8%)[7].

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De novo sequencing of horticultural plant genomes

As of December 31, 2018, the genomes of 181 horticultural species have been sequenced (Table 1). These include 4 beverage, 47 fruit, 44 medicinal, 44 ornamental, and 42 vegetable plants (Fig. 1a). In terms of taxonomic distribution, these plants include 175 angiosperms, 2 gymnosperms, 3 lycophytes, and 1 moss (Fig. 1b). As shown in Fig. 1c, the number of sequenced genomes of horticultural plants completed each year has significantly increased from 1 in 2007 to 40 in 2018. Although most of the horticultural plants are angiosperms, the genome sequencing of non-angiosperm species has also demonstrated steady growth (Fig. 1c). Vegetables and fruits have been a focus of plant research in the past few years. However, only two vegetables and seven fruits had their genomes sequenced in 2018 (Fig. 1d). This is probably because many economically important vegetables and fruits were already sequenced prior to 2018.

Some angiosperms have a significant role in the economy[8]. The 181 horticultural plants with sequenced genomes are distributed in 30 of the 64 angiosperm orders. Among these 30 orders, 7 (Fabales, Rosales, Cucurbitales, Brassicales, Sapindales, Solanales, and Laminales) have >10 species whose genomes have been sequenced (Fig. 1e), suggesting their vital importance to humans.

Most of the genome-sequenced plants fall into the Rosaceae family, which is a medium-sized family with approximately 4800 species (http://www.theplantlist.org), including many popular fruit-bearing and ornamental plants. The genome-decoded fruit-producing species include breadnut (*Artocarpus camansi*)[9], ficus (*Ficus carica*)[10], jujube (*Ziziphus jujuba*)[11], strawberry and its close relatives (*Fragaria* × *ananassa*, *Fragaria iinumae*, *Fragaria nipponica*, *Fragaria nubicola*, *Fragaria orientalis*, *Fragaria vesca*)[12–14], apple (*Malus domestica*)[15], morus (*Morus notabilis*)[16], sweet cherry (*Prunus avium*)[17], peach (*Prunus persica*)[18], Chinese pear (*Pyrus bretschneideri*)[19], European pear (*Pyrus communis*)[20], and black raspberry (*Rubus occidentalis*)[21]. The genome-decoded ornamentals include mei (*Prunus mume*)[22], sakura (*Prunus yedoensis*)[23], and rose and its close relatives (*Rosa* × *damascene*, *Rosa chinensis*, *Rosa multiflora*, and *Rosa roxburghii*)[24–26]. However, the genomes of many important fruit-bearing Rosales plants, such as *Crataegus pinnatifida*, *Malus prunifolia*, *Eriobotrya japonica*, *Armeniaca vulgaris*, and *Prunus salicina*, and of Rosales ornamentals, such as *Photinia serrulata*, *Spiraea thunbergii*, *Cotoneaster multiflorus*, and *Rubus japonicas*, have not yet been sequenced. The available genome sequences of Rosales species have largely improved our understanding of the biology of fruits and flowers. For example, the high-quality apple genome sequence showed that a single allele is responsible for red fruit peal coloration[27], and the reference genome of rose has provided insights into the floral color and scent pathways[25].

The Solanaceae family consists of ~2700 species (http://www.theplantlist.org) that include a number of vegetable, medicinal, and ornamental species. The genomes of several important Solanaceae vegetable species have been sequenced, such as tomato (*Solanum lycopersicum*, *Solanum pimpinellifolium*)[28,29], potato (*Solanum tuberosum*)[30], pepper (*Capsicum annuum*, *Capsicum baccatum*, *Capsicum chinense*)[31–33], and eggplant (*Solanum melongena*)[34]. Solanaceae ornamentals include ivy morning glory (*Ipomoea nil*)[35], ornamental tobacco (*Nicotiana sylvestris*)[36], and petunia (*Petunia axillaris*, *Petunia inflate*)[37]. Although these genomes have helped to understand the evolution of Solanaceae plants, additional Solanaceae horticultural genomes need to be sequenced. These include the sequences of the medicinal plants *Datura arborea*, *Datura metel*, and *Datura innoxia* and the ornamentals *Petunia* spp., *Nicotiana* spp., *Lycium* spp., *Solanum* spp., *Cestrum* spp., *Calibrachoa* spp., and *Solandra* spp. These available genome sequences have helped to decipher the evolution and genomic basis of metabolites such as vitamin C (or ascorbic acid)[38] in tomato and alkaloids in tobacoo[39].

The Fabaceae family, consisting of ~19,000 known species, is the third largest angiosperm family by number of species richness, followed by the Orchidaceae and Asteraceae families. Although only dozens of Fabaceae genomes have been sequenced[8], many of them are from horticultural species. The genome-decoded Fabaceae vegetable plants include pigeon pea (*Cajanus cajan*)[40], chickpea and its relative (*Cicer arietinum*, *Cicer reticulatum*)[41,42], soybean (*Glycine max*)[43], barrelclover (*Medicago truncatula*)[44], common bean (*Phaseolus vulgaris*)[45], faba bean (*Vicia faba*)[46], adzuki bean (*Vigna angularis*)[47], and mung bean (*Vigna radiata*)[48]. The genome-sequenced Fabaceae ornamentals include eastern redbud (*Cercis canadensis*)[49], narrowleaf lupin (*Lupinus angustifolius*)[50], and mimosa (*Mimosa pudica*). The Fabaceae medicinal plants with sequenced genomes include Chinese uralensis (*Glycyrrhiza uralensis*)[51] and red clover (*Trifolium pratense*)[52]. Legumes are considered a valuable source of food in the future[53]; thus the sequencing of their genomes would be valuable. Determining the genomic basis of legume–rhizobium interactions would help not only to solve a classic fundamental problem in biology but also to improve nitrogen utilization in horticultural plants.

The Brassicaceae family is a medium-sized family with ~4000 species, including many horticultural plant species. The Brassicaceae vegetable plants with sequenced genomes include Zhacai (*Brassica juncea*)[54], cabbage (*Brassica oleracea*)[55], napa cabbage (*Brassica rapa*)[56], Capsella (*Capsella bursa-pastoris* and *Capsella rubella*)[57,58], radish (*Raphanus sativus*)[59], and field pennycress (*Thlaspi*

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Table 1 List of genome-sequenced horticultural plant species and their close relatives

Species	Common name	Taxonomy	Type	DB-url
Zoysia japonica	Japanese lawn grass	Angiosperm/ Alismatales/Poaceae	Ornamental	zoysia.kazusa.or.jp
Zoysia matrella	Manila grass	Angiosperm/ Alismatales/Poaceae	Ornamental	zoysia.kazusa.or.jp
Zoysia pacifica	Mascarene grass	Angiosperm/ Alismatales/Poaceae	Ornamental	zoysia.kazusa.or.jp
Cocos nucifera	Coconut palm	Angiosperm/ Arecales/Arecaceae	Fruit	gigadb.org
Phoenix dactylifera	Date palm	Angiosperm/ Arecales/Arecaceae	Fruit	drdb.big.ac.cn
Asparagus officinalis	Garden asparagus	Angiosperm/ Asparagales/ Asparagaceae	Vegetable	phytozome.jgi.doe.gov
Dendrobium catenatum	N.A.	Angiosperm/ Asparagales/ Orchidaceae	Medicinal	herbalplant.ynau.edu.cn
Gastrodia elata	Tianma	Angiosperm/ Asparagales/ Orchidaceae	Medicinal	herbalplant.ynau.edu.cn
Phalaenopsis aphrodite	Aphrodite's phalaenopsis	Angiosperm/ Asparagales/ Orchidaceae	Ornamental	genomevolution.org; chibba.agtec.uga.edu/duplication; orchidstra2.abrc.sinica.edu.tw
Phalaenopsis equestris	Horse phalaenopsis	Angiosperm/ Asparagales/ Orchidaceae	Ornamental	genomevolution.org; chibba.agtec.uga.edu/duplication; orchidstra2.abrc.sinica.edu.tw
Dioscorea rotundata	White Guinea yam	Angiosperm/ Dioscoreales/ Dioscoreaceae	Vegetable	genomevolution.org/CoGe; plants.ensembl.org
Ananas comosus	Pineapple	Angiosperm/Poales/ Bromeliaceae	Fruit	phytozome.jgi.doe.gov; genomevolution.org/CoGe; pineapple.angiosperms.org/pineapple/html/index.html
Echinochloa crus-galli	Cockspur grass	Angiosperm/Poales/ Poaceae	Medicinal	horticulture.eplant.org
Lolium perenne	Perennial ryegrass	Angiosperm/Poales/ Poaceae	Ornamental	pgsb.helmholtz-muenchen.de
Zizania latifolia	Jiaobai	Angiosperm/Poales/ Poaceae	Vegetable	plants.ensembl.org
Musa acuminata	Wild banana	Angiosperm/ Zingiberales/ Musaceae	Ornamental	chibba.agtec.uga.edu/duplication; plants.ensembl.org/; phytozome.jgi.doe.gov; banana-genome-hub.southgreen.fr
Musa balbisiana	Wild banana	Angiosperm/ Zingiberales/ Musaceae	Ornamental	banana-genome-hub.southgreen.fr
Musa itinerans	Yunnan banana	Angiosperm/ Zingiberales/ Musaceae	Fruit	banana-genome-hub.southgreen.fr

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Table 1 (continued)

