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REVIEW ARTICLE

Construction, characteristics and high throughput molecular screening methodologies in some special breeding populations: a horticultural perspective

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Abstract. Advanced marker technologies are widely used for evaluation of genetic diversity in cultivated crops, wild ancestors, landraces or any special plant genotypes. Developing agricultural cultivars requires the following steps: (i) determining desired characteristics to be improved, (ii) screening genetic resources to help find a superior cultivar, (iii) intercrossing selected individuals, (iv) generating genetically hybrid populations and screening them for agro-morphological or molecular traits, (v) evaluating the superior cultivar candidates, (vi) testing field performance at different locations, and (vii) certifying. In the cultivar development process valuable genes can be identified by creating special biparental or multiparental populations and analysing their association using suitable markers in given populations. These special populations and advanced marker technologies give us a deeper knowledge about the inherited agronomic characteristics. Unaffected by the changing environmental conditions, these provide a higher understanding of genome dynamics in plants. The last decade witnessed new applications for advanced molecular techniques in the area of breeding, with low costs per sample. These, especially, include next-generation sequencing technologies like reduced representation genome sequencing (genotyping by sequencing, restriction site-associated DNA). These enabled researchers to develop new markers, such as simple sequence repeat and single- nucleotide polymorphism, for expanding the qualitative and quantitative information on population dynamics. Thus, the knowledge acquired from novel technologies is a valuable asset for the breeding process and to better understand the population dynamics, their properties, and analysis methods.

Keywords. population; backcross; double haploid; recombinant inbred line; near-isogenic line; nested association mapping; multiparent advanced generation intercross.

History of breeding

Since the transition from hunter-gatherer primitive human communities to settled lifestyle, mankind has made immence efforts in cultivating a wide range of plant species, giving rise to agriculture (Gepts 2014; Milla *et al.* 2015; Abbo and Gopher 2017). Researchers estimated that this trend in cultivation started in the late Paleolithic age, nearly 10,000 years ago; it was concentrated in four different locations in the middle latitudes of the world. The major origins of the Neolithic agriculture were near Eastern centre, Central American centre, Chinese centre and New Guinean centre (Mazoyer and Roudart 2006). These centres were further extended with two or three secondary diversification centres. According to one theory, the hunter-gatherer communities were divided into subpopulations and found marginal places (Neolithic agriculture centres) to live in Pleistocene age (Flannery 1969). To

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meet the basic necessities for their survival, these subpopulations enlarged their dietary resources with deliberately selected, protected, germinated and planted weed types in addition to their original hunter diet. Morgan (2015) termed this deliberate usage of plants as 'intensification' (Morgan 2015). Therefore, with these initiatives, early applications of domestication process have begun long time ago. Natural and artificial selections (especially long-term artificial selection) were two indispensable forces for domestication (Gregory 2009; Flint-Garcia 2013). These led to permanent heritable genetic alterations via gene recombinations, transposable elements, shifts, mutations, and polyploidization (Soltis and Soltis 1999; Doebley *et al.* 2006; Pathirana 2011; Belyayev 2014; Sidhu *et al.* 2017). As a result of fixed genetic differences throughout generations, newly formed alleles spread to the weed populations in some of those marginal places. Further, long-term cultivation of weeds with the new alleles increased the desirable allele frequency and gradually differentiated in genetic, morphological, and physiological properties. Hence, the domestication process by the early farmers shaped the modern cultivars that emerged from the ancestral populations (Gepts and Harlan 2012; Turcotte *et al.* 2017).

Breeding is an important process for the domestication of plants. Plant breeding is a manipulation method for generating highly heritable variations among populations and selecting the desirable ones beneficial for humanity. The breeding activity can also be defined as an accelerated way of domestication. This also indicates that the origin of breeding is as old as domestication.

Breeders, who professionally manage breeding activities, determine the ultimate direction of the programme and design the details to be implemented. The direction of a breeding programme depends on many factors, such as productivity, nutritional value, disease and environmental stress resistance, adaptation to agricultural lands and/or climatic conditions, agricultural mechanization and food processing (Dwivedi *et al.* 2016; Li *et al.* 2018b). Among these, productivity could be increased by introducing new genes to resist pathogens and to increase tolerance to environmental stress, screening and bringing major polygenic traits into new cultivars, and using effective biofertilizers, conventional fertilizers and irrigation systems (Ashikari and Matsuoka 2006; Wahid *et al.* 2007; Balconi *et al.* 2012; Nadeem *et al.* 2013). The nutritional value of a plant is directly correlated to its protein composition, amino acid content, macronutrient and micronutrient composition, fibre content, and increased oil and sugar content; additionally, it is inversely correlated to the toxic components (Hayat *et al.* 2014; Strobbe *et al.* 2018).

The key factor for improvement of any given characteristic is the variation among individual genotypes or populations. Breeding programmes, effecting these improvements, are built on three main foundations: variation, heritability and selection. Genetic variation within a population or its diversity index is measured by fixation index (F_{ST}), widely estimated using simple sequence repeat (SSR) and single- nucleotide polymorphism (SNP) markers. Other equivalents of F_{ST} are (i) Q_{ST}, metric measurement units of genetic differentiation used for analysing quantitative traits, (ii) G_{ST}, multiallelic version of F_{ST}, (iii) Nei's D, genetic distance, (iv) Jost's D, and (v) sequence divergence (Nei 1973; Hedrick 2005, 2011; Jost 2008; Whitlock and Guillaume 2009; Ma *et al.* 2015; Filiz *et al.* 2018). DNA sequence divergence or variations are not always morphologically and physiologically observable. In any case, base-pair differences create variations within individuals. Various agricultural traits, e.g. yield, are polygenic and quantitative in nature. Distinct genes on the same or different chromosomes and their interactions under different environmental conditions are responsible for such traits (Nadeem *et al.* 2018; Saba Rahim *et al.* 2018). Demographic, genetic, or environmental factors could be the reason for the variability in quantitative traits (Heino 2014).

From early farmers to modern breeders, the agro-morphological traits selected in edible crops include higher yield, larger fruit and seed size, uniform germination and ripening of seeds and fruits, annual nature of crop, and enhanced taste and fragrance (Taiz 2013). Phenotypic selection of these traits in every generation allows desirable and uniform production, at the cost of reduced genetic variation (Nogue *et al.* 2016). Thus, continuously choosing an allele results in some undesirable consequences. Gene frequencies in a population change dynamically under the pressure of natural selection. Natural selection along with artificial selection sometimes could result in a genetic bottleneck in breeding by the accumulation of specific genes among the cultivated forms (Wright 2005). On one hand, uniformity of genes is a desired property; on the other hand, induced uniformity at the hands of breeders is dangerous in many ways, particularly for large-scale production. According to van de Wouw *et al.* (2010), the replacement of landraces with modern cultivars led to a gradual loss of variations in crops. Finally, the loss of variation due to the introduction of uniformity makes large cultivation areas susceptible to the new emerging epidemic threats. Such epidemics were previously recorded in some locations of the world.

Subsequent to ancient practices, the earliest efforts for breeding were observed in the 18th century. The detail elucidation of sexual reproduction system in plants led to the initiation of modern-day breeding. The first report of sexual reproduction in plants was recorded by Ceamerarius (1694). Sexual reproduction—selfing, crossing, incompatibility or sterility—have been one of the most significant features in determining breeding methodology. Thomas Fairchild performed the first hybrid cross, a cross between two distinct species (Qaim 2016). Major milestones in plant improvement emerged over time that included the pedigree method of breeding, first scientific hybrid, hybridization by Mendel, pure-line theory of

selection, the law of equilibrium of populations, development of inbreeds to produce hybrids, bulk-breeding selection method, recurrent selection method, and finally the development of genetically modified organisms. The emergence of new methods had a cumulative effect on plant improvement and triggered many reactions toward agricultural speciation.

Importance of breeding

Today, there are 7.53 billion people in this world, and is estimated that they may reach 9.7 billion by 2050. According to the Food and Agriculture Organization (FAO) of the UN, 815 million people (about 11% of the global population) will suffer from undernourishment, where individuals would lack enough calories, proteins or micronutrients. Both, population and production growth rates are increasing, but the production rate is far slower than that of the population. According to the FAO statistics, food production rate must be increased by at least 70% to supply enough nutrients for humanity (FAO 2017).

In the coming decades, mankind will have to face major, inevitable food crisis. Due to population growth as well as fragile climatic and environmental factors, a new green revolution is of vital importance to meet global food demands. Until now, cereals have been the most important part of the human diet. In addition, the consumption of vegetables is expected to increase significantly in the next decade due to their indispensable role in the human diet (Slavin and Lloyd 2012). Vegetable-based diets have proven to increase the quality of life and prevent many diseases, owing to the rich nutritional values in the form of dietary fibres, proteins, vitamin, antioxidants, and minerals. In 2013, over one billion tons of food was produced in a harvested area of 58.1 million hectares (FAO 2017). From the point of land usage, vegetable production has almost reached its upper limits. Inevitably, this has led the breeders to develop new, more resistant (to diseases and pests) and tolerant (to abiotic stress factors) varieties to increase yield per unit area.

The screening of plant offspring with markers, guides the breeders to select the desirable traits, thus accelerating the process. Since selection is the simplest, longest and most continuous activity of plant improvement, the early selection of desirable offspring among created populations speeds up the releasing new cultivars (Hallauer 2011). Considering the above reasons, incorporating genomic tools with conventional breeding will accelerate the development of varieties with higher yields, richer nutritional values, and wider adaptation capabilities. Eathington *et al.* (2007) reviewed this evidence of acceleration.

The effectiveness of breeding may be increased many folds by using molecular marker technologies in vegetable crops. This means that the genomic tools integrated into the selection of progeny increase and accelerate the breeding programmes, which conventionally depended on the labour-intensive and time-consuming selection process. Next-generation sequence (NGS) analysis applied to plant science provides an abundance of information at low cost, as well as generates quick, accurate and reliable results. Hence, the breeders use it extensively in population screening studies. Particularly, marker-assisted selection (MAS) and quantitative trait loci (QTL) analysis were employed in screening to develop superior cultivars from individuals in a population (Varshney *et al.* 2014; Torkamaneh *et al.* 2018). In this case, the positions of QTL must be exactly known to minimize the number of recombinations between the QTL and markers used for selection. Phenotypic variations arising from QTLs must be well documented to eliminate any negative impacts that may lead to false positive results. Thus, cross-validation is required for the detected QTLs. For this, each population should be divided into two subsets: an estimation subset and an independent validation subset. To achieve precise selection, researchers employ whole genome sequencing (WGS), resequencing (RS) and NGS-based reduced representation sequencing. These high-throughput analyses produce endless data for discovering new SNP, SSR, cleaved amplified polymorphic sequence (CAPS) and other markers, detecting new major and minor QTLs, understanding genetic variations among individuals, and associating traits and DNA sequence with high accuracy (Barabaschi *et al.* 2016; Gramazio *et al.* 2018).

This review aims to meet the following objectives: (i) provide a detailed insight on creating breeding populations, (ii) explain properties of these populations, (iii) introduce newly developed breeding populations and (iv) to build a bridge between these populations and the appropriate high-throughput molecular screening methods. For this, the populations are discussed according to their contribution rates from parental lines as being biparental population (derived from two parental lines) and multiparental population (derived from multiple parental lines).