Species	Common name	Taxonomy	Type	DB-url
Ensete ventricosum	Ethiopian banana	Angiosperm/ Zingiberales/ Musaceae	Medicinal	horticulture.eplant.org
Liriodendron chinense	Chinese tulip tree	Angiosperm/ Magnoliales/ Magnoliaceae	Ornamental	www.hardwoodgenomics.org
Manihot esculenta	Cassava	Angiosperm/ Malpighiales/ Euphorbiaceae	Vegetable	genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza; plants.ensembl.org; www.plantgdb.org/; phytozome.jgi.doe.gov
Rhizophora apiculata	Tall-stilt mangrove	Angiosperm/ Malpighiales/ Rhizophoraceae	Medicinal	genomevolution.org/coge
Begonia fuchsioides	Shrub Begonia	Angiosperm/ Cucurbitales/ Begoniaceae	Ornamental	
Cucumis melo	Muskmelon	Angiosperm/ Cucurbitales/ Cucurbitaceae	Fruit	cucurbitgenomics.org/; bioinformatics.psb.ugent.be/plaza
Citrullus lanatus	Watermelon	Angiosperm/ Cucurbitales/ Cucurbitaceae	Fruit	www.coolseasonFoodlegume.org; bioinformatics.psb.ugent.be/plaza; chibba.agtec.uga.edu/duplication; cucurbitgenomics.org
Siraitia grosvenorii	Monk fruit	Angiosperm/ Cucurbitales/ Cucurbitaceae	Medicinal	herbalplant.ynau.edu.cn
Cucumis sativus	Cucumber	Angiosperm/ Cucurbitales/ Cucurbitaceae	Vegetable	genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza; phytozome.jgi.doe.gov; chibba.agtec.uga.edu/duplication; plants.ensembl.org; www.plantgdb.org; cucurbitgenomics.org
Cucurbita argyrosperma	Silver-seed gourd	Angiosperm/ Cucurbitales/ Cucurbitaceae	Vegetable	cucurbitgenomics.org
Cucurbita maxima	Winter squash	Angiosperm/ Cucurbitales/ Cucurbitaceae	Vegetable	cucurbitgenomics.org
Cucurbita moschata	Pumpkin	Angiosperm/ Cucurbitales/ Cucurbitaceae	Vegetable	cucurbitgenomics.org
Cucurbita pepo	Summer squash	Angiosperm/ Cucurbitales/ Cucurbitaceae	Vegetable	cucurbitgenomics.org
Lagenaria siceraria	Bottle gourd	Angiosperm/ Cucurbitales/ Cucurbitaceae	Vegetable	genomevolution.org; cucurbitgenomics.org
Momordica charantia	Bitter melon	Angiosperm/ Cucurbitales/ Cucurbitaceae	Vegetable	

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Table 1 (continued)

Species	Common name	Taxonomy	Type	DB-url
Glycyrrhiza uralensis	Chinese liquorice	Angiosperm/Fabales/ Fabaceae	Medicinal	ngs-data-archive.psc.riken.jp
Trifolium pratense	Red clover	Angiosperm/Fabales/ Fabaceae	Medicinal	http://www.cacaogenomedb.org; bioinformatics.psb.ugent.be/plaza; plants.ensembl.org; phytozome.jgi.doe.gov
Cercis canadensis	Eastern redbud	Angiosperm/Fabales/ Fabaceae	Ornamental	genomevolution.orgauth.iplantc.org
Lupinus angustifolius	Narrow-leaved lupine	Angiosperm/Fabales/ Fabaceae	Ornamental	plants.ensembl.org
Mimosa pudica	Sensitive plant	Angiosperm/Fabales/ Fabaceae	Ornamental	www.medicagogenome.org
Cajanus cajan	Pigeon pea	Angiosperm/Fabales/ Fabaceae	Vegetable	brassicadb.org/brad; genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza; chibba.agtec.uga.edu/duplication
Cicer arietinum	Chick pea	Angiosperm/Fabales/ Fabaceae	Vegetable	genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza; chibba.agtec.uga.edu/duplication; phytozome.jgi.doe.gov
Cicer reticulatum	Chick pea	Angiosperm/Fabales/ Fabaceae	Vegetable	www.coolseasonfoodlegume.org
Glycine max	Soybean	Angiosperm/Fabales/ Fabaceae	Vegetable	genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza; phytozome.jgi.doe.gov; chibba.agtec.uga.edu/duplication/; plants.ensembl.org; www.plantgdb.org
Medicago truncatula	Barrelclover	Angiosperm/Fabales/ Fabaceae	Vegetable	phytozome.jgi.doe.gov; bioinformatics.psb.ugent.be/plaza; chibba.agtec.uga.edu/duplication; /plant/plantsdb.jsp; plants.ensembl.org; www.plantgdb.org
Phaseolus vulgaris	Common bean	Angiosperm/Fabales/ Fabaceae	Vegetable	genomevolution.org/CoGe; chibba.agtec.uga.edu/duplication; plants.ensembl.org; phytozome.jgi.doe.gov
Vicia faba	Fava bean	Angiosperm/Fabales/ Fabaceae	Vegetable	
Vigna angularis	Adzuki bean	Angiosperm/Fabales/ Fabaceae	Vegetable	plants.ensembl.org
Vigna radiata	Mungbean	Angiosperm/Fabales/ Fabaceae	Vegetable	plants.ensembl.org
Casuarina equisetifolia	Australian pine tree	Angiosperm/Fagales/ Casuarinaceae	Ornamental	hardwoodgenomics.org
Castanea mollissima	Chinese chestnut	Angiosperm/Fagales/ Fagaceae	Fruit	genomevolution.org/CoGe
Juglans cathayensis	Chinese walnut	Angiosperm/Fagales/ Juglandaceae	Fruit	www.hardwoodgenomics.org
Juglans hindsii	Northern California walnut	Angiosperm/Fagales/ Juglandaceae	Fruit rootstock	www.hardwoodgenomics.org
Juglans microcarpa	Texas black walnut	Angiosperm/Fagales/ Juglandaceae	Fruit	www.hardwoodgenomics.org
Juglans nigra	Eastern black walnut	Angiosperm/Fagales/ Juglandaceae	Fruit rootstock	www.hardwoodgenomics.org
Juglans regia	Common walnut	Angiosperm/Fagales/ Juglandaceae	Fruit	www.hardwoodgenomics.org
Juglans sigillata	Iron walnut		Fruit	www.hardwoodgenomics.org

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Table 1 (continued)

Species	Common name	Taxonomy	Type	DB-url
		Angiosperm/Fagales/Juglandaceae		
Morella rubra	Red bayberry	Angiosperm/Fagales/Myricaceae	Fruit	
Nelumbo nucifera	Sacred lotus	Angiosperm/Proteales/Nelumbonaceae	Ornamental	bioinformatics.psb.ugent.be/plaza; chibba.agtec.uga.edu/duplication
Macadamia integrifolia	Macadamia nut	Angiosperm/Proteales/Proteaceae	Fruit	www.hardwoodgenomics.org
Macleaya cordata	Plume poppy	Angiosperm/Ranunculales/Papaveraceae	Medicinal	herbalplant.ynau.edu.cn
Papaver somniferum	Opium poppy	Angiosperm/Ranunculales/Papaveraceae	Medicinal	genomevolution.orgauth.iplantc.org
Eschscholzia californica	California poppy	Angiosperm/Ranunculales/Papaveraceae	Ornamental	eschscholzia.kazusa.or.jp
Aquilegia coerulea	Colorado blue columbine	Angiosperm/Ranunculales/Ranunculaceae	Medicinal	genome.jgi.doe.gov; genomevolution.org/CoGe; phytozome.jgi.doe.gov
Cannabis sativa	Hemp	Angiosperm/Rosales/Cannabaceae	Medicinal	genome.ccbr.utoronto.ca
Parasponia andersonii	Caoye shanhuangma	Angiosperm/Rosales/Cannabaceae	Medicinal	www.bioinformatics.nl/parasponia
Trema orientalis	Indian charcoal tree	Angiosperm/Rosales/Cannabaceae	Medicinal	www.bioinformatics.nl/parasponia
Artocarpus camansi	Breadnut	Angiosperm/Rosales/Moraceae	Fruit	sites.northwestern.edu/zerega-lab/research/artocarpus-genomics
Ficus carica	Common fig	Angiosperm/Rosales/Moraceae	Fruit	
Ziziphus jujuba	Jujube	Angiosperm/Rosales/Rhamnaceae	Fruit	genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza
Fragaria iinumae	Nogo strawberry	Angiosperm/Rosales/Rosaceae	Fruit	strawberry-garden.kazusa.or.jp
Fragaria nipponica	Japanese strawberry	Angiosperm/Rosales/Rosaceae	Fruit	strawberry-garden.kazusa.or.jp
Fragaria nubicola	Tibet strawberry	Angiosperm/Rosales/Rosaceae	Fruit	strawberry-garden.kazusa.or.jp
Fragaria orientalis	Eastern strawberry	Angiosperm/Rosales/Rosaceae	Fruit	strawberry-garden.kazusa.or.jp
Fragaria vesca	Woodland strawberry	Angiosperm/Rosales/Rosaceae	Fruit	strawberry-garden.kazusa.or.jp; genomevolution.org/CoGe;bioinformatics.psb.ugent.be/plaza; chibba.agtec.uga.edu/duplication; phytozome.jgi.doe.gov

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Table 1 (continued)