Biparental crossing populations

F_2 populations

An F_2 population depends on the crosses between two selected parents. F_2 progenies are the most preferred populations for a variety of studies because they can be easily produced and screened at molecular and morphological levels. Most of the derived special populations depend on the production of F_1–F_2 hybrid genotypes. F_2 progenies emerge as a reflection of Mendel's laws (Kumar *et al.* 2018). The F_2 populations are ideal for basic and advanced studies, as they allow applying all three marker systems (restriction, PCR, and sequence-based), and also certain morphological markers owing to their distinct genetic background.

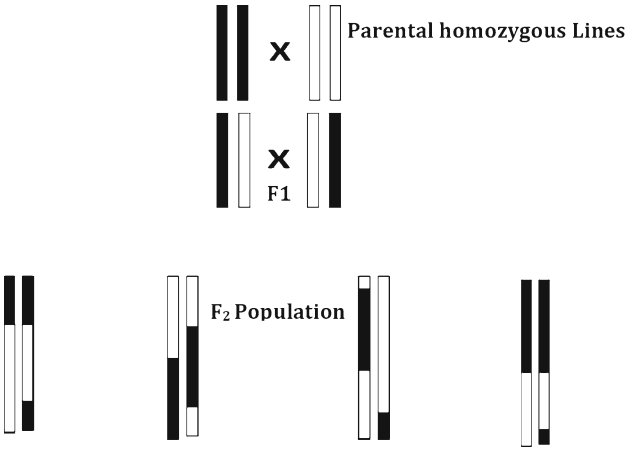

Figure 1. Schematic representation of an F_2 population. Parental homozygous lines are represented as diploid 2 chromosomes with black and white colours. F_1, first cross between parental homozygous lines; F_2, selfed of each F_1 individuals, modified from Zhang (2012).

Certain criteria need to be met when creating an F_2 population. In general, parental genotypes should be pure and express different phenotypes. If they are not pure, F_1 progeny will not be uniform as expected. According to Mendelian inheritance, 100% of the F_1 population must have the same phenotype. Thus, the purity level of parental lines is very important for creating the F_2 population (Baret *et al.* 1998). Production of doubled haploids is an alternative way to produce pure lines. It eliminates any chance of heterozygous genotype in the parental lines. In addition to pure genotypes, phenotypes of the parental lines should be different from one another (Muylle *et al.* 2005; Anhalt *et al.* 2008). In this way, the genetic and morphological polymorphisms between individuals can be identified and be associated correctly with specific characteristics. Although genetic and morphological diversities in parental lines can increase polymorphism rate, high levels of differences—arising from close relatives or interspecies crosses—sometimes cause fertility barriers in offspring. In conclusion, the derived F_2 population includes the largest diversity and gene combinations of the following generations (figure 1) (Feldman and Levy 2005). Therefore, codominant markers generate maximum information about this population.

Intentional selfing or backcrossing or a combination of both could be applied to the next generations for segregating any desired trait. The number of individuals in an F_2 population may vary from 50 to 1000 (Ferreira *et al.* 2006). Ideally, 100–300 F_2 progenies are sufficient to associate morphological traits with screened genetic markers and to detect QTLs (Mackay 2001; Zhang and Xu 2004). An F_2 population is also widely used to create other populations (Zhu *et al.* 2007). The reliability and resolution of the constructed genetic maps are directly proportional to the population size. Populations used in genetic studies are classified at two levels: temporary structure and permanent structure. The main disadvantage of the F_2 population is that it becomes unstable or unsustainable structure (Schneider 2005).

As seen in table 1, F_2 populations are mainly used for detecting QTLs, screening for resistant genes, constructing linkage maps and screening for special characteristics for different purposes. Populations that are suitable for all marker systems—codominant (e.g. SSR), dominant (e.g. ISSR, RAPD) and sequence-based (e.g. SNP) markers—for detection and genotyping enable the researchers to implement high-throughput methodologies (e.g. KASP genotyping, InDel, RNA-seq, WGS/R whole genome sequencing, whole genome resequencing, QTL-sequencing) on vegetables (Pradhan *et al.* 2018; Han *et al.* 2019; Jat *et al.* 2019). For instance, average SNP detection per study produces thousands of data points for mapping or converting previously detected SNP markers to dCAPS. SNP markers are detected in two different ways: (i) whole genome resequencing, used for detection in plants with small genome structures and (ii) reduced libraries, used for detection in highly repetitive or polyploidy and complex plants (Deschamps *et al.* 2012). For SNP calling, a reference genome can be used to align sequence data.

Backcross populations

A backcross population is derived from traditional breeding techniques and allows researchers to detect specific fragments of DNA (single dominant/recessive allele or several alleles) from a desirable parental line (Peng *et al.* 2014; De Beukelaer *et al.* 2015). The two parental lines, donor parents with desirable alleles and recurrent parents with more cultivation properties can generate a backcross population. It is derived from F_1 and F_2 generations, and advanced by repeatedly crossing with a recurrent parent (figure 2). The choice of recurrent parents depends on the alleles that carry certain characteristics. These alleles can be found either in wild relatives, as in the case of wild tomatoes (Celik *et al.* 2017), or in different populations of the same species (Kumar *et al.* 2014). Backcrossing achieves two main purposes: (i) decreasing undesirable traits of the donor DNA without losing the desirable traits, and (ii) reducing the observed number of individuals in a backcross population (Schneider 2005). Each backcross generation results in decrease in the percentage of donor genome at the rate of $1-(1/2)^{t+1}$, where t is the number of generations (Babu *et al.* 2004). The recovery rate of the created population reaches 99.2% at the end of six generations of continuous backcross activities.

Backcrosses are mostly applied to the populations as MAS or marker-assisted breeding. MAS is composed

Table 1. F_2 population studies from some vegetables and their analysis methods.

Vegetable	Population	Analysis method/platform/ marker system	Single/QTL character	References
Mugbean (*Vigna radiate*)	F_2	Phenotypic evaluation	Inheritance of gene-specific mungbean yellow mosaic virus (MYMV) resistance	Bhanu *et al.* (2019)
	F_2	Bulk segregant analysis	SCAR markers development for MYMV	Sai *et al.* (2017)
Pepper (*Capsicum annuum*)	F_2	GBS, SNP	Mapping of Pun3 gene	Han *et al.* (2019)
	F_2	SNP, CAPS development	CaPhyto gene mapping	Wang *et al.* (2016)
Brassica napus	F_2	BSA-seq, dCAPS development	Genetic mapping of DS-4 locus	Zhao *et al.* (2019)
	F_2	RNA-seq, SNP, QTL	Fatty acid levels, flowering time, and growth-related QTLs	Li *et al.* (2018c)
Chinese Cabbage (*Brassica rapa*)	F_2	InDel SNP	Heading degree, several heading QTLs	Sun *et al.* (2018)
Coriander (*Coriandrum sativum*)	F_2	Phenotypic evaluation	Heritability of some phenotypic character	Gholizadeh *et al.* (2019)
Tomato (*Solanum lycopersicum*)	F_2	WGR, InDel	Cf-10 gene mapping	Liu *et al.* (2019)
	F_2	Molecular characterizations	Tomato leaf curl virus resistance	Singh *et al.* (2015)
Purple cai-tai (*Brassica rapa* ssp. *purpurea*)	F_2	2000 pairs of SSR	BrCER4 gene mapping	Wang *et al.* (2019)
Pumpkin (*Cucurbita moschata*)	F_2	1277 pairs of SSR	Chilling index QTLs	Xu *et al.* (2017)
	F_2	ddRAD-sequencing	Carotenoids, sugars, tuberculate fruit, fruit diameter, thickness and chamber width QTLs	Zhong *et al.* (2017)
Cucumber (*Cucumis sativus*)	F_2	WGR, QTL-sequencing	Subgynoecy QTLs	Win *et al.* (2019)
	F_2	SSR, resequencing, SNP	Mapping of Cul-1 gene	Rong *et al.* (2019)
	F_2	SSR	Mapping of gynoecious (F) locus	Jat *et al.* (2019)
	F_2	WGS, marker development	Mapping of female (F) locus	Win *et al.* (2015)
Soybean (*Glycine max*)	F_2	Phenotypic evaluation	Heritability of agronomic traits	Michelle *et al.* (2018)
Lima Bean (*Phaseolus lunatus*)	F_2	Phenotypic evaluation	Resistance status of Phytophthora phaseoli	Santamaria *et al.* (2018)
Potato (*Solanum tuberosum*)	F_2	KASP genotyping	Tuber shape, flesh and skin colour QTLs	Meijer *et al.* (2018)
Melon (*Cucumis melo*)	F_2	CAPS	Melon fruit QTLs	Baloch *et al.* (2016)
Eggplant (*Solanum melongena*)	F_2	RAD-tag	Fruit properties QTLs	Toppino *et al.* (2016)

of three stages: (i) identification of sufficient molecular markers to represent the genome at a good coverage, (ii) association between major traits and markers, and (iii) detection of recombination events between markers, traits, and the rest of the genome (Babu *et al.* 2004). It has helped to improve many crops or to introduce new characters, as in the case of common bean (Brinez *et al.* 2017). MAS is generally used for single or major QTL mapping throughout generations (Hasan *et al.* 2015). To monitor these genes or QTLs, the ideal markers need to be located at the desired loci. Such markers may also exhibit linkage disequilibrium, which offers possibilities of inheritance of a gene with markers (Babu *et al.* 2004). Nevertheless, it is difficult to identify these markers. SSR and SNP markers have been used for monitoring QTLs. To date, MAS has been applied to many vegetable crops, qualitatively and quantitatively (table 2).

As seen in table 2, backcross populations are used in various forms in breeding studies. The forms of backcross populations include backcross inbred line and F_1 generation backcrossed several times. The derivatives of these different and classic backcross populations depend on the serial crossing and backcrossing strategy. Nearly all of these populations have been analysed with high-throughput molecular methods like genotyping by sequencing (GBS), specific locus amplified fragment sequencing (SLAF-seq), GoldenGate genotyping, InDel and restriction enzyme sequence comparison analysis (RESCAN). All these efforts significantly help in accelerating the process of releasing new cultivars and dissecting special genes.