Species	Common name	Taxonomy	Type	DB-url
Fragaria × ananassa	Strawberry	Angiosperm/Rosales/Rosaceae	Fruit	strawberry-garden.kazusa.or.jp
Malus domestica	Apple	Angiosperm/Rosales/Rosaceae	Fruit	genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza; phytozome.jgi.doe.gov; www.rosaceae.org
Morus notabilis	Mulberry	Angiosperm/Rosales/Rosaceae	Fruit	morus.swu.edu.cn
Prunus avium	Sweet cherry	Angiosperm/Rosales/Rosaceae	Fruit	www.rosaceae.org
Prunus persica	Peach	Angiosperm/Rosales/Rosaceae	Fruit	genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza; chibba.agtec.uga.edu/duplication; plants.ensembl.org; phytozome.jgi.doe.gov
Pyrus bretschneideri	Chinese pear	Angiosperm/Rosales/Rosaceae	Fruit	bioinformatics.psb.ugent.be/plaza; chibba.agtec.uga.edu/duplication
Pyrus communis	European pear	Angiosperm/Rosales/Rosaceae	Fruit	www.rosaceae.org
Rubus occidentalis	Black raspberry	Angiosperm/Rosales/Rosaceae	Fruit	www.rosaceae.org
Prunus mume	Mei	Angiosperm/Rosales/Rosaceae	Ornamental	genomevolution.org/CoGe; chibba.agtec.uga.edu/duplication
Prunus yedoensis	Yoshino cherry	Angiosperm/Rosales/Rosaceae	Ornamental	www.rosaceae.org
Rosa × damascena	Damask rose	Angiosperm/Rosales/Rosaceae	Ornamental	gigadb.org; www.rosaceae.org
Rosa chinensis	Chinese rose	Angiosperm/Rosales/Rosaceae	Ornamental	www.rosaceae.org
Rosa multiflora	Many-flowered rose	Angiosperm/Rosales/Rosaceae	Ornamental	www.rosaceae.org
Rosa roxburghii	Chestnut rose	Angiosperm/Rosales/Rosaceae	Ornamental	www.rosaceae.org
Daucus carota	Carrot	Angiosperm/Apiales/Apiaceae	Vegetable	bioinformatics.psb.ugent.be/plaza; plants.ensembl.org; phytozome.jgi.doe.gov
Panax ginseng	Asian ginseng	Angiosperm/Apiales/Araliaceae	Medicinal	herbalplant.ynau.edu.cn
Panax notoginseng	Sanchi ginseng	Angiosperm/Apiales/Araliaceae	Medicinal	herbalplant.ynau.edu.cn
Artemisia annua	Sweet wormwood	Angiosperm/Asterales/Asteraceae	Medicinal	herbalplant.ynau.edu.cn
Conyza canadensis	Horseweed	Angiosperm/Asterales/Asteraceae	Medicinal	genomevolution.org/CoGe
Erigeron breviscapus	Chinese fleabane	Angiosperm/Asterales/Asteraceae	Medicinal	www.ncbi.nlm.nih.gov/genome/?term=Eleusine+coracana
Chrysanthemum nankingense	Juhuanao	Angiosperm/Asterales/Asteraceae	Vegetable	genomevolution.org/CoGe
Cynara cardunculus	Cardoon	Angiosperm/Asterales/Asteraceae	Vegetable	www.artichokegenome.unito.it

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Table 1 (continued)

Species	Common name	Taxonomy	Type	DB-url
Lactuca sativa	Lettuce	Angiosperm/ Asterales/Asteraceae	Vegetable	phytozome.jgi.doe.gov
Eutrema yunnanense	Shan yu cai	Angiosperm/ Brassicales/ Brassicaceae	Medicinal	
Lepidium meyenii	Maca	Angiosperm/ Brassicales/ Brassicaceae	Medicinal	maca.eplant.org
Brassica juncea	Zhacai	Angiosperm/ Brassicales/ Brassicaceae	Vegetable	brassicadb.org
Brassica oleracea	Cabbage	Angiosperm/ Brassicales/ Brassicaceae	Vegetable	brassicadb.org; genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza; chibba.agtec.uga.edu/duplication; plants.ensembl.org
Brassica rapa	Chinese cabbage	Angiosperm/ Brassicales/ Brassicaceae	Vegetable	plants.ensembl.org; genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza; phytozome.jgi.doe.gov; chibba.agtec.uga.edu/duplication; plants.ensembl.org; www.plantgdb.org
Capsella bursa-pastoris	Shepherd's purse	Angiosperm/ Brassicales/ Brassicaceae	Vegetable	genome.ccbr.utoronto.ca/cgi-bin/hgGateway
Capsella rubella	Red shepherd's purse	Angiosperm/ Brassicales/ Brassicaceae	Vegetable	genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza; chibba.agtec.uga.edu/duplication; phytozome.jgi.doe.gov
Raphanus sativus	Radish	Angiosperm/ Brassicales/ Brassicaceae	Vegetable	radish.kazusa.or.jp
Thlaspi arvense	Field pennycress	Angiosperm/ Brassicales/ Brassicaceae	Vegetable	pennycress.umn.edu
Carica papaya	Papaya	Angiosperm/ Brassicales/Caricaceae	Fruit	genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza; phytozome.jgi.doe.gov; chibba.agtec.uga.edu/duplication; www.plantgdb.org
Tarenaya hassleriana	Spider flower	Angiosperm/ Brassicales/ Cleomaceae	Ornamental	genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza
Moringa oleifera	Moringa	Angiosperm/ Brassicales/ Moringaceae	Vegetable	bioinformatics.psb.ugent.be/plaza
Amaranthus hypochondriacus	Prince's feather	Angiosperm/ Caryophyllales/ Amaranthaceae	Ornamental	phytozome.jgi.doe.gov; genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza
Beta vulgaris	Sugar beet	Angiosperm/ Caryophyllales/ Amaranthaceae	Vegetable	bioinformatics.psb.ugent.be/plaza; chibba.agtec.uga.edu/duplication; plants.ensembl.org
Spinacia oleracea	Spinach		Vegetable	spinachbase.org

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Table 1 (continued)

Species	Common name	Taxonomy	Type	DB-url
		Angiosperm/ Caryophyllales/ Amaranthaceae		
Carnegiea gigantea	Saguaro cactus	Angiosperm/ Caryophyllales/ Cactaceae	Ornamental	phytozome.jgi.doe.gov
Dianthus caryophyllus	Carnation	Angiosperm/ Caryophyllales/ Caryophyllaceae	Ornamental	carnation.kazusa.or.jp
Casuarina glauca	Swamp oak	Angiosperm/ Caryophyllales/ Casuarinaceae	Ornamental	
Drosera capensis	Cape sundew	Angiosperm/ Caryophyllales/ Droseraceae	Ornamental	
Camptotheca acuminata	Happy tree	Angiosperm/ Cornales/Nyssaceae	Ornamental	www.plantkingdomgdb.com; genomevolution.org/CoGe
Actinidia chinensis	Kiwifruit	Angiosperm/Ericales/ Actinidiaceae	Fruit	bdg.hfut.edu.cn/kir; genomevolution.org/coge
Diospyros lotus	Date-plum	Angiosperm/Ericales/ Ebenaceae	Fruit	gigadb.org
Vaccinium corymbosum	Blueberry	Angiosperm/Ericales/ Ericaceae	Fruit	www.vaccinium.org
Vaccinium macrocarpon	American cranberry	Angiosperm/Ericales/ Ericaceae	Fruit	gigadb.org
Rhododendron delavayi	Tree rhododendron	Angiosperm/Ericales/ Ericaceae	Ornamental	
Primula vulgaris	Common primrose	Angiosperm/Ericales/ Primulaceae	Medicinal	phytozome.jgi.doe.gov
Primula veris	Cowslip	Angiosperm/Ericales/ Primulaceae	Ornamental	plantgenie.org
Camellia sinensis	Tea tree	Angiosperm/Ericales/ Theaceae	Beverage	tpia.teaplant.org
Eucommia ulmoides	Hardy rubber tree	Angiosperm/ Garryales/ Eucommiaceae	Medicinal	
Calotropis gigantea	Crown flower	Angiosperm/ Gentianales/ Apocynaceae	Medicinal	
Catharanthus roseus	Madagascar periwinkle	Angiosperm/ Gentianales/ Apocynaceae	Medicinal	genomevolution.org/CoGe
Coffea arabica	Arabian coffee	Angiosperm/ Gentianales/ Rubiaceae	Beverage	www.coffee-genome.org; phytozome.jgi.doe.gov

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Table 1 (continued)

Species	Common name	Taxonomy	Type	DB-url
Coffea canephora	Robusta Coffee	Angiosperm/ Gentianales/ Rubiaceae	Beverage	genomevolution.org/CoGe; www.coffee-genome.org; bioinformatics.psb.ugent.be/plaza
Andrographis paniculata	Green chireta	Angiosperm/ Lamiales/ Acanthaceae	Medicinal	
Handroanthus impetiginosus	Pink trumpet tree	Angiosperm/ Lamiales/ Bignoniaceae	Ornamental	www.hardwoodgenomics.org
Boea hygrometrica	N.A.	Angiosperm/ Lamiales/ Gesneriaceae	Ornamental	genomevolution.org
Mentha longifolia	Horse mint	Angiosperm/ Lamiales/Lamiaceae	Medicinal	phytozome.jgi.doe.gov
Ocimum sanctum	Holy basil	Angiosperm/ Lamiales/Lamiaceae	Medicinal	caps.ncbs.res.in/Ote
Scutellaria baicalensis	Baikal skullcap	Angiosperm/ Lamiales/Lamiaceae	Medicinal	
Lavandula angustifolia	Lavender	Angiosperm/ Lamiales/Lamiaceae	Ornamental	
Salvia splendens	Scarlet sage	Angiosperm/ Lamiales/Lamiaceae	Ornamental	gigadb.org
Osmanthus fragrans	Sweet osmanthus	Angiosperm/ Lamiales/Oleaceae	Medicinal	sweetolive.eplant.org
Fraxinus excelsior	European ash	Angiosperm/ Lamiales/Oleaceae	Ornamental	www.hardwoodgenomics.org
Mimulus guttatus	Seep monkeyflower	Angiosperm/ Lamiales/Phrymaceae	Ornamental	phytozome.jgi.doe.gov; www.plantgdb.org
Theobroma cacao	Cacao	Angiosperm/ Malvales/Malvaceae	Beverage	bioinformatics.psb.ugent.be/plaza/; chibba.agtec.uga.edu/duplication; plants.ensembl.org; phytozome.jgi.doe.gov
Durio zibethinus	Durian	Angiosperm/ Malvales/Malvaceae	Fruit	
Corchorus olitorius	Chang shuo huang ma	Angiosperm/ Malvales/Malvaceae	Medicinal	bioinformatics.psb.ugent.be/plaza
Bombax ceiba	Red silk-cotton tree	Angiosperm/ Malvales/Malvaceae	Ornamental	
Hibiscus syriacus	Rose of Sharon	Angiosperm/ Malvales/Malvaceae	Ornamental	
Aquilaria agallocha	Agarwood	Angiosperm/ Malvales/ Thymelaeaceae	Medicinal	
Santalum album	Indian sandalwood	Angiosperm/ Santalales/ Santalaceae	Medicinal	