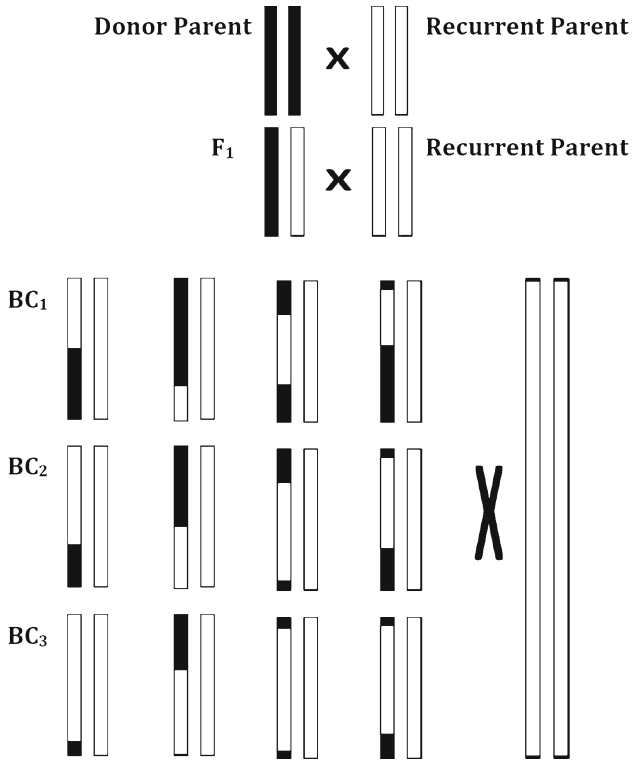

Figure 2. Schematic representation of backcross population. Respectively, donor and recurrent parents are represented as diploid 2 chromosomes with black and white colours. F_1, first cross between donor and recurrent parents. BC_1, first backcross with recurrent parent. BC_2, second backcross with recurrent parent. BC_3, third backcross with recurrent parent, modified from Schneider (2005).

Doubled haploid lines

Doubled haploids (DHs) can either occur naturally or be induced *in vitro*. They were first discovered in the early 20th century and were intensely used in the breeding of Brassicaceae family, over the last decade (Hasan *et al.* 2016; Lv *et al.* 2016; Mang *et al.* 2016). DH lines are mostly produced from suitable diploid species, and until now, more than 200 species have been generated (Ren *et al.* 2017). Nevertheless, there are some limitations in using DH lines. Major limiting factors for DH production include lifespan (annual, biennial or perennial), mating systems (autogamy, allogamy or propagation), and reproductive stages (flowering periods) of the plants.

The three common methods for inducing DH are gynogenesis, androgenesis, and wide hybridization (interspecies cross), each followed by chemical treatment for chromosome doubling (Bohanec 2009; Guha and Maheshwari 1964; Kasha and Kao 1970; Ravi and Chan 2010). All selected pollens and ovules from DH candidate cells must be in immature form for their regeneration capabilities to be at higher degrees (Yang and Zhou 1982; Bhojwani and Razdan 1996). These cells are particularly stable maternal cells and the offspring arising from them tend not to be infertile or albino (Dwivedi *et al.* 2015). In gynogenesis and androgenesis, immature ovules and pollens each have one set of chromosomes that need to be doubled. Wide hybridization is a cross between two distinct species. In this, one set of chromosomes disappears after the first division of embryonic cells. Due to the intentional elimination of alien chromosome sets, haploid plant production is stimulated via one set of chromosomes. Haploid plants are distinct from their diploid counterparts. They have smaller and thinner forms, low vigor, and are mostly infertile (Delaat *et al.* 1987). After this stage, upon colchicine treatment, all three types of haploid plants regenerate normal diploid plants. Colchicine and its alternatives, like amiprophos-methyl (APM), pronamid, oryzalin, and trifluralin, block mitotic filament formation during cell division; thus, two identical chromosomes remain in the cells without separation (Schneider 2005; Semagn *et al.* 2006; Ren *et al.* 2017; Yan *et al.* 2017).

In breeding, DHs can be derived from both F_1 hybrids and F_2 generation. However, sometimes they can be produced from F_2 populations if more genetic diversity is required (figure 3) (Melchinger *et al.* 2011; Sleper and Bernardo 2016). DH lines are ideal for observing recessive, non or imperfect dominant traits, as they carry identical chromosome pairs containing only one set of alleles for all the traits, desired and otherwise. There are several advantages of using DH lines. They enable detection of genotype–phenotype relations. They eliminate inbreeding depression, arising in cross-pollinated species and self-incompatibility systems (Pen *et al.* 2018). DH lines remove any residual heterozygosity and reduce the time for generation of pure lines, which would otherwise require at least six generations of selfing (Velmurugan *et al.* 2018). Most importantly, they shorten the duration of cultivar development, producing true breeding lines that are 100% homozygous (Segui-Simarro 2015). DH population structure is stable compared to F_2 populations. However, there are some disadvantages of using DH lines, such as genotype-dependency, low genetic diversity, infertility, albinism, aneuploidy and high levels of segregation distortion compared to backcross populations (Semagn *et al.* 2006; Tanhuanpaa *et al.* 2008; Kumari *et al.* 2009; Yan *et al.* 2017).

As seen in table 3, the members of the Brassicaceae family exemplify DHs. This is due to the compatibility of their mating systems and reproductive organs. This family shows a high tendency toward anther culture and chromosome doubling. Table 3 summarizes the DH populations combined with high-throughput analysis methods, like Golden Gate SNP genotyping, InDel, RAD-Seq, SLAF sequencing, Illumina Infinium array, WGR, QTL-seq, and GBS. The whole genome sequencing or reduced representation genome sequencing methods have been commonly used for different purposes like discovering SSR and

Table 2. MAS population studies from some vegetables and their analysis methods.

Vegetable	Population	Analysis method/platform/ marker system	Single/QTL character	References
Tomato (*Solanum lycopersicum*)	BC	WGR, InDel	Cf-10 gene mapping	Liu *et al.* (2019)
	BIL	Illumina Platform	MetaboliteQTLs	Brog *et al.* (2019)
	BC	Phenotypic evaluation	Polygene inheritance model	Sun *et al.* (2019)
	BC	GBS	Fruit quality QTLs	Celik *et al.* (2017)
	BIL	RESCAN	Leaf QTL	Fulop *et al.* (2016)
Cabbage (*Brassica oleracea* ssp. *capitata*)	BC	Gene sequencing, gene expression	BoCER1 gene identification	Ji *et al.* (2018)
Chilli pepper (*Capsicum annuum*)	BC	Genetic and phenotypic evaluation	Leaf curl virus resistance	Thakur *et al.* (2019)
	BC	GBS	Capsinoids	Jeong *et al.* (2015)
Potato (*Solanum tuberosum*)	BC	MAS	Late blight resistance	Sanetomo *et al.* (2019)
Eggplant (*Solanum melongena*)	BC	First interspecific hybrid	Introduction of distant genepool for eggplant breeding	García-Fortea *et al.* (2019)
	F_2 and BC	SSR, SNP	Parthenocarpy QTL	Miyatake *et al.* (2012)
Soybean (*Glycine max*)	BC	SSR	Oil content QTLs	Xia *et al.* (2017)
Cowpea (*Vigna unguiculata*)	BC	SSR	Fusarium wilt resistance pattern and marker development	Omoigui *et al.* (2018)
Mungbean (*Vigna radiata*)	BC	Phenotypic evaluation	Inheritance pattern of yellow mosaic disease resistance	Akbar *et al.* (2018)
Spinach (*Spinacia oleracea*)	BC_1	SLAF-seq	Mapping of the sex-determining gene	Qian *et al.* (2017)
Pumpkin (*Cucurbita pepo*)	F_1, BC	Illumina platform	Agronomic traits QTLs	Esteras *et al.* (2012)
Bean (*Phaseolus vulgaris*)	IBL	InDel	E. kraemeri and E. fabae related 14 QTLs	Brisco *et al.* (2014)

BC, backcross; BC_1, first backcrossed population; BIL, backcross inbreed line; BC_2F_1, two times backcrossed F_1 generation; BC_1F_1, backcrossed F_1 generation; IBL, inbreed backcross line; MAB, marker assisted breeding; SLAF-seq, specific locus amplified fragment sequencing.

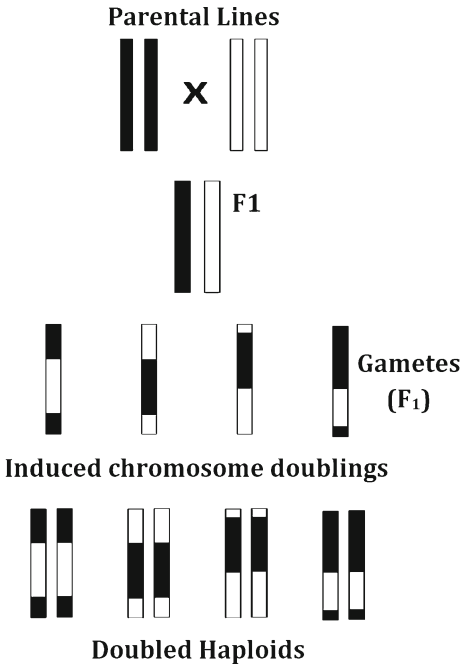

Figure 3. Schematic representation of DHs population. Respectively, parental and F_1 DHs are represented as diploid 2 chromosomes with black and white colours. F_1: means first cross between two distinct parents (modified from Seymour *et al.* (2012).

SNP, creating draft genome sequence, detecting SNP and aligning to the reference genome. DHs are very useful population for breeding (Bhatia *et al.* 2018), Also, it is possible to analyse classical marker systems and apply nearly all the high-throughput methods. Regrettably, limited application to various species of vegetables is its major disadvantage.

Recombinant inbred lines

Recombinant inbred line (RIL) is a powerful fine-mapping population, useful for the association and genetic mapping studies. The ultimate purpose of RIL production is to obtain true breeding lines (Takuno *et al.* 2012). RILs are used to construct mapping population not only in self-pollinating species but also in cross-pollinating species by means of crosses for half-sib and full-sib families (Doerge 2002). RILs are expected to be stable, permanent and homozygous populations compared with the F_2 population. They can be multiplied without any genetic change within the genome. They have been tested over years for documenting their acquired properties and exchanged with different research groups (Broman 2005; Yan *et al.*

Table 3. DHs population studies from some vegetables and their analysis methods.

Vegetable	Population	Analysis method/platform/ marker system	Single/QTL character	References
Brassica rapa	DH	SSR, SNP, AFLP	Flowering time QTL	Xiao *et al.* (2019)
	DH	Phenotypic evaluation	Sclerotinia resistance	Ding *et al.* (2019)
	DH	Illumina Infinium array	Heading related traits QTLs	Sun *et al.* (2018)
	DH	Phenotypic evaluation	Agronomic and seed quality traits	Szała *et al.* (2018)
Brassica napus	DH	DArT, KASP	Agronomic trait QTLs	Fattahi *et al.* (2018)
	DH	AFLP, SSR	Seed germination, seedling vigour QTLs	Nguyen *et al.* (2018)
Broccoli (*Brassica oleracea* ssp. *italica*)	DH	SLAF sequencing	Hollow stem trait QTLs	Yu *et al.* (2019)
	DH	WGR, QTL-seq	Heat tolerance QTLs	Branham and Farnham (2019)
	DH	GBS	Heat tolerance QTL	Branham *et al.* (2017)
Chinese cabbage (*Brassica campestris* ssp. *chinensis*)	DH	Microspore culture	Efficient doubled haploid production	Niu *et al.* (2019)
Chinese cabbage and Chinese kale	DH	SSR	Characterization	Wei *et al.* (2018)
Cucumber (*Cucumis sativus*)	DH	Anther culture, SSR	Doubled haploids production	Asadi *et al.* (2018)
	DH	Improved chromosome doubling	Parthenogenetic haploid plants	Ebrahimzadeh *et al.* (2018)
Cauliflower (*Brassica oleracea*)	DH	DH	Antioxidant	Singh *et al.* (2018)
	DH	SLAF sequencing	Genetic map construction	Zhao *et al.* (2016)
Allohexaploid hybrid from brassica species	DH	RAD-Seq, QTL	Pollen viability and fertility-related QTLs	Yang *et al.* (2018)
Pepper (*Capsicum annuum*)	DH	SSR development	Construction of a high-density linkage map	Sugita *et al.* (2013)
Melon (*Cucumis melo*)	DH	WGS	Draft genome	Garcia-Mas *et al.* (2012)
Cabbage (*Brassica oleracea* ssp. *capitata*)	DH	InDel, SSR and specific marker	Cabbage *Fusarium* wilt resistance line	Liu *et al.* (2017)
Garden asparagus (*Asparagus officinalis*)	DH	Illumina Platform	Genetic relationships	Mercati *et al.* (2015)

BC, backcross; DH, doubled haploid; SLAF-seq, specific locus amplified fragment sequencing.

2017). These properties make them one of the most important breeding populations.

RILs are constructed via single seed descendent (SSD) selection approach, which depends on creating F_2 population and repeated selecting of desirable seeds from F_2 to F_6 or F_8 (figure 4) (van Berloo and Stam 1998; Keurentjes *et al.* 2011). The selection process is continued for at least six to eight generations to attain a high degree of purity. About 99% of purity is expected at the end of eight generations of selfing (Seymour *et al.* 2012). Besides this, RILs are used for high-quality mapping resolution (Broman 2005). During the construction of SSD lines, not only one but also multiple lines (seeds) may be selected from each generation to achieve the ultimate breeding goals. These selected seeds represent different genotypes and contain different genetic segments of introgression in their genome (Dole and Weber 2007). In the selection of parental genotypes, highly homozygous inbred lines should be used to construct new breeding populations (RIL) (Lander and Botstein 1989). To achieve high purity, RILs must be constructed from self-compatible species as opposed to self-incompatible species and the species should be suitable for selfing throughout generations (Madhusudhana 2015).

At the end of the selfing process, RILs consist of homozygous individuals like DHs, but with some differences. As a result of crossing over through generations, RILs include some residual heterozygosity as well as exhibit links between markers and QTLs. When sufficient homozygosity is achieved, crossing over no longer causes differentiation in the genomic content (Schneider 2005). As a result of genomic stability, the ratio of information from RILs, in terms of dominant and codominant markers, is expected to be 1:1 (Yan *et al.* 2017). Therefore, genetic diversity and linkage disequilibrium can be assessed for both dominant and codominant marker systems. Further, QTL detection and fine-mapping can be achieved efficiently with these populations. The aforementioned reasons make RILs ideal for QTL mapping (Ashrafi *et al.* 2009). As seen in table 4, RILs are widely used to map QTLs by using various high-throughput

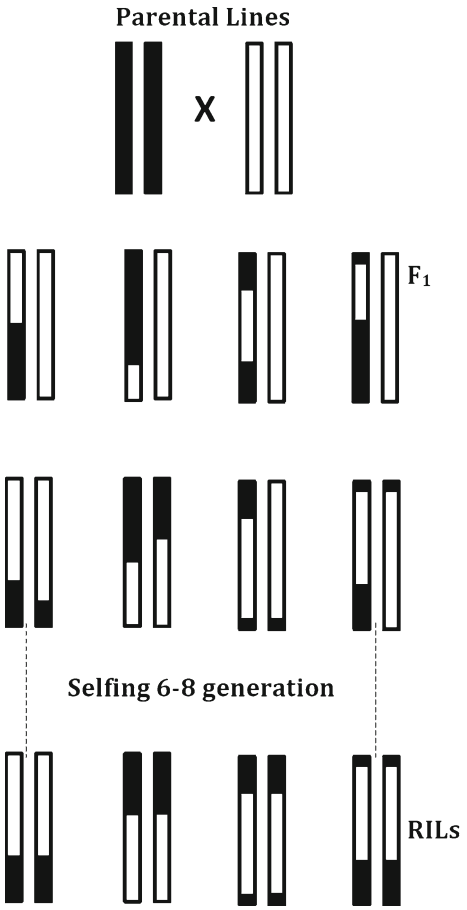

Figure 4. Schematic representation of RILs. Respectively, F_2 and offspring are represented as diploid 2 chromosomes with black and white colours, modified from Burr and Burr (1991).

array platforms like Fluidigm, Illumina, iSelect, InDel. In addition to these, SSR, RFLP and EST-based classical QTL mapping can also be done by using these fine-mapping populations.

Near-isogenic lines

Near-isogenic line (NIL) is another important fine-mapping population for self-pollinating species in the breeding programmes (Argyris *et al.* 2017). NILs carry a single, desirable gene from a donor parent and the remaining genomic content is isoform with the recipient parents (Eshed and Zamir 1995). Since all the other genes in the genome are the same except for the gene of interest, it can be assumed that the gene of interest produces phenotypical differences. Due to their highly homozygous structures, dominant and codominant markers have equal information contents on NILs (Semagn *et al.* 2006). They show heterozygosity with respect to the gene of interest (Farre *et al.* 2016). The number of markers required for mapping population is quite low compared to the other populations (Yano *et al.* 1997). Additionally, NILs transform quantitative traits into qualitative traits.

The development of NILs requires several steps of selfing and backcrossing. The first step is to find parental inbred lines—a donor and a recipient. Donor parents may be selected from elite backcross populations, RILs, DHs, heterogeneous inbred families (HIF) or wild progenitors (Kooke *et al.* 2012a). Mostly, elite cultivars are preferred as recipient parents, as they are highly homozygous without any remnants of undesired traits and include a superior desired trait. After the first cross, the F_1 generation is backcrossed with the selected recipient parent for several generations to ensure adequate homozygosity. Backcrossing enhances the chances of the gene of interest being fixed and the remaining parts of introgressed DNA segment being removed from the offspring. Finally, two rounds of selfing are needed for fixation of the target gene (figure 5).

The chief goals of creating NIL populations are the production of congenic strains, dissection of quantitative trait locus, identification of target gene functions, positional identification and cloning of the gene of interest, and development of markers tightly linked with the interested segment of genome (Yan *et al.* 2017). NILs are also immortal along with the immortalized F_2, RILs, and advanced BC populations. Nonetheless, the major disadvantages of construction of NILs are that it is a highly labour-intensive and a time-consuming process. Further, tightly linked undesirable traits may also pose a problem within these populations due to limited recombination rates between the undesirable traits and the genes of interest. As an advantage, NILs enable detection of minor QTL that could be missed in RILs (Keurentjes *et al.* 2007). All these characteristics emphasize that NILs can be easily integrated with high-throughput molecular methods and efficiently used for developing better cultivars, as seen in table 5.

Multiparental crossing populations

Nested association mapping population

From the perspective of breeding, valuable traits are generally inherited as polygenic characteristics (Liang *et al.* 2015). In this regard, linkage and association mapping are two main population analysis methods for identifying these complex inherited traits. The ultimate goals of any breeder are to identify these complex traits and to accumulate them into a cultivar, which is finally renamed as an elite cultivar (Hamawaki *et al.* 2019; Deokar *et al.* 2019; Obi *et al.* 2019; Sapkota *et al.* 2019; Vallarino *et al.* 2019). Breeders can achieve these goals in two ways. First is to use numerous markers for generating a high-resolution genomic map. Second is to construct dissected populations in terms of complex traits (Gibson 2012; Stadlmeier *et al.* 2018).

Table 4. Schematic representation of RILs. Respectively, F_2 and offspring are represented as diploid 2 chromosomes with black and white colours (modified from Burr and Burr (1991)).

Vegetables	Population	Analysis method/platform/ marker system	Single/QTL Character	References
Soybean (*Glycine max*)	RIL	GBS	Domestication-related traits QTLs	Swarm *et al.* (2019)
	RIL	GBS	Root hairless loci identification	Yang *et al.* (2019)
	RIL	Affymetrix platform	Seed protein and oil QTLs	Seo *et al.* (2019)
	RIL	SSR, RFLP, EST	Seed hardness QTL	Bu *et al.* (2018)
	RIL	SLAF-Seq, SSR, InDel	Seed oil content QTLs	Cao *et al.* (2017)
Watermelon (*Citrullus lanatus*)	RIL	SNP array	Flesh quality QTLs	Fall *et al.* (2019)
Pepper (*Capsicum annuum*)	RIL	GBS, RNA-seq	Pun3 gene mapping	Han *et al.* (2019)
	RIL	WGR	Bacterial wilt resistance SNP markers	Kang *et al.* (2016)
Cowpea (*Vigna unguiculata*)	RIL	Illumina platform	CAPS development for rust resistance	Wu *et al.* (2018)
Bean (*Phaseolus vulgaris*)	RIL	Illumina platform	Symbiotic nitrogen fixation QTLs	Kamfwa *et al.* (2019)
	RIL	Illumina platform	Pod dehiscence QTL	Parker *et al.* (2019)
	RIL	Illumina platform	Bean Weevil resistance QTLs	Kamfwa *et al.* (2018)
	RIL	Illumina platform	Fusarium root rot and root architecture QTLs	Nakedde *et al.* (2016)
Melon (*Cucumis melo*)	RIL	GBS	Fruit quality QTLs	Pereira *et al.* (2018)
Tomato (*Solanum lycopersicum*)	RIL	Illumina platform	Volatile organic compound QTLs	Rambla *et al.* (2017)
Cucumber (*Cucumis sativus*)	RIL	Bin map	Cotyledon regeneration QTLs	Wang *et al.* (2018)
	RIL	Fluidigm	Chromosomal rearrangements, regional recombination rate	Rubinstein *et al.* (2015)
Pea (*Pisum sativum*)	RIL	GBS	Genomic selection (GS) for grain yield	Annicchiarico *et al.* (2017)

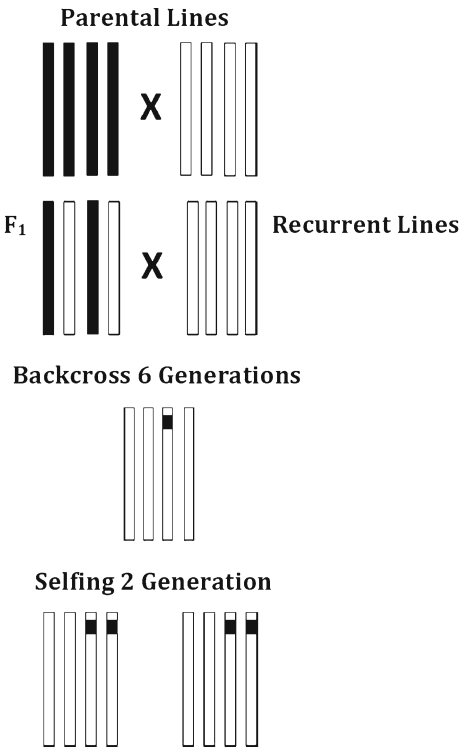

Figure 5. Schematic representation of NILs. Respectively, F_1 and offspring are represented as diploid 4 chromosomes with black and white colours, modified from Kooke *et al.* (2012b).