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Table 1 (continued)

Species	Common name	Taxonomy	Type	DB-url
Citrus clementina	Clementine citrus	Angiosperm/ Sapindales/Rutaceae	Fruit	genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza; phytozome.jgi.doe.gov
Citrus grandis	Pummelo	Angiosperm/ Sapindales/Rutaceae	Fruit	www.citrusgenomedb.org
Citrus ichangensis	Ichang papeda	Angiosperm/ Sapindales/Rutaceae	Fruit	www.citrusgenomedb.org
Citrus paradisi × *Poncirus trifoliata*	Citrumelo	Angiosperm/ Sapindales/Rutaceae	Fruit	
Citrus reticulata	Mandarin orange	Angiosperm/ Sapindales/Rutaceae	Fruit	www.citrusgenomedb.org
Citrus sinensis	Sweet orange	Angiosperm/ Sapindales/Rutaceae	Fruit	www.citrusgenomedb.org
Citrus unshiu	Cold hardy mandarin	Angiosperm/ Sapindales/Rutaceae	Fruit	www.citrusgenomedb.org
Atalantia buxifolia	Jiu bing le	Angiosperm/ Sapindales/Rutaceae	Medicinal	www.citrusgenomedb.org
Citrus medica	Citron	Angiosperm/ Sapindales/Rutaceae	Medicinal	www.citrusgenomedb.org
Dimocarpus longan	Longan	Angiosperm/ Sapindales/ Sapindaceae	Fruit	gigadb.org
Rhodiola crenulata	Tibetan Rhodiola	Angiosperm/ Saxifragales/ Crassulaceae	Medicinal	gigadb.org
Kalanchoe fedtschenkoi	Lavender-scallops	Angiosperm/ Saxifragales/ Crassulaceae	Ornamental	phytozome.jgi.doe.gov
Cuscuta australis	Australian dodder	Angiosperm/ Solanales/ Convolvulaceae	Medicinal	
Cuscuta campestris	Prairie dodder	Angiosperm/ Solanales/ Convolvulaceae	Medicinal	plabipd.de/project_cuscuta2/start.ep
Ipomoea nil	Japanese morning glory	Angiosperm/ Solanales/ Convolvulaceae	Ornamental	viewer.shigen.info/asagao
Nicotiana sylvestris	Flowering tobacco	Angiosperm/ Solanales/Solanaceae	Ornamental	solgenomics.net
Petunia axillaris	N.A.	Angiosperm/ Solanales/Solanaceae	Ornamental	genome.jgi.doe.gov; bioinformatics.psb.ugent.be/plaza; solgenomics.net
Petunia inflata	N.A.	Angiosperm/ Solanales/Solanaceae	Ornamental	solgenomics.net
Solanum pennellii	Wild tomato	Angiosperm/ Solanales/Solanaceae	Vegetable relative	

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Table 1 (continued)

Species	Common name	Taxonomy	Type	DB-url
Capsicum annuum	Spanish pepper	Angiosperm/ Solanales/Solanaceae	Vegetable	bioinformatics.psb.ugent.be/plaza; chibba.agtec.uga.edu/duplication; solgenomics.net
Capsicum baccatum	Berry-like pepper	Angiosperm/ Solanales/Solanaceae	Vegetable	genomevolution.org/CoGe
Capsicum chinense	Bonnet pepper	Angiosperm/ Solanales/Solanaceae	Vegetable	www.pepperpan.org:8012
Solanum lycopersicum	Tomato	Angiosperm/ Solanales/Solanaceae	Vegetable	bioinformatics.psb.ugent.be/plaza; phytozome.jgi.doe.gov; chibba.agtec.uga.edu/duplication;pgsb.helmholtz-muenchen.de; plants.ensembl.org; www.plantgdb.org; solgenomics.net
Solanum melongena	Eggplant	Angiosperm/ Solanales/Solanaceae	Vegetable	solgenomics.net; genomevolution.org/CoGe
Solanum pimpinellifolium	Currant tomato	Angiosperm/ Solanales/Solanaceae	Vegetable	solgenomics.net
Solanum tuberosum	Potato	Angiosperm/ Solanales/Solanaceae	Vegetable	genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza; chibba.agtec.uga.edu/duplication; plants.ensembl.org; www.plantgdb.org; phytozome.jgi.doe.gov; solgenomics.net
Vitis vinifera	Grape	Angiosperm/Vitales/ Vitaceae	Fruit	phytozome.jgi.doe.gov; genomevolution.org/CoGe; bioinformatics.psb.ugent.be/plaza; chibba.agtec.uga.edu/duplication; plants.ensembl.org; www.plantgdb.org
Punica granatum	Pomegranate	Angiosperm/ Myrtales/Lythraceae	Fruit	www.hardwoodgenomics.org
Marchantia polymorpha	Umbrella liverwort	Bryophyta/ Marchantiales/ Marchantiaceae	Medicinal	bioinformatics.psb.ugent.be/plaza; phytozome.jgi.doe.gov
Ginkgo biloba	Ginkgo tree	Gymnosperms/ Ginkgoales/ Ginkgoaceae	Medicinal	gigadb.org/site/index
Gnetum montanum	Jointfir	Gymnosperms/ Gnetales/Gnetaceae	Medicinal	www.datadryad.org/resource/doi:10.5061/dryad.0vm37; genomevolution.org/coge
Selaginella lepidophylla	Resuscitation moss	Lycophyta/ Selaginellales/ Selaginellaceae	Medicinal	plantgdb.org/SmGDB/
Selaginella moellendorffii	Spikemoss	Lycophyta/ Selaginellales/ Selaginellaceae	Medicinal	phytozome.jgi.doe.gov; genomevolution.org/CoGe; chibba.agtec.uga.edu/duplication; bioinformatics.psb.ugent.be/plaza; plants.ensembl.org; www.plantgdb.org/
Selaginella tamariscina	Little club moss	Lycophyta/ Selaginellales/ Selaginellaceae	Medicinal	www.ncbi.nlm.nih.gov/assembly/GCA_003024785.1; genomevolution.org/coge

N.A. not available

arvense)[60]. The genomes of the Brassicaceae medicinal plants *Eutrema yunnanense*[61] and maca (*Lepidium meyenii*)[62] have also been sequenced. With these genome sequences at hand, the genomic features of common ancestors and the subsequent evolution of the Brassicaceae can be clarified, such as the intron evolution within the Brassicaceae[63], and gene and genome duplication events within the Brassicaceae[64,65]. These genomes would also shed light on the evolution of the hypocotyl, as has been reported in maca[62] and radish[59]. Within the Brassicaceae family, we could foresee a growing demand for the genome sequencing of horticultural Brassicaceae plants, both for evolutionary research and for decoding the molecular basis of economically important traits.

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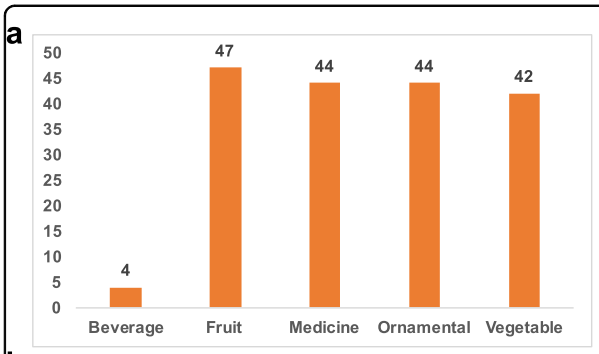