One such dissected population is the nested association mapping (NAM) population. NAM populations are a kind of multi-parental genetic mating strategies that consist of a large number of founder parents and one maintainer or reference parent (Ladejobi *et al.* 2016). Further, derived progenies and donor parents are screened with a number of markers and phenotypes to recognize the substituted chromosomal segments or loci, as in the case of maize breeding programme (Kump *et al.* 2011; Hung *et al.* 2012). NAM populations also help in detecting the origin of rare alleles from a wide range of founder parents (McMullen *et al.* 2009). Additionally, the NAM population forms a powerful tool for analysing complex traits as it can be used for linkage and association analyses in the same population, giving it a significant advantage over other methods (Zhang *et al.* 2005; Yu *et al.* 2008). In diploid species, diversity is limited to two parental lines, but these barriers can be exceeded via multiparental founders that consist of divergent genetic background (Welsh and McMillan 2012). A multiparental population offers observing many allelic variations into the phenotype and increasing the efficient detection of QTLs because of its own diverse genetic background (Yu *et al.* 2008). This background consists of varieties, inbreeds, accessions, ecotypes, races, DHs, mutants and wild types.

Table 5. Schematic representation of NILs. Respectively, F_1 and offspring are represented as diploid 4 chromosomes with black and white colours (modified from Kooke *et al.* (2012a)).

Vegetable	Population	Analysis method/platform/ marker system	Single/QTL character	References
Watermelon (*Citrullus lanatus*)	NIL	RNA-seq, transcriptome	Identify fruit cracking genes	Jiang *et al.* (2019)
	NIL	RNA sequencing	Soluble sugar- and organic acid accumulation gene identified	Gao *et al.* (2018)
	NIL	RAPD, CAPS, SNP	Powdery mildew disease resistance marker development	Han *et al.* (2016)
Common mustard (*Brassica juncea*)	NIL	NGS of BAC-clones	BjuWRR1 first white rust resistance gene	Arora *et al.* (2019)
Melon (*Cucumis melo*)	NIL	Illumina platform	Sugar content QTLs	Argyris *et al.* (2017)
Cowpea (*Vigna unguiculata*)	NIL, RIL	Illumina platform	Resistance loci to root-knot nematodes	Huynh *et al.* (2016)
Tomato (*Solanum lycopersicum*)	NIL	WGS	Detects flower number and inflorescence architecture loci	Zhang *et al.* (2018)
	NIL	MassARRAY platform	Water relations QTL for chilling stress	Arms *et al.* (2015)
Pepper (*Capsicum annuum*)	NIL	GBS, CAPS marker development	Genic male sterility genes	Naresh *et al.* (2018)
	NIL	DArT	Fruit PWL QTL	Popovsky-Sarid *et al.* (2017)
Pea (*Pisum sativum*)	NIL	SSR	Aphanomyces euteiches resistance QTL	Lavaud *et al.* (2015)
Chinese cabbage (*Brassica campestris* ssp. chinensis)	NIL	Gene expression	BrSWEET gene expression	Li *et al.* (2018a)
	NIL	RNA-seq,	Gene expression under infection of Plasmodiophora	Chen *et al.* (2016)
Broccoli (*Brassica oleracea*)	NIL	GBS	Mutation detected in wax synthesis genes	Branham and Farnham (2017)

To create a NAM population, classical breeding activities of crossing, selfing and selecting are used to generate a large number of RILs that have a wide range of founders and a reference line. This strategy is more suitable for cultivated plants that have multiple germplasm and progenitor species collections. After crossing with a wide range of founders, multiple RILs are maintained via selfing and selecting over at least six generations. As in the case with RIL population, immortality is achieved by selfing it through six generations (figure 6). Up to now, NAM populations have been applied to grain species such as maize, wheat, barley and rice (Fragoso *et al.* 2017; Draicchio *et al.* 2018; Jordan *et al.* 2018; Liang *et al.* 2019). Besides, they have also helped to enhance the vegetable species such as common bean and soybean (Hoyos-Villegas *et al.* 2016; Chen *et al.* 2017; Li *et al.* 2017; Diers *et al.* 2018; Khan *et al.* 2018; Scott *et al.* 2019).

RIL and NAM populations are suitable for application with high-throughput molecular marker systems. SNP and other marker systems offer to construct integrated genetic maps, such as linkage and association maps. Derived and maintained individuals enable linkage analysis. Phenotype and marker data for each generation allows finding an association for agronomically important traits. GBS studies can easily be applied to these populations because the reference sequence information, as well as the founder or reference parents are good sources for observing chromosomal substitutions.

Multiparent advanced generation intercross

Multiparental populations provide precise details of the desired phenotypic traits as well as increase detection and resolution of QTLs due to higher recombination rates (Cavanagh *et al.* 2008). According to Huang *et al.* (2015), it is a panoramic angle of population studies. Constructing a multiparent advanced generation intercross (MAGIC) population may render many genomic regions into a single individual. In other words, all the founder parents contribute to a certain extend to the final product.

The selection of parental lines for creating MAGIC populations requires several considerations, as parental genetic background significantly affects the genetic diversity of the population. The primary deposit of founder parents consists of elite breeding lines, formed by farmer's

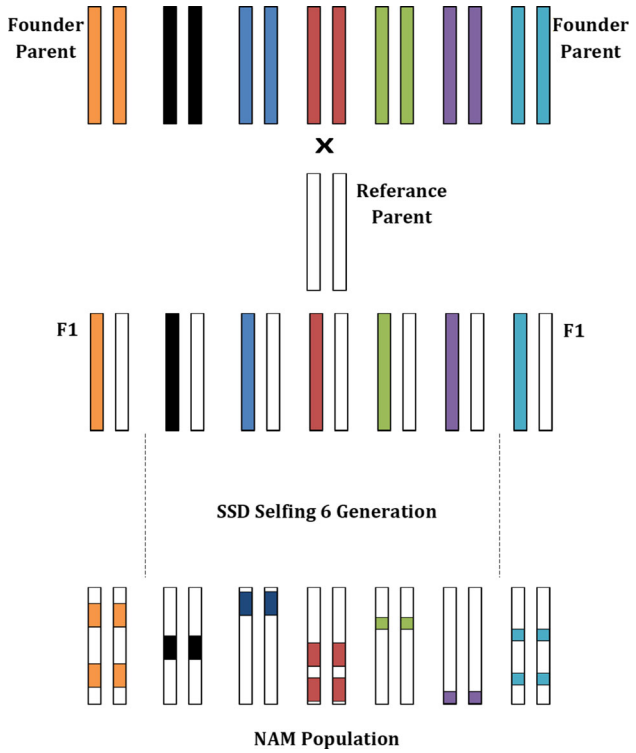

Figure 6. Schematic representation of NAM. Respectively, F_1 and offspring are represented as diploid 2 chromosomes. Each colour represents different progenitor parents. White colour is the reference parent, SSD, single seed descendant selection, modified from Yu *et al.* (2008).

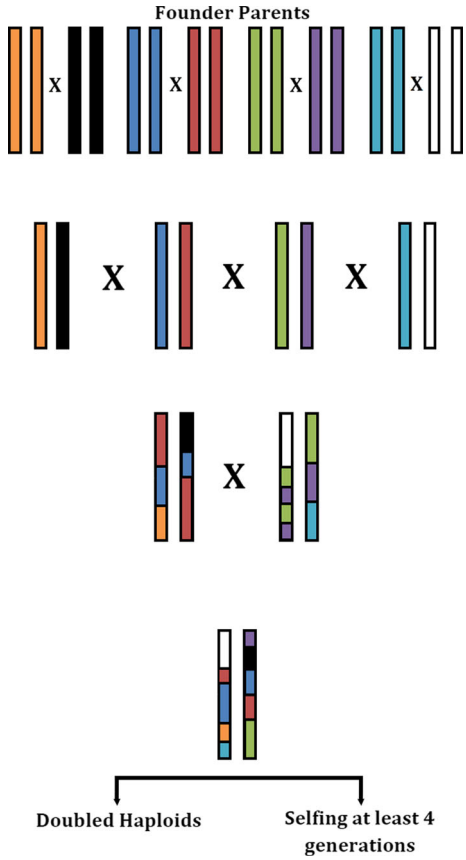

Figure 7. Schematic representation of MAGIC. Respectively, F_1 and offspring are represented as diploid 2 chromosomes. Each colour represents different progenitor parents, modified from Bandillo *et al.* (2013).

recurrent selection, landraces, wild relatives, and germplasms (Aliyu *et al.* 2014). Huang *et al.* (2014) proposed a formula that estimates the contribution of founder alleles, the alleles affected by population number, the genetic relatedness of founder, and density of markers. Thus, parental lines are selected according to the purpose of breeding and are incorporated with balanced contributions of the founder lines that ensure the ideal recombination rate for genetic diversity. The construction of MAGIC population is based on three steps: mixing, advanced intercrossing, and inbreeding (Huang *et al.* 2015). Mixing is performed for producing an outbreed population. Wide founder lines are intercrossed to create adequate diversity via the funnel design. This design is necessary for accumulating different gene combinations from each parent into a single individual. Advanced intercrossing is 'n' number of intercrossing of F_1 generation with each other to introduce different gene combinations via recombination events. In inbreeding, as in the RIL, homozygous lines are generated via SSD selection. Alternatively, doubled haploid lines are used to save time from the top of the funnel. After this point, the final product is either used for selfing or for generating doubled haploid (Kover *et al.* 2009). If selfed, additional recombination events could be observed throughout offspring. However, the lines would be homozygous, if doubled haploids are generated (figure 7).

The MAGIC population is a suitable mating system for cereals, such as rice, wheat and maize (Guan *et al.* 2017; Descalsota *et al.* 2018; Sannemann *et al.* 2018). There are also some examples of vegetable crops, such as soybean, pigeon pea, tomato, fava bean, cowpea and strawberry (Pascual *et al.* 2015; Sallam and Martsch 2015; Shivakumar *et al.* 2016; Ripoll *et al.* 2016; Huynh *et al.* 2018; Wada *et al.* 2017). However, it is not applicable in vegetables due to limitations in their mating systems compared to field crops. For example, some vegetables have a biennial mating system.

Although high-throughput molecular methods can be applied to MAGIC population progenies, only a few give desired results. Residual heterozygosity causes loss of function in molecular markers and generates false positive results (Dickson *et al.* 2010; Korte and Farlow 2013). Additionally, huge structural variations make sequence readings complicated during genotyping by sequencing or next-generation sequencing methods (Elshire *et al.*

2011). Also, MAGIC population construction is a labour-intensive and a time-consuming process.

Conclusion

Nowadays, under the constantly changing environmental conditions, sustaining and increasing agricultural production have gained more importance than ever before. Previously, two methods were widely used: (i) examining the existing germplasm with genome-wide association studies by using thousands of markers and (ii) investigating the breeding populations generated by using available genetic resources. Conventional breeding simply depended on the selection of superior traits from the ordinary ones. However, genotype–environment interaction was a major limitation faced in this selection process.

The introduction of novel technologies paved the way for identification of new genes and development of highly adaptable varieties. The limitations were resolved by discovering constitutive quantitative traits loci and integrating them into any genome of the breeding populations. Thus, these technologies empowered breeders to manipulate plants at genomic levels. In addition, a decrease in cost per sample for DNA sequencing led to the widespread use of next-generation sequencing technologies by breeders. Thus, the major goal of numerous studies was to integrate agronomically valuable traits into the selected elite cultivars.

Breeding populations are used to obtain various combinations of parental alleles, fix inheritance of desirable alleles, shorten the breeding time, ensure homozygosity and test additive or dominance effects. They also provide greater mapping resolutions, transform quantitative traits to qualitative traits and allow biparental allele barrier to be exceeded. Thus, population studies along with the integrated advanced molecular tools have powerful applications in agriculture.

References

Abbo S. and Gopher A. 2017 Near eastern plant domestication: a history of thought. *Trends Plant Sci.* **22**, 491–511.

Akbar W., Aslam M., Maqbool M. A., Ali M. and Arshad M. 2018 Inheritance pattern of mungbean yellow mosaic disease resistance and gene action for different traits in mungbean (*Vigna radiata* (L.) Wilczek) under protected and unprotected field conditions. *Plant Breed.* **137**, 763–772.

Aliyu S., Massawe F. and Mayes S. 2014 Beyond landraces: developing improved germplasm resources for underutilized species – a case for Bambara groundnut. *Biotechnol. Genet. Eng. Rev.* **30**, 127–141.

Anhalt U. C. M., Heslop-Harrison P., Byrne S., Guillard A. and Barth S. 2008 Segregation distortion in Lolium: evidence for genetic effects. *Theor. Appl. Genet.* **117**, 297–306.

Annicchiarico P., Nazzicari N., Pecetti L., Romani M., Ferrari B., Wei Y. L. *et al.* 2017 GBS-Based genomic selection for pea grain yield under severe terminal drought. *Plant Genome* **10**, 1–13.

Argyris J. M., Diaz A., Ruggieri V., Fernandez M., Jahrmann T., Gibon Y. *et al.* 2017 QTL analyses in multiple populations employed for the fine mapping and identification of candidate genes at a Locus affecting sugar accumulation in melon (*Cucumis melo* L.). *Front. Plant Sci.* **8**, article ID 1679.

Arms E. M., Bloom A. J. and St Clair D. A. 2015 High-resolution mapping of a major effect QTL from wild tomato Solanum habrochaites that influences water relations under root chilling *Theor. Appl. Genet.* **128**, 1713–1724.

Arora H., Padmaja K. L., Paritosh K., Mukhi N., Tewari A. K., Mukhopadhyay A. *et al.* 2019 BjuWRR1, a CC-NB-LRR gene identified in *Brassica juncea*, confers resistance to white rust caused by Albugo candida. *Theor. Appl. Genet.* **32**, 2223–2236.

Asadi A., Zebarjadi A., Abdollahi M. R. and Seguí-Simarro J. M. 2018 Assessment of different anther culture approaches to produce doubled haploids in cucumber (*Cucumis sativus* L.). *Euphytica* **214**, 216.

Ashikari M. and Matsuoka M. 2006 Identification, isolation and pyramiding of quantitative trait loci for rice breeding. *Trends Plant Sci.* **11**, 344–350.

Ashrafi H., Kinkade M. and Foolad M. R. 2009 A new genetic linkage map of tomato based on a Solanum lycopersicum x S. pimpinellifolium RIL population displaying locations of candidate pathogen response genes. *Genome* **52**, 935–956.

Babu R., Nair S. K., Prasanna B. M. and Gupta H. S. 2004 Integrating marker-assisted selection in crop breeding - prospects and challenges. *Curr. Sci. India* **87**, 607–619.

Balconi C., Stevanato P., Motto M. and Biancardi E. 2012 Breeding for biotic stress resistance/tolerance in plants. In *Crop production for agricultural improvement.* (ed. M. Ashraf M., M. Öztürk M., M. S. A. Ahmad and A. Aksoy), pp. 57–114. Springer Netherlands, Dordrecht.

Baloch A. M., Baloch A. W., Liu S., Gao P., Baloch M. J., Wang X. Z. *et al.* 2016 Linkage map construction and Qtl analysis of fruit traits in melon (*Cucumis Melo* L.) based on caps. *Markers Pak. J. Bot.* **48**, 1579–1584.

Bandillo N., Raghavan C., Muyco P. A., Sevilla M. A. L., Lobina I. T., Dilla-Ermita C. J. *et al.* 2013 Multi-parent advanced generation inter-cross (MAGIC) populations in rice: progress and potential for genetics research and breeding. *Rice* **6**, 11.

Barabaschi D., Tondelli A., Desiderio F., Volante A., Vaccino P., Vale G. *et al.* 2016 Next generation breeding. *Plant Sci.* **242**, 3–13.

Baret P. V., Knott S. A. and Visscher P. M. 1998 On the use of linear regression and maximum likelihood for QTL mapping in half-sib designs. *Genet. Res.* **72**, 149–158.

Belyayev A. 2014 Bursts of transposable elements as an evolutionary driving force. *J. Evol. Biol.* **27**, 2573–2584.

Bhanu A. N., Singh M. N. and Srivastava K. 2019 Genetic analysis of gene-specific resistance to mungbean yellow mosaic virus in mungbean (Vigna radiata). *Plant Breed.* https://doi.org/10.1111/pbr.12675.

Bhatia R., Dey S. S., Parkash C., Sharma K., Sood S., Kumar R. 2018 Modification of important factors for efficient microspore embryogenesis and doubled haploid production in field grown white cabbage (*Brassica oleracea* var. *capitata* L.) genotypes in India. *Sci. Hortic.* **233**,178–187.

Bhojwani S. S. and Razdan M. K. (ed.) 1996 Plant tissue culture : theory and practice, a revised edition. In *Studies in plant science*. p ix. Elsevier.

Bohanec B. 2009 Doubled haploids via gynogenesis. In *Advances in haploid production in higher plants* (ed. A. Touraev, B. P.

Forster and S. M. Jain), pp. 35–46. Springer Netherlands, Dordrecht.
Branham S. E. and Farnham M. W. 2017 Genotyping-by-sequencing of waxy and glossy near-isogenic broccoli lines. *Euphytica* **213**, 84.
Branham S. E. and Farnham M. W. 2019 Identification of heat tolerance loci in broccoli through bulked segregant analysis using whole genome resequencing. *Euphytica* **215**, 34.
Branham S. E., Stansell Z. J., Couillard D. M. and Farnham M. W. 2017 Quantitative trait loci mapping of heat tolerance in broccoli (*Brassica oleracea* var. *italica*) using genotyping-by-sequencing. *Theor. Appl. Genet.* **130**, 529–538.
Brinez B., Perseguini J., Rosa J. S., Bassi D., Goncalves J. G. R., Almeida C. *et al.* 2017 Mapping QTLs for drought tolerance in a SEA 5 x AND 277 common bean cross with SSRs and SNP markers. *Genet. Mol. Biol.* **40**, 813–823.
Brisco E. I., Porch T. G., Cregan P. B. and Kelly J. D. 2014 Quantitative trait loci associated with resistance to Empoasca in common bean. *Crop Sci.* **54**, 2509–2519.
Brog Y. M., Osorio S., Yichie Y., Alseekh S., Bensal E., Kochevenko A. *et al.* 2019 A *Solanum neorickii* introgression population providing a powerful complement to the extensively characterized *Solanum pennellii* population. *Plant J.* **97**, 391–403.
Broman K. W. 2005 The genomes of recombinant inbred lines. *Genetics* **169**, 1133–1146.
Bu Y., Zhang X., Wang C., Guo J., Zhang X., Li X. *et al.* 2018 Conditional and unconditional QTL analyses of seed hardness in vegetable soybean (*Glycine max* L. Merr.). *Euphytica* **214**, 237.
Burr B. and Burr F. A. 1991 Recombinant inbreds for molecular mapping in maize - theoretical and practical considerations. *Trends Genet.* **7**, 55–60.
Cao Y. C., Li S. G, Wang Z. L., Chang F. G., Kong J. J., Gai J. Y. *et al.* 2017 Identification of major quantitative trait Loci for seed oil content in soybeans by combining linkage and genome-wide association mapping. *Front. Plant Sci.* **8**, 1222.
Cavanagh C., Morell M., Mackay I. and Powell W. 2008 From mutations to MAGIC: resources for gene discovery, validation and delivery in crop plants. *Curr. Opin. Plant Biol.* **11**, 215–221.
Ceamerarius R. J. 1694 Rudolphi Jacobi Camerarii ad Thessalum, D. Mich. Bernardum Valentini De sexu plantarum epistola [microform]. Tybingai: Typis Viduae Rommeili.
Celik I., Gurbuz N., Uncu A. T., Frary A. and Doganlar S. 2017 Genome-wide SNP discovery and QTL mapping for fruit quality traits in inbred backcross lines (IBLs) of solanum pimpinellifolium using genotyping by sequencing. *BMC Genomics* **18**, 1.
Chen J., Pang W., Chen B., Zhang C. and Piao Z. 2016 Transcriptome analysis of *Brassica rapa* near-isogenic lines carrying clubroot-resistant and –susceptible alleles in response to *Plasmodiophora brassicae* during early infection. *Front. Plant Sci.* **6**, 1183.
Chen S. S., Han X. J., Fang J., Lu Z. C., Qiu W. M., Liu M. Y. *et al.* 2017 Sedum alfredii SaNramp6 metal transporter contributes to cadmium accumulation in transgenic *Arabidopsis thaliana*. *Sci. Rep.* **7**, 13318.
Da F. S. Michelle, Möller M., Clough S. J. and Pinheiro J. B. 2018 Heritability of agronomic traits correlated with reduced stink bug damage in an $F_{2:3}$ soybean population derived from IAC-100. *J. Crop Improv.* **32**, 1–18.
De Beukelaer H., De Meyer G. and Fack V. 2015 Heuristic exploitation of genetic structure in marker-assisted gene pyramiding problems. *BMC Genet.* **16**, 2.
Delaat A. M. M., Gohde W. and Vogelzang M. J. D. C. 1987 Determination of ploidy of single plants and plant-populations by flow-cytometry. *Plant Breed.* **99**, 303–307.
Deokar A., Sagi M., Daba K. and Tar'an B. 2019 QTL sequencing strategy to map genomic regions associated with resistance to ascochyta blight in chickpea. *Plant Biotechnol. J.* **17**, 275–288.
Descalsota G. I. L, Swamy B. P. M., Zaw H., Inabangan-Asilo M. A., Amparado A., Mauleon R. *et al.* 2018 Genome-wide association mapping in a Rice MAGIC plus population detects QTLs and genes useful for biofortification. *Front. Plant Sci.* **9**, 1347.
Deschamps S., Llaca V. and May G. D. 2012 Genotyping-by-sequencing in plants. *Biology* **1**, 460–483.
Dickson S. P., Wang K., Krantz I., Hakonarson H. and Goldstein D. B. 2010 Rare variants create synthetic genome-wide associations. *PLoS Biol.* **8**, e1000294.
Diers B. W., Specht J., Rainey K. M., Cregan P., Song Q., Ramasubramanian V. *et al.* 2018 Genetic architecture of soybean yield and agronomic traits. *G3 (Bethesda)* **8**, 3367–3375.
Ding Y., Mei J., Wu Q., Xiong Z., Li Y., Shao C. *et al.* 2019 Synchronous improvement of subgenomes in allopolyploid: a case of Sclerotinia resistance improvement in *Brassica napus*. *Mol. Breed.* **39**, 10.
Doebley J. F., Gaut B. S. and Smith B. D. 2006 The molecular genetics of crop domestication. *Cell* **127**, 1309–1321.
Doerge R. W. 2002 Mapping and analysis of quantitative trait loci in experimental populations. *Nat. Rev. Genet.* **3**, 43–52.
Dole J. and Weber D. F. 2007 Detection of quantitative trait loci influencing recombination using recombinant inbred lines. *Genetics* **177**, 2309–2319.
Draicchio F., Sharma R., Flavell A. J., Bull H., Thomas W. T. B., Maurer A. *et al.* 2018 Genome-wide association of yield traits in a nested association mapping population of barley reveals new gene diversity for future breeding. *J. Exp. Bot.* **69**, 3811–3822.
Dwivedi S. L., Britt A. B., Tripathi L., Sharma S., Upadhyaya H. D. and Ortiz R. 2015 Haploids: constraints and opportunities in plant breeding. *Biotechnol. Adv.* **33**, 812–829.
Dwivedi S. L., Ceccarelli S., Blair M. W., Upadhyaya H. D., Are A. K. and Ortiz R. 2016 Lancrace Germplasm for improving yield and abiotic stress adaptation. *Trends Plant Sci.* **21**, 31–42.
Eathington S. R., Crosbie T. M., Edwards M. D., Reiter R., Bull J. K. 2007 Molecular markers in a commercial breeding program. *Crop Sci.* **47**, S154–S163.
Ebrahimzadeh H., Soltanloo H., Shariatpanahi M. E., Eskandari A. and Ramezanpour S. S. 2018 Improved chromosome doubling of parthenogenetic haploid plants of cucumber (*Cucumis sativus* L.) using colchicine, trifluralin, and oryzalin. *Plant Cell Tissue Organ Cult.* **135**, 407–417.
Elshire R. J., Glaubitz J. C., Sun Q., Poland J. A., Kawamoto K., Buckler E. S. *et al.* 2011 A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS One.* https://doi.org/10.1371/journal.pone.0019379.
Eshed Y. and Zamir D. 1995 An introgression line population of *Lycopersicon pennellii* in the cultivated tomato enables the identification and fine mapping of yield-associated QTL. *Genetics* **141**, 1147–1162.
Esteras C., Gomez P., Monforte A. J., Blanca J., Vicente-Dolera N., Roig C. *et al.* 2012 High-throughput SNP genotyping in *Cucurbita pepo* for map construction and quantitative trait loci mapping. *BMC Genomics* **13**, 80.
Fall L. A., Perkins-Veazie P., Ma G. and McGregor C. 2019 QTLs associated with flesh quality traits in an elite × elite watermelon population. *Euphytica* **215**, 30.