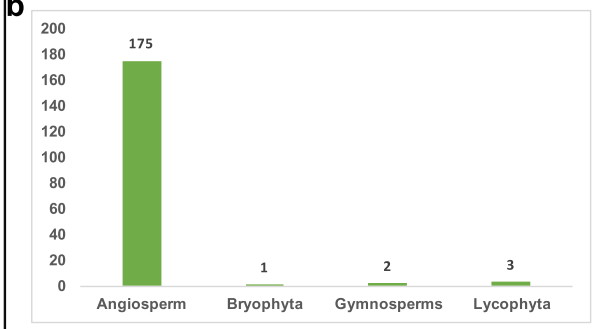

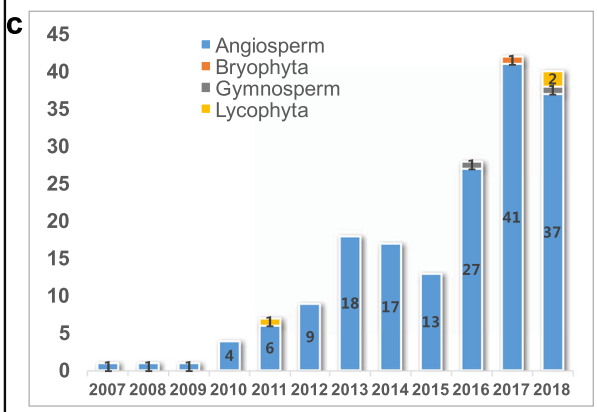

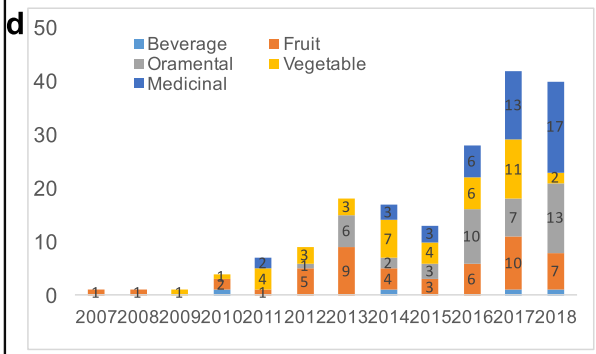

e

Clade	Genomes	Clade	Genomes
Basal		Malpighiales	2
Amborellales	0	Celastrales	0
Nymphaeales	0	Zygophyllales	0
Austrobaileyales	0	Geraniales	0
Monocots		Myrtales	1
Arecales	2	Crossosomatales	0
Poales	4	Picramniales	0
Commelinales	0	Malvales	6
Zingiberales	4	Brassicales	12
Asparagales	5	Huerteales	0
Liliables	0	Sapindales	10
Dioscoreales	1	Vitales	1
Pandanales	0	Saxifragales	2
Petrosaviales	0	Dilleniales	0
Alismatales	3	Berberidopsidales	0
Acorales	0	Santalales	1
Magnoliids		Caryophyllales	7
Magnoliales	1	Cornales	1
Laurales	0	Ericales	8
Piperales	0	Aquifoliables	0
Canellales	0	Asterales	6
Ceratophyllales	0	Escalloniales	0
Chloranthales	0	Bruniales	0
Eudicots		Apiales	3
Ranunculales	4	Dipsacales	0
Proteales	2	Paracryphiales	0
Trochodendrales	0	Solanales	14
Buxales	0	Lamiales	11
Gunnerales	0	Vahliales	0
Fabales	14	Gentianales	4
Rosales	25	Boraginales	0
Fagales	9	Garryales	1
Cucurbitales	11	Metteniusales	0
Oxalidales	0	Icacinales	0
Total Orders = 64, Orders with sequenced genomes = 30			
Total sequenced Angiosperms genomes = 175			

f

Speices	Type	Taxonomy	size (Mb)
Coffea eugenioides	Drink	Angiosperm, Gentianales,Rubiaceae	699.904
Juglans mandshurica	Fruit	Angiosperm, Fagales,Juglandaceae	558.071
Passiflora edulis	Fruit	Angiosperm, Malpighiales,Passifloraceae	165.657
Psidium guajava	Fruit	Angiosperm, Myrtales,Passifloraceae	386.852
Xanthoceras sorbifolium	Fruit	Angiosperm, Sapindales,Sapindaceae	504.383
Vitis aestivalis	Fruit	Angiosperm, Vitales,Vitaceae	432.755
Vitis cinerea × Vitis riparia	Fruit	Angiosperm, Vitales,Vitaceae	514.63
Persea americana	Fruit	Angiosperms, Laurales,Lauraceae	446.756
Citrus cavaleriei	Fruit	Angiosperms, Sapindales,Rutaceae	357.621
Citrus maxima	Fruit	Angiosperms, Sapindales,Rutaceae	345.757
Quillaja saponaria	Medicine	Angiosperm, Fabales,Quillajaceae	248.908
Perilla citriodora	Medicine	Angiosperm, Lamiales,Lamiaceae	618.797
Solanum americanum	Medicine	Angiosperm, Solanales,Solanaceae	9.83576
Embelia ribes	Medicine	Angiosperms, Ericales,Primulaceae	660.51
Monotropa hypopitys	Medicine	Angiosperms, Ericales,Ericaceae	2197.49
Nothapodytes nimmoniana	Medicine	Angiosperms, Gunnerales,Icacinaceae	1.36527
Euphorbia esula	Medicine	Angiosperms, Malpighiales,Euphorbiaceae	1124.89
Geum urbanum	Medicine	Angiosperms, Rosales,Rosaceae	1217.04
Cissus quadrangularis	Medicine	Angiosperms, Vitales,Vitaceae	281.704
Pachycereus pringlei	Ornamental	Angiosperm, Caryophyllales,Cactaceae	629.656
Stenocereus thurberi	Ornamental	Angiosperm, Caryophyllales,Cactaceae	853.348
Ruellia speciosa	Ornamental	Angiosperm, Lamiales,Acanthaceae	740.036
Eugenia uniflora	Ornamental	Angiosperms, Myrtales,Myrtaceae	639.02
Berberis thunbergii	Ornamental	Angiosperms, Ranunculales,Berberidaceae	2240.74
Pisum sativum	Vegetable	Angiosperm, Fabales,Fabaceae	4275.93
Erythranthe guttata	Vegetable	Angiosperm, Lamiales,Phrymaceae	1402.73
Cicer echinospermum	Vegetable	Angiosperms, Fabales,Fabaceae	644.721

Fig. 1 Statistics of genome-sequenced horticultural plant species. a Distribution of genome-sequenced horticultural plants. **b** Botanical distribution of genome-sequenced horticultural plants. **c** Annual increase in the genome-sequenced horticultural plants by botanical taxonomy. **d** Annual increase in the genome-sequenced horticultural plants by horticultural category. **e** The reported 181 horticultural plant species fall into 30 angiosperm orders. **f** List of the released but not reported horticultural plant species

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Table 2 Pan-genome information of horticultural plants

Pan-genome	Covered population	Year of release	Horticultural category	Tool	Pan-genome database
Glycine soja	7 cultivars	2014	Wild relatives of vegetable	N.A.	N.A.
Brassica oleracea	9 cultivars	2016	Vegetable	Gbrowse, BLAST, Gbrowse	http://brassicagenome.net/
Capsicum spp.	383 cultivars, including 355 *C. annuum*, four *C. baccatum*, 11 *C. chinense*, 13 *C. frutescens*	2018	Vegetable	Search, Jbrowse	http://www.pepperpan.org:8012/
Helianthus annuus	493 accessions	2018	Ornamental	N.A.	www.sunflowergenome.org
Solanum lycopersicum	725 accessions	2019	Vegetable	N.A.	N.A.

N.A. not available

The Cucurbitaceae family includes >3700 species belonging to 134 genera (www.theplantlist.org). Within this family, the genome-decoded vegetable plants include silver-seed gourd (*Cucurbita argyrosperma*)[66], winter squash (*Cucurbita maxima*)[67], pumpkin (*Cucurbita moschata*)[67], summer squash (*Cucurbita pepo*)[68], bottle gourd (*Lagenaria siceraria*)[69], and bitter melon (*Momordica charantia*)[70]. The genome-decoded fruit species include muskmelon (*Cucumis melo*)[71] and watermelon (*Citrullus lanatus*)[72]. The only genome-decoded medicinal plant is monk fruit (*Siraitia grosvenorii*)[73,74]. Via analysis of these available genome sequences, it was found that a tetraploid-inducing event occurred in the last common ancestor of the Cucurbitaceae species[75]. These genome sequences can also help to better understand the domestication history[76] and fruit development[77]. Increasing numbers of the wild relatives of these economically important crop species, as well as those of thousands of plant cultivars, will be sequenced in the near future, providing additional details and surprises.

The Rutaceae or citrus family consists of 158 genera and 6686 species (www.theplatlist.org). The Rutaceae fruit-bearing plants with sequenced genomes include clementine (*Citrus clementina*)[78], pomelo (*Citrus grandis*)[79], Ichang papeda (*Citrus ichangensis*)[79], citrumelo (*Citrus paradisi* × *Poncirus trifoliate*)[80], mandarin orange (Citrus reticulata)[81], sweet orange (*Citrus sinensis*)[82], and cold-hardy mandarin (*Citrus unshiu*)[83]. The Rutaceae medicinal plants with sequenced genomes include jiu bing le (*Atalantia buxifolia*)[79] and citron (*Citrus medica*)[79]. Via analysis of these genome sequences, the evolutionary origin and evolutionary changes in the *Citrus* genus during domestication were mapped[84]. In the future, the genome sequences of Rutaceae fruit-bearing plants including lemon (*Citrus limon*), calamansi (*Citrofortunella microcarpa*), lime (*Citrus* spp. hybrids), kumquat (*Citrus japonica*), and grapefruit (*Citrus* × *paradisi*) will require genome sequencing.

Genome resequencing and the pan-genome of horticultural plants

A single reference genome sequence is not sufficient for identifying the best candidate genes for molecular breeding or for understanding the genomic background of a population due to the prevalence of genomic structural variations. Compared to the construction of a reference genome, genome resequencing usually requires less sequencing coverage. It is feasible to obtain a high-quality resequenced genome via mapping to a reference genome. A pan-genome is the summary of genomes of a species obtained by comparing a large number of resequenced genomes of a species or, occasionally, a genus. A pan-genome can help to understand the size of a core genome (defined as the conserved part among the related genomes), the size of a pan-genome, and the amount and nature of variations within a species or a genus, which improve our understanding of the evolution of a species/genu, as well as of agronomic traits. Currently, a growing number of pan-genomes among horticultural plants have been constructed (Table 2).

Soybean is an economically important vegetable crop; in addition to being a source of human protein, it is an important source of vegetable oil. *Glycine soja* is the closest wild relative to cultivated soybean (*Glycine max*). The *G. soja* pan-genome was the first horticultural pan-genome released, which occurred in 2014 and consisted of seven wild accessions[85] (Table 2). This pan-genome revealed that, when more genomes were added, the number of shared genes decreased, and in contrast, the number of total genes increased when more genomes were added. In addition, this pan-genome confirmed that

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a single reference genome does not adequately represent the genomic and genetic diversity of a species. Because the reference genome of *G. soja* was not previously available, those researchers assembled all seven genomes with the de novo assembly method, but this method was not adopted by subsequent researchers.

Assembly of the *B. oleracea* pan-genome[86] is another early trial in the genomic research of horticultural plants (Table 2). It is relatively small, created using nine morphologically diverse varieties (covering two cabbage, one broccoli, one brussels sprout, one kohlrabi, two cauliflowers, and one kale plant) and a wild relative, *Brassica macrocarpa*. Through the analyses of this pan-genome, we observed that 20% of genes are absent in some cultivar (s), and there are presence–absence variations (PAVs), including those related to major agronomic traits. This is a pioneering study that provided assembled pan-genome contigs, pan-genome annotations, and the GBrowse tool, available at http://brassicagenome.net.