FAO 2017 FAO statistical databases FAOSTAT. Food and Agricultural Organization. http://www.fao.org/faostat/en/#data. 2017.

Farre A., Sayers L., Leverington-Waite M., Goram R., Orford S, Wingen L. *et al.* 2016 Application of a library of near isogenic lines to understand context dependent expression of QTL for grain yield and adaptive traits in bread wheat. *BMC Plant Biol.* **16**, 161–173.

Fattahi F., Fakheri B. A., Solouki M., Möllers C. and Rezaizad A. 2018 Mapping QTL controlling agronomic traits in a doubled haploid population of winter oilseed rape (*Brassica napus* L.). *J. Genet.* **97**, 1389–1406.

Feldman M. and Levy A. A. 2005 Allopolyploidy - a shaping force in the evolution of wheat genomes. *Cytogenet. Genome Res.* **109**, 250–258.

Ferreira A., Silva M. Fd, Silva LdCe and Cruz C. D. 2006 Estimating the effects of population size and type on the accuracy of genetic maps. *Genet. Mol. Biol.* **29**, 187–192.

Filiz E., Uras M. E., Ozyigit., II, Sen U. and Gungor H. 2018 Genetic diversity and phylogenetic analyses of Turkish rice varieties revealed by Issr markers and chloroplast trnL-F Region. *Fresenius Environ. Bull.* **27**, 8351–8358.

Flannery K. V. 1969 Origins and ecological effects of early domestication in Iran and the near east. In *The domestication and exploitation of plants and animals* (ed. P. J. Ucko and G. W Dimbleby), pp. 73–100. Gerald Duckworth, London.

Flint-Garcia S. A. 2013 Genetics and consequences of crop domestication. *J. Agr. Food Chem.* **61**, 8267–8276.

Fragoso C. A., Moreno M., Wang Z., Heffelfinger C., Arbelaez L. J., Aguirre J. A. *et al.* 2017 Genetic architecture of a rice nested association mapping population. *G3 (Bethesda)* **7**, 1913–1926.

Fulop D., Ranjan A., Ofner I., Covington M. F., Chitwood D. H., West D. *et al.* 2016 A new advanced backcross tomato population enables high resolution leaf QTL mapping and gene identification. *G3 (Bethesda)* **6**, 3169–3184.

Gao L., Zhao S., Lu X., He N., Zhu H., Dou J. *et al.* 2018 Comparative transcriptome analysis reveals key genes potentially related to soluble sugar and organic acid accumulation in watermelon. *PLoS One* **13**, e0190096.

García-Fortea E., Gramazio P., Vilanova S., Fita A., Mangino G., Villanueva G. *et al.* 2019 First successful backcrossing towards eggplant (*Solanum melongena*) of a New World species, the silverleaf nightshade (*S. elaeagnifolium*), and characterization of interspecific hybrids and backcrosses. *Sci. Hortic.* **246**, 563–573.

Garcia-Mas J., Benjak A., Sanseverino W., Bourgeois M., Mir G., Gonzalez V. M. *et al.* 2012 The genome of melon (*Cucumis melo* L.). *Proc. Natl. Acad. Sci. USA* **109**, 11872–11877.

Gepts P. 2014 Domestication of plants. In *Encyclopedia of agriculture and food system* (ed. N. V. Alfen), vol. 2, pp. 474–486. Elsevier, San Diego.

Gepts P. L. and Harlan S. 2012 *Biodiversity in agriculture: domestication, evolution, and sustainability*. Cambridge University Press, New York.

Gholizadeh A., Dehghani H. and Khodadadi M. 2019 Quantitative genetic analysis of water deficit tolerance in coriander through physiological traits. *Plant Genet. Resour.* **17**, 255–264.

Gibson G. 2012 Rare and common variants: twenty arguments. *Nat. Rev. Genet.* **13**, 135–145.

Gramazio P., Prohens J., Plazas M., Mangino G., Herraiz F. J., Garcia-Fortea E. *et al.* 2018 Genomic tools for the enhancement of vegetable crops: a case in Eggplant. *Not. Bot. Horti. Agrobo* **46**, 1–13.

Gregory T. R. 2009 Artificial selection and domestication: modern lessons from Darwin's enduring analogy. *Evol. Edu. Outreach* **2**, 5–27.

Guan H., Ali F. and Pan Q. 2017 Dissection of recombination attributes for multiple maize populations using a common SNP assay. *Front. Plant Sci.* **8**, article ID 2063.

Guha S. and Maheshwari S. C. 1964 *In vitro* production of embryos from anthers of datura. *Nature* **204**, 497–497.

Hallauer A. R. 2011 Evolution of plant breeding. *Crop Breed. Appl. Biot.* **11**, 197–206.

Hamawaki R. L., Hamawaki O. T., Nogueira A. P. O., Juliatti F. C., Glasenapp J. S. and Hamawaki C. D. L 2019 New high-yielding conventional soybean adapted to the states of Goiás, Minas Gerais and Mato Grosso. *Acta Sci. Agron.* **41**, e39913.

Han B. K., Rhee S. J., Jang Y. J., Sim T. Y., Kim Y. J., Park T. S. *et al.* 2016 Identification of a causal pathogen of watermelon powdery mildew in Korea and development of a genetic linkage marker for resistance in watermelon (*Citrullus lanatus*). *Korean J. Hortic. Sci.* **34**, 912–923.

Han K., Jang S., Lee J.-H., Lee D.-G., Kwon J.-K., Kang B.-C. 2019 A MYB transcription factor is a candidate to control pungency in *Capsicum annuum*. *Theor. Appl. Genet.* **132**, 1235–1246.

Hasan M. M., Rafii M. Y., Ismail M. R., Mahmood M., Rahim H. A., Alam M. A. *et al.* 2015 Marker-assisted backcrossing: a useful method for rice improvement. *Biotechnol. Biotechnol. Equip.* **29**, 237–254.

Hasan Y., Briggs W., Matschegewski C., Ordon F., Stutzel H., Zetzsche H. *et al.* 2016 Quantitative trait loci controlling leaf appearance and curd initiation of cauliflower in relation to temperature. *Theor. Appl. Genet.* **129**, 1273–1288.

Hayat I., Ahmad A., Masud T., Ahmed A. and Bashir S. 2014 Nutritional and health perspectives of beans (*Phaseolus vulgaris* L.): an overview. *Crit. Rev. Food Sci.* **54**, 580–592.

Hedrick P. W. 2005 A standardized genetic differentiation measure. *Evolution* **59**, 1633–1638.

Hedrick P. W. 2011 *Genetics of populations*, 4th edition. Jones and Bartlett, Sudbury.

Heino M. 2014 Quantitative traits. In *Stock identification methods* (ed. S. X. Cadrin, L. A. Kerr and S. Mariani), pp. 59–76. Academic Press, San Diego.

Hoyos-Villegas V., Song Q. J., Wright E. M., Beebe S. E. and Kelly J. D. 2016 Joint linkage QTL mapping for yield and agronomic traits in a composite map of three common bean RIL populations. *Crop Sci.* **56**, 2546–2563.

Huang B. E., Raghavan C., Mauleon R., Broman K. W. and Leung H. 2014 Efficient imputation of missing markers in low-coverage genotyping-by-sequencing data from multiparental crosses *Genetics* **197**, 401–404.

Huang B. E., Verbyla K. L., Verbyla A. P., Raghavan C., Singh V. K., Gaur P. *et al.* 2015 MAGIC populations in crops: current status and future prospects. *Theor. Appl. Genet.* **128**, 999–1017.

Hung H. Y., Browne C., Guill K., Coles N., Eller M., Garcia A. *et al.* 2012 The relationship between parental genetic or phenotypic divergence and progeny variation in the maize nested association mapping population. *Heredity* **108**, 490–499.

Huynh B.-L., Ehlers J. D., Huang B. E., Muñoz-Amatriaín M., Lonardi S., Santos J. R. P. *et al.* 2018 A multi-parent advanced generation inter-cross (MAGIC) population for genetic analysis and improvement of cowpea (*Vigna unguiculata* L. Walp.). *Plant J.* **93**, 1129–1142.