Pepper plants are important vegetable plants with distinct fruit morphologies. The pepper pan-genome has been generated for the pepper genus *Capsicum*[87]. This pan-genome consists of 5 species and 383 cultivars, all of which have 15 chromosomes. In addition to the comparison of PAVs among this large amount of pepper cultivars, the pan-genome is also useful in linking the association between important agronomic traits and corresponding genes. These valuable pan-genome data and JBrowse and other search tools are available (www.pepperpan.org:8012).

Sunflower plants provide seed that can be used for cooking oil and serve as popular ornamentals. The sunflower pan-genome was created by sequencing 493 accessions, including cultivars, landraces, and wild relatives[5]. A total of 61,205 genes have been identified within the gene set of the sunflower pan-genome. Via the aid of this pan-genome, the understanding of the evolutionary history of sunflower species has significantly improved, and genes linked to biotic stress resistance have been identified[5]. Although pan-genome data can be found in the sunflower genome database (www.sunflowergenome.org), no publicly accessible tool has been built to date (accessed March 31, 2019).

Reference genome sequences are necessary to identify genes and to understand evolutionary trajectory. However, a pan-genome can help to uncover additional details. For example, relying on the tomato genome sequence, researchers mapped only several genes and pathways controlling fruit ripening[28]. These flesh- and flavor-related genes are the best targets in breeding. Moreover, genome sequences allow comprehensive and systematic analyses of fruit biology. Furthermore, via the sequencing of a tomato population and analysis of its pan-genome consisting of 725 accessions, the genes selected during domestication and quality improvement were identified[88]. Thus a pan-genome not only improves our understanding of crop evolution but also is useful for the discovery of novel genes and breeding.

Data storage and visualization

In addition to comprehensive plant-centric databases such as Phytozome (https://phytozome.jgi.doe.gov) and EnsemblPlants (http://plants.ensembl.org), 27 horticultural plant-specific genome databases have been constructed (Table 3). Among these, 22 provide data for downloading. Some databases are freely accessible to all users, while others provide only limited access to specific data or users. For example, the Genome Database for Rosaceae[89] requires user registration and a login to access the breeding data.

Visualization of genomic data of horticultural plants is challenging due to the heterogeneous nature of the different types of data. GBrowse[90] and JBrowse[91–93] are powerful tools that provide a visualization of various levels of genomic features. The availability of genomic analysis tools also varies greatly among databases. BLAST-related tools such as NCBI-BLAST[94] and viroBLAST[95] are provided by some databases for homologous sequence searches and sequence comparisons. Gene query tools can help to obtain details of genes such as their sequence, annotation, and expression. HMMER[96] searches allow the inference and extraction of gene families from genomes in the database. Syntenic tools allow the identification and visualization of genome-wide syntenic relationships across genomes. The BioCyc tools (https://biocyc.org) allow users to navigate individual pathways or the whole metabolic map of a genome for functional analyses[97].

The Genome Database for Rosaceae (GDR), which was developed by the main bioinformatics laboratory at Washington State University[89], is well known among the Rosaceae research community and even the plant research community. It covers the genome sequences of 18 Rosaceae species (*Fragaria vesca*, *F. ananassa*, *F. iinumae*, *F. nipponica*, *F. nubicola*, *F. orientalis*, *Malus domestica*, *Potentilla micrantha*, *Prunus avium*, *Prunus domestica*, *Prunus dulcis*, *Prunus persica*, *Prunus yedoensis*, *Pyrus bretschneideri*, *Pyrus communis*, *Rosa chinensis*, *Rosa multiflora*, and *Rubus occidentalis*), which are categorized into seven genera: *Fragaria*, *Malus*, *Potentilla*, *Prunus*, *Pyrus*, *Rosa*, and *Rubus*. To facilitate online analyses, a series of tools are provided, including genomic tools (BLAST+, JBrowse, Primer3, Sequence Retrieval, MapViewer, Synteny Viewer), metabolomic tools (GDRcyc, Pathway Inspector), and breeding tools (Breeding information Management System (BMS), Breeders Toolbox). The same team at Washington State University also developed a series of horticultural plant-themed

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Table 3 List of horticultural plant-centric genome databases

Database name	Covered species	Tools
Herbal Medicine Omics Database	*Calotropis gigantea*	BLAST
(herbalplant.ynau.edu.cn)	*Catharanthus roseus*	GBrowse
	Rhodiola rosea	
	Gastrodia elata	
	Eucommia ulmoides	
	Camptotheca acuminata	
	Ginkgo biloba	
	Dioscorea rotundata	
	Panax ginseng	
	Punica granatum	
	Boea hygrometrica	
	Jatropha curcas	
	Glycyrrhiza uralensis	
	Cannabis sativa	
	Macleaya cordata	
	Mentha longifoli	
	Erigeron breviscapus	
	Panax notoginseng	
	Moringa oleifera	
	Lepidium meyenii	
	Dendrobium officinale	
	Salvia miltiorrhiza	
Genome Database for Rosaceae (GDR)	*Fragaria vesca*	Breeding Information Management System
(www.rosaceae.org)	*Fragaria* x *ananassa*	BLAST+
	Malus x *domestica*	Breeders Toolbox
	Prunus armeniaca	GDRCyc
	Prunus avium	JBrowse
	Prunus cerasus	MapViewer
	Prunus dulcis	Pathway Inspector
	Prunus persica	Primer3
	Prunus serotina	Sequence Retrieval
	Pyrus communis	Synteny Viewer
	Rubus occidentalis	
Sol Genomics Network	*Solanum pennellii*	BLAST
(solgenomics.net)	*Solanum lycopersicoides*	VIGS Tool
	Nicotiana attenuata	Alignment Analyzer
	Nicotiana benthamiana	Tree Browser
	Nicotiana tabacum	Genome Browser (JBrowse)
	Petunia axillaris	Comparative Map Viewer
	Petunia inflata	CAPS Designer
	Solanum pimpinellifolium	solQTL: QTL Mapping
	Solanum lycopersicum	In Silico PCR
	Solanum tuberosum	Tomato Expression Atlas (TEA)
	Solanum phureja	Tomato Expression Database (TED)
	Capsicum annuum	SolCyc Biochemical Pathways
	Petunia axillaris	Coffee Interactomic Data
	Petunia x *hybrida*	SGN Ontology Browser
	Petunia integrifolia var inflata	Breeders Toolbox
		FTP Site
		Download Gene Sequences
		Clones, Arrays, Unigenes and BACs
		Unigene Converter
Citrus Genome Database (CGD)	*Citrus clementina*	Breeding Information Management System
(www.citrusgenomedb.org)	*Citrus ichangensis*	BLAST+
	Citrus sinensis	Breeders Toolbox
	Citrus reticulata	GDRCyc
	Citrus maxima	JBrowse
	Citrus medica	MapViewer
	Poncirus trifoliata	Pathway Inspector
	Atalantia buxifolia	Primer3
		Sequence Retrieval
		Synteny Viewer
Cool Season Food Legume Database (CSFL)	*Cicer arietinum*	JBrowse
(www.coolseasonfoodlegume.org)	*Cicer reticulatum*	PathwayCyc
	Vicia faba	Breeding Information Management System
	Pisum sativum	MapViewer
	Lens culinaris	Synteny Viewer
		BLAST+
Cucurbit Genomics Database (CuGenDB)	*Cucumis sativus*	BLAST
(cucurbitgenomics.org)	*Cucumis melo*	JBrowse
	Citrullus lanatus	Batch Query
	Cucurbita maxima	Synteny Viewer
	Cucurbita moschata	CMAP
	Cucurbita pepo	CucurbitCyc
	Lagenaria siceraria	Pathway enrichment
		GO enrichment

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Table 3 (continued)

Database name	Covered species	Tools
		Gene classification
Banana Genome Hub	*Musa acuminata* DH-Pahang	BLAST
(banana-genome-hub.southgreen.fr)	*Musa acuminata* Banksii	JBrowse
	Musa acuminata Zebrina	GBrowser
	Musa acuminata Calcutta 4	Generic Maps
	Musa balbisiana PKW	Gene Family
	Musa Itinerans	Chromosome viewer
	Musa schizocarpa	Transcriptomic Search
		Design primer
		Ontology Browser
		Dotplot
Brassica database (BRAD)	*Brassica rapa*	BLAST
(brassicadb.org)	*Brassica juncea*	Gbrowse
	Brassica napus	Markers and Maps
	Brassica oleracea	Gene families
		Glucosinolate genes
		Anthocyanin genes
		Resistance genes
		Flower genes
		Transcription factors
		Auxin genes
		Phenotypes
		People/Labs
Pepper Pangenome Browser (PepperPan)	*Capsicum annuum*	Generic genome browser
(www.pepperpan.org:8012)	*Capsicum baccatum*	
	Capsicum frutescens	
Cofffee Genome Hub (CGH)	*Coffea canephora*	Advanced Search
(www.coffee-genome.org/coffeacanephora)	*Coffea arabica*	Chromosome Viewer
		Gene annotation
		Gene Expression
		Gene Families
		Genetic Map
		Primer Blaster
		Primer Designer
		SNPs
		Blast
		JBrowse
		GBrowser
Viggs	Vigna marina subsp. oblonga	Gbrowse
(viggs.dna.affrc.go.jp)	*Vigna angularis*	BLAST
	Vigna angularis (Willd.)	BLAT
	Vigna vexillata	
Cannabis genome project (CCBR)	*Cannabis sativa*	BLAST

Table 3 (continued)

Database name	Covered species	Tools
(genome.ccbr.utoronto.ca/cgi-bin/hgGateway)		GBrowser
		Design primer
Carnation DB	*Dianthus caryophyllus*	BLAST
(carnation.kazusa.or.jp)		
HopBase	*Humulus lupulus*	BLAST
(hopbase.cgrb.oregonstate.edu)		Gbrowse
Medicago truncatula Genome Database (MTGD)	*Medicago truncatula*	JBrowse
(www.medicagogenome.org)		BLAST
		Web Services
		CMap (LegumeInfo.org)
		GO Analysis
		InterPro Annotations
Tea Plant Information Archive (TPIA)	*Camellia sinensis*	BLAST
(tpia.teaplant.org/)		Gbrowse
		Pathway
		Correlation Analysis
		Function Erichment
		Batch Retrival
Mulberry Genome Database (MorusDB)	*Morus notabilis*	Transposable Element Analysis
(morus.swu.edu.cn/morusdb)		Horizontal Gene Transfer Analysis
		Ortholog and Paralog Group Analysis
		BLAST
		WEGO
		HMMER
		Browse GO
		Search GO
		Find Motifs
Pear Genome Project	*Pyrus bretschneideri*	Download
(peargenome.njau.edu.cn)		
Radish Genome database	*Raphanus sativus*	BLAST
(www.radish-genome.org/)		Gbrowse
		Expression
CsiDB	*Citrus sinensis*	Gene Search
(citrus.hzau.edu.cn)		BLAST
		GBrowser
		PPI
		Pathway
Mint Genomics Resource	*Mentha longifolia*	BLAST
(langelabtools.wsu.edu/mgr/organism/Mentha/longifolia)		Gbrowse
		Pathway
CeleryDB	*Apium graveolens*	BLAST
(apiaceae.njau.edu.cn)		GBrowser
		Transcription factors
CarrotDB	*Daucus carota*	BLAST
(apiaceae.njau.edu.cn/)		Gbrowse
		Transcription factors

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Table 3 (continued)

Database name	Covered species	Tools
		Germplasm Resources Collection
Banana Genome Hub	*Musa acuminata* DH-Pahang	BLAST
(banana-genome-hub.southgreen.fr)	*Musa acuminata* Banksii	JBrowse
	Musa acuminata Zebrina	GBrowser
	Musa acuminata Calcutta 4	Generic Maps
	Musa balbisiana PKW	Gene Family
	Musa Itinerans	Chromosome viewer
	Musa schizocarpa	Transcriptomic Search
		Design primer
		Ontology Browser
		Dotplot
Brassica database (BRAD)	*Brassica rapa*	BLAST
(brassicadb.org)	*Brassica juncea*	Gbrowse
	Brassica napus	Markers and Maps
	Brassica oleracea	Gene families
		Glucosinolate genes
		Anthocyanin genes
		Resistance genes
		Flower genes
		Transcription factors
		Auxin genes
		Phenotypes
		People/Labs
Pepper Pangenome Browser (PepperPan)	*Capsicum annuum*	Generic genome browser
(www.pepperpan.org:8012)	*Capsicum baccatum*	
	Capsicum frutescens	
Cofffee Genome Hub (CGH)	*Coffea canephora*	Advanced Search
(www.coffee-genome.org/coffeacanephora)	*Coffea arabica*	Chromosome Viewer
		Gene annotation
		Gene Expression
		Gene Families
		Genetic Map
		Primer Blaster
		Primer Designer
		SNPs
		Blast
		JBrowse
		GBrowser
Viggs	Vigna marina subsp. oblonga	Gbrowse
(viggs.dna.affrc.go.jp)	*Vigna angularis*	BLAST
	Vigna angularis (Willd.)	BLAT
	Vigna vexillata	
Cannabis genome project (CCBR)	*Cannabis sativa*	BLAST

Table 3 (continued)

Database name	Covered species	Tools
(genome.ccbr.utoronto.ca/cgi-bin/hgGateway)		GBrowser
		Design primer
Carnation DB	*Dianthus caryophyllus*	BLAST
(carnation.kazusa.or.jp)		
HopBase	*Humulus lupulus*	BLAST
(hopbase.cgrb.oregonstate.edu)		Gbrowse
Medicago truncatula Genome Database (MTGD)	*Medicago truncatula*	JBrowse
(www.medicagogenome.org)		BLAST
		Web Services
		CMap (LegumeInfo.org)
		GO Analysis
		InterPro Annotations
Tea Plant Information Archive (TPIA)	*Camellia sinensis*	BLAST
(tpia.teaplant.org/)		Gbrowse
		Pathway
		Correlation Analysis
		Function Erichment
		Batch Retrival
Mulberry Genome Database (MorusDB)	*Morus notabilis*	Transposable Element Analysis
(morus.swu.edu.cn/morusdb)		Horizontal Gene Transfer Analysis
		Ortholog and Paralog Group Analysis
		BLAST
		WEGO
		HMMER
		Browse GO
		Search GO
		Find Motifs
Pear Genome Project	*Pyrus bretschneideri*	Download
(peargenome.njau.edu.cn)		
Radish Genome database	*Raphanus sativus*	BLAST
(www.radish-genome.org/)		Gbrowse
		Expression
CsiDB	*Citrus sinensis*	Gene Search
(citrus.hzau.edu.cn)		BLAST
		GBrowser
		PPI
		Pathway
Mint Genomics Resource	*Mentha longifolia*	BLAST
(langelabtools.wsu.edu/mgr/organism/Mentha/longifolia)		Gbrowse
		Pathway
CeleryDB	*Apium graveolens*	BLAST
(apiaceae.njau.edu.cn)		GBrowser
		Transcription factors
CarrotDB	*Daucus carota*	BLAST
(apiaceae.njau.edu.cn/)		Gbrowse
		Transcription factors
		Germplasm Resources Collection

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databases, including the Citrus Genome Database, Cool-Season Food Legume Crop Database resources, and Genome Database for Vaccinium (GRIN). All these databases share a similar data process standard and have built-in bioinformatics tools.

The Sol Genomics Network (SGN)[98], a database of Solanaceae genomic and phenotypic data and tools, was developed by Mueller's team from the Boyce Thompson Institute for Plant Research and Cornell University. The SGN includes 11 genomes: those of *Solanum lycopersicum*, *S. lycopersicoides*, *S. pimpinellifolium*, *S. tuberosum*, *S. pennellii*, *Capsicum annuum*, *Nicotiana attenuata*, *N. benthamiana*, *N. tabacum*, *Petunia axillaris*, and *P. inflata*. These species are categorized into four economically important genera: *Solanum*, *Capsicum*, *Nicotiana*, and *Petunia*. For online analyses of genomic sequences, BLAST, Alignment Analyzer, Tree Browser, and VIGS tools are available. For mapping of various data, JBrowse, Comparative Map Viewer, CAPS Designer, and solQTL are provided. Some tools have been developed for common molecular wet laboratory experiments, including In-Silico PCR, the Tomato Expression Atlas, and the Tomato Expression Database. Systems biology tools such as SolCyc Biochemical Pathways[99], Coffee Interactome Data, and the SGN Ontology Browser are provided. The Breeders Toolbox was developed for breeders. The same team also developed a series of horticultural plant-themed databases, including the YamBase (https://yambase.org), CassavaBase (https://cassavabase.org), and MusaBase (https://musabase.org) databases. All these databases adhere to the release of genomic data before publication (the Toronto Agreement)[100].

The Cucurbit Genomics Database (CuGenDB)[101] currently hosts eight high-quality genome sequences corresponding to those of cucumber (*Cucumis sativus*), water melon (*Citrullus lanatus*), winter squash (*Cucurbita maxima*), pumpkin (*Cucurbita moschata*), summer squash (*Cucurbita pepo*), muskmelon (*Cucumis melo*), bottle gourd (*Lagenaria siceraria*), and silver-seed gourd (*Cucurbita argyrosperma*). The search and batch query system allow searching for sequences and annotations. To display genomic details, the JBrowse, BLAST, Gene Ontology (GO), Synteny Viewer, CAMP, and expression viewer tools are available. To display metabolic pathways, CucurbitCyc and Pathway enrichment tools are available.

The Brassica Database (BARD)[102], a database of important *Brassica* species, covers the vegetable species *Brassica rapa* and *B. oleracea*, as well as the model plant *Arabidopsis* and Brassicaceae close relatives. In addition to its genomic data, the BRAD database hosts a curated list of genes involved with anthocyanins, resistance, auxin, flowering, and glucosinolates and a full list of gene families that are of considerable importance in *Brassica* research. BLAST and JBrowse tools were built for visualization of genomic data, and syntenic tools are useful for comparative analyses.

The Herbal Medicine Omics Database[103] includes genomic, transcriptomic, pathway, and metabolomic data for medicinal plants, although the medicinal properties of some plants are recognized only in some parts of the world. In this database, hundreds of medicinal plants are included. However, the database currently provides only the BLAST and GBrowse tools for the visualization of omics data. Other collected omic data can be downloaded but cannot be analyzed or visualized online.

There are other tool-specific databases that can be very useful for the visualization and online analyses of horticultural plant genome sequences. The Plant Genome Duplication Database (PGDD)[104] offers online analyses of gene synteny and visualization of different results, such as dot plots (macrosynteny) and local genomic comparison plots (microsynteny). The built-in Map-View tool allows mapping of a given sequence to the genomes of 47 species from the PGDD (data accessed on March 31, 2019). The Plant Duplicate Gene Database[105] is a collection of 141 plant species and offers online analysis and visualization of duplicated genes in select species.

Discussions and future perspectives

The horticultural plant genome project

It is challenging to determine the exact number of species or cultivars that exist for horticultural plants. In terms of fruit-bearing plants, at least 91 species are economically important and produce fruit that are consumed (https://simple.wikipedia.org/wiki/List_of_fruits). More than 200 vegetable plants are consumed (https://simple.wikipedia.org/wiki/List_of_vegetables). The exact number of ornamentals is also unclear, as novel cultivars are produced each year. However, it has been estimated that there are >6000 ornamental cultivars (https://www.rhs.org.uk/plants/pdfs/agm-lists/agm-ornamentals-(1).pdf), and many cultivars are created and disappear each year. Up to December 2018, genome sequences had been decoded for only 181 species, accounting for only a small proportion of the total horticultural plant species. Hence, there is a strong need to sequence additional genomes for more horticultural plants that would be valuable for comparative genomics, to better understand their evolutionary history, and to possibly make genetic modifications to better utilize these plant species.