Huynh B. L., Matthews W. C., Ehlers J. D., Lucas M. R., Santos J. R. P., Ndeve A. *et al.* 2016 A major QTL corresponding to the Rk locus for resistance to root-knot nematodes in cowpea (*Vigna unguiculata* L. Walp.). *Theor. Appl. Genet.* **129**, 87–95.

Jat G. S., Das Munshi A., Behera T. K., Choudhary H., Dash P., Ravindran A. *et al.* 2019 Genetics and molecular mapping of gynoecious (F) locus in cucumber (*Cucumis sativus* L). *J. Hortic. Sci. Biotech.* **94**, 24–32.

Jeong H. S., Jang S., Han K., Kwon J. K. and Kang B. C. 2015 Marker-assisted backcross breeding for development of pepper varieties (*Capsicum annuum*) containing capsinoids. *Mol. Breed.* **35**, 266–275.

Ji J., Cao W., Dong X., Liu Z., Fang Z., Zhuang M. *et al.* 2018 A 252-bp insertion in BoCER1 is responsible for the glossy phenotype in cabbage (*Brassica oleracea* L. var. capitata) *Mol. Breed.* **38**, 128.

Jiang H., Tian H., Yan C., Jia L., Wang Y., Wang M. *et al.* 2019 RNA-seq analysis of watermelon (*Citrullus lanatus*) to identify genes involved in fruit cracking. *Sci. Hortic.* **248**, 248–255.

Jordan K. W., Wang S., He F., Chao S., Lun Y., Paux E. *et al.* 2018 The genetic architecture of genome-wide recombination rate variation in allopolyploid wheat revealed by nested association mapping. *Plant J.* **95**, 1039–1054.

Jost L. 2008 GST and its relatives do not measure differentiation. *Mol. Ecol.* **17**, 4015–4026.

Kamfwa K., Beaver J. S., Cichy K. A. and Kelly J. D. 2018 QTL mapping of resistance to bean Weevil in common bean. *Crop Sci.* **58**, 2370–2378.

Kamfwa K., Cichy K. A. and Kelly J. D. 2019 Identification of quantitative trait loci for symbiotic nitrogen fixation in common bean. *Theor. Appl. Genet.* **132**, 1375–1387.

Kang Y. J., Ahn Y. K., Kim K. T. and Jun T. H. 2016 Resequencing of *Capsicum annuum* parental lines (YCM334 and Taean) for the genetic analysis of bacterial wilt resistance. *BMC Plant Biol.* **16**, 235.

Kasha K. J. and Kao K. N. 1970 High frequency haploid production in barley (*Hordeum vulgare* L). *Nature* **225**, 874–876.

Keurentjes J. J. B., Bentsink L., Alonso-Blanco C., Hanhart C. J., Vries H. B. D., Effgen S. *et al.* 2007 Development of a near-isogenic line population of *Arabidopsis thaliana* and comparison of mapping power with a recombinant inbred line population. *Genetics* **175**, 891–905.

Keurentjes J. J. B., Willems G., van Eeuwijk F., Nordborg M. and Koornneef M. 2011 A comparison of population types used for QTL mapping in *Arabidopsis thaliana*. *Plant Genet. Resour.* **9**, 185–188.

Khan M. A., Tong F., Wang W., He J., Zhao T. and Gai J. 2018 Analysis of QTL–allele system conferring drought tolerance at seedling stage in a nested association mapping population of soybean (*Glycine max* (L.) Merr.) using a novel GWAS procedure. *Planta* **248**, 947–962.

Kooke R., Wijnker E. and Keurentjes J. J. 2012a Backcross populations and near isogenic lines. *Methods Mol. Biol.* **871**, 3–16.

Kooke R., Wijnker E. and Keurentjes J. J. B. 2012b Quantitative trait Loci (QTL): methods and protocols. In *Quantitative trait loci (QTL)* (ed. S. A. Rifkin), vol. 871, pp. XI, 331. Humana Press, Totowa.

Korte A. and Farlow A. 2013 The advantages and limitations of trait analysis with GWAS: a review. *Plant Methods* **9**, 29–29.

Kover P. X., Valdar W., Trakalo J., Scarcelli N., Ehrenreich I. M., Purugganan M. D. *et al.* 2009 A multiparent advanced generation inter-cross to fine-map quantitative traits in *Arabidopsis thaliana*. *PLoS Genet.* **5**, e1000551.

Kumar A., Tiwari K. L., Datta D. and Singh M. 2014 Marker assisted gene pyramiding for enhanced Tomato leaf curl virus disease resistance in tomato cultivars. *Biol. Plant.* **58**, 792–797.

Kumar A., Ranjan T., Kumar R. R., Rajani K., Kishore C. and Kumar J. 2018 Development of mapping populations. In *Plant biotechnology* (ed. B. Prasad, S. Sahni, P. Kumar and M. Siddiqui), vol. 1. Apple Academic Press, New York.

Kumari M., Clarke H. J., Small I. and Siddique K. H. M. 2009 Albinism in plants: a major bottleneck in wide hybridization, androgenesis and doubled haploid culture. *Crit. Rev. Plant Sci.* **28**, 393–409.

Kump K. L., Bradbury P. J., Wisser R. J., Buckler E. S., Belcher A. R., Oropeza-Rosas M. A. *et al.* 2011 Genome-wide association study of quantitative resistance to southern leaf blight in the maize nested association mapping population. *Nat. Genet.* **43**, 163.

Ladejobi O., Elderfield J., Gardner K. A., Gaynor R. C., Hickey J., Hibberd J. M. *et al.* 2016 Maximizing the potential of multi-parental crop populations. *Appl. Trans. Genom.* **11**, 9–17.

Lander E. S. and Botstein D. 1989 Mapping mendelian factors underlying quantitative traits using Rflp linkage maps. *Genetics* **121**, 185–199.

Lavaud C., Lesne A., Piriou C., Le Roy G., Boutet G., Moussart A. *et al.* 2015 Validation of QTL for resistance to Aphanomyces euteiches in different pea genetic backgrounds using near-isogenic lines. *Theor. Appl. Genet.* **128**, 2273–2288.

Li H., Li X. N., Xuan Y. H., Jiang J., Wei Y. D. and Piao Z. Y. 2018a Genome wide identification and expression profiling of SWEET genes family reveals its role during *Plasmodiophora* brassicae-ınduced formation of clubroot in *Brassica rapa*. *Front. Plant Sci.* **9**, 207.

Li H. H., Rasheed A., Hickey L. T. and He Z. H. 2018b Fast-forwarding genetic gain. *Trends Plant Sci.* **23**, 184–186.

Li R., Jeong K., Davis J. T., Kim S., Lee S., Michelmore R. W. *et al.* 2018c Integrated QTL and eQTL Mapping provides insights and candidate genes for fatty acid composition, flowering time, and growth traits in a F_2 population of a novel synthetic allopolyploid *Brassica napus*. *Front. Plant Sci.* **9**, 1632

Li S., Cao Y., He J., Zhao T. and Gai J. 2017 Detecting the QTL-allele system conferring flowering date in a nested association mapping population of soybean using a novel procedure. *Theor. Appl. Genet.* **130**, 2297–2314.

Liang D., Hu Q., Xu Q., Qi X., Zhou F. and Chen X. 2015 Genetic inheritance analysis of melon aphid (*Aphis gossypii* Glover) resistance in cucumber (*Cucumis sativus* L.). *Euphytica* **205**, 361–367.

Liang Z., Qiu Y. and Schnable J. 2019 Distinct characteristics of genes associated with phenome-wide variation in maize (*Zea mays*). (in press).

Liu G., Zhao T., You X., Jiang J., Li J. and Xu X. 2019 Molecular mapping of the Cf-10 gene by combining SNP/InDel-index and linkage analysis in tomato (*Solanum lycopersicum*). *BMC Plant Biol.* **19**, 15.

Liu X., Han F. Q., Kong C. C., Fang Z. Y., Yang L. M., Zhang Y. Y. *et al.* 2017 Rapid introgression of the Fusarium wilt resistance gene into an elite cabbage line through the combined application of a microspore culture, genome back ground analysis, and disease resistance-Sspecific marker assisted fore ground selection. *Front. Plant Sci.* **8**. 354.

Lv H. H, Wang Q. B., Liu X., Han F. Q., Fang Z. Y., Yang L. M. *et al.* 2016 Whole-genome mapping reveals novel QTL clusters associated with main agronomic traits of cabbage (*Brassica oleracea* var. capitata L.). *Front. Plant Sci.* **7**, 989.

Ma L., Ji Y. J. and Zhang D. X. 2015 Statistical measures of genetic differentiation of populations: rationales, history and current states. *Curr. Zool.* **61**, 886–897.

Mackay T. F. C. 2001 The genetic architecture of quantitative traits. *Annu. Rev. Genet.* **35**, 303–339.

Madhusudhana R. 2015 Linkage mapping. In *Sorghum molecular breeding* (ed. R. Madhusudhana, P. Rajendrakumar and J. V. Patil), pp. 47–70. Springer India, New Delhi.

Mang X. L., Su Y. B., Liu Y. M., Fang Z. Y., Yang L. M., Zhuang M. *et al.* 2016 Genetic analysis and QTL mapping of traits related to head shape in cabbage (*Brassica oleracea* var. capitata L.). *Sci. Hortic.* **207**, 82–88.

Mazoyer M. and Roudart L. 2006 Centers of origin of neolithic agriculture. In *A history of world agriculture*, pp. 74. Earthscan, London.

McMullen M. D., Kresovich S., Villeda H. S., Bradbury P., Li H., Sun Q. *et al.* 2009 Genetic properties of the Maize nested association mapping population. *Science* **325**, 737–740.

Meijer D., Viquez-Zamora M., van Eck H. J., Hutten R. C. B., Su Y., Rothengatter R. *et al.* 2018 QTL mapping in diploid potato by using selfed progenies of the cross *S. tuberosum* × *S. chacoense*. *Euphytica* **214**, 121.

Melchinger A. E., Technow F. and Dhillon B. S. 2011 Gene stacking strategies with doubled haploids derived from biparental crosses: theory and simulations assuming a finite number of loci. *Theor. Appl. Genet.* **123**, 1269–1279.

Mercati F., Riccardi P., Harkess A., Sala T., Abenavoli M. R., Leebens-Mack J. *et al.* 2015 Single nucleotide polymorphism-based parentage analysis and population structure in garden asparagus, a worldwide genetic stock classification. *Mol. Breed.* **35**, 59–70.

Milla R., Osborne C. P., Turcotte M. M. and Violle C. 2015 Plant domestication through an ecological lens. *Trends Ecol. Evol.* **30**, 463–469.

Miyatake K., Saito T., Negoro S., Yamaguchi H., Nunome T., Ohyama A. *et al.* 2012 Development of selective markers linked to a major QTL for parthenocarpy in eggplant (*Solanum melongena* L.). *Theor. Appl. Genet.* **124**, 1403–1413.

Morgan C. 2015 Is it intensification yet? Current archaeological perspectives on the evolution of hunter