Here we propose a horticultural plant genome project (HPGP) with three goals (Fig. 2). The first goal of the HPGP is to generate reference genome sequences for all horticultural plants, after which pan-genomes and core collections would be generated as genetic banks for horticultural plants. Two recently developed genome assembly methods could be applied to decode highly ploidy[71] and highly heterozygous[106–108] horticultural

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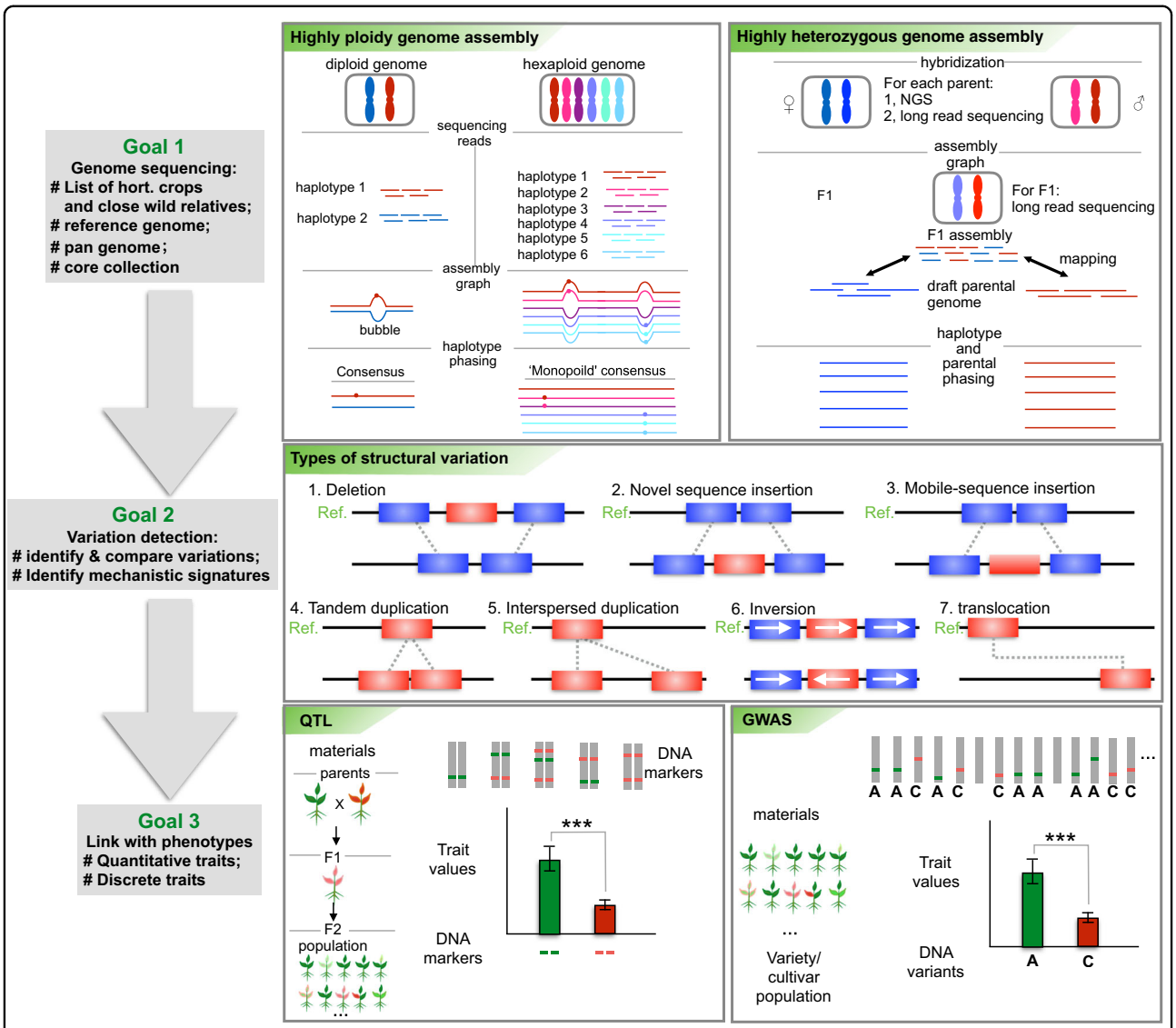

Fig. 2 The proposed roadmap to the horticultural plant genome project (HPGP). The first goal of HPGP is to generate all reference genome sequences for horticultural plants, after which pan-genomes and core collections will be generated as a gene bank for horticultural plants. Two recently developed methods would be applied to decode the highly ploidy and highly heterozygous horticultural genomes. The second goal is to detect the various genomic variations within a pan-genome. In addition, the mechanistic signatures leading to the variations would be explored. The third goal is to link the phenotypes with the genomic regions. Two methods would be applied: the quantitative trait locus (QTL) method to correlate genomic variations with a quantitative trait and the genome-wide association study (GWAS) method to associate genomic variation with many genomic variations from different individuals ***$p < 0.001$

genomes. The second goal is to identify the various genomic variations within a pan-genome. In addition, the mechanistic signatures leading to the variations would be explored. The third goal is to link the phenotypes to the genomic regions. Two methods would be applied: quantitative trait locus methods to correlate genomic variations with a quantitative trait and genome-wide association study methods to associate genomic variation with many genomic variations from different individuals[109,110]. The good news is that the Earth Genome Project and the 1000-Plant Genome Project will accelerate the genome sequencing process of horticultural plants.

The timeline for obtaining the genome sequences of all horticultural plants at both draft and reference scales (goal one of the HPGP) would be short—within 3–5 years—because the cost for sequencing is dropping rapidly. However, collecting and sequencing the population definitely requires worldwide collaborations and would take >10 years. The second goal is to analyze the genomic variations to identify the mechanistic signatures within a

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population, which is also time consuming and would be gradually achieved. The third goal is an advanced step that occurs after or concurrently with the second goal. Although these last two goals appear to be enormous challenges, we are confident in the ability to achieve most of these two goals in model horticultural plants such as the tomato, cucumber, and strawberry in the coming years.

In addition, the quality of assembly and annotation of existing reference genomes of horticultural plants need to be further improved. Although a few tools such as BUSCO[111] and CEGMA[112] have been widely used to evaluate the quality of genome annotations, a good standard is still not available for the systematic evaluation of the quality of genome assemblies. As a result, the quality of the genome assemblies is very uneven and is sometimes related to the complexity or heterozygosity of the taxa. This situation is changing as sequencing platforms are being upgraded. For example, since the first apple genome sequence was released in 2010 based on next-generation sequencing technology[15], an improved version produced by next-generation sequencing (NGS) and PacBio technologies was released in 2016[113]. The third improved version of the apple genome, which was obtained using a combination of NGS, PacBio, and Bionano technologies, was released in 2017[114]. The fourth improved version was released in 2019, based on the utilization of NGS, PacBio, and Hi-C technologies[27]. In the future, the quality of the reference genome should reach certain minimal standards upon which the community can agree, similar to the proposal for bacteria and archaea[115], thereby leading to more accurate pan-genome analyses and biotechnology.

Storage and access of genomic data constitute another problem concerning horticultural biologists and bioinformatics scientists. For access to genome sequences and raw sequencing data, a number of public databases are usually the first choice of researchers due to the nature of their stability, low cost, and ease of access. The well-known public databases include the NCBI (https://ncbi.nlm.nih.gov), EMBL (www.embl.org), CNGB (www.cngb.org), BIGD (bigd.big.ac.cn), DDBJ (www.ddbj.nig.ac.jp), GigaDB (gigadb.org), Dryad (www.datadryad.org), and Phytozome (https://phytozome.jgi.doe.gov) databases. To share these data with worldwide researchers, we encourage the release of data before publication, as was suggested by the Toronto Agreement in 2009[100].

The need for a horticultural plant-centric database

Unlike agricultural plants, horticultural plants share multiple features. For example, plant growth requires controlled conditions with specific equipment or facilities; plants generally need grafting, postharvest treatment, and a long juvenile phase; and plants usually undergo asexual reproduction and have unique specialized metabolism. All of these concerns make it hard to study these traits in model plants or via regular tools. Uniting the various omic data and the development of novel tools for horticultural plants are needed. Moreover, aside from the comprehensive plant databases and the 27 horticultural plant-specific databases mentioned above, there is still an increasing need to find and compare an increased amount of data for horticultural plants. However, horticultural biologists usually need to frequently deal with breeders; thus the need to create a comprehensive horticultural database to meet the interests of basic biologists and breeders is largely required. Such a database should cover as many horticultural plant genomes as possible and should provide an integrated set of bioinformatics tools. We believe that, in the future, the need for such a comprehensive database of all horticultural plants will satisfy additional horticulture researchers and breeders.

Given the advancement of sequencing technologies and reduced costs, the genome sequencing data of horticultural plants are accumulating rapidly. The storage, analyses, and sharing of large collections of genome sequencing data are becoming even more laborious and time consuming. The integrative analysis of various omic data, such as genomic, transcriptomic, metabolomic, phenomic, and breeding data, have become a major challenge for many horticultural biologists and requires coordinated efforts of scientists from different fields. For data processing and visualization, we recommend using BioMart tools, which could be easily built into a database. For database construction, we suggest following the template of the Tripal series (www.tripal.infor)[8]. Finally, we believe that, with a fostered collaboration of the horticultural community, the HPGP and subsequent knowledge and experiences will greatly benefit biology researchers and breeders.

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Conflict of interest

The authors declare that they have no conflict of interest.

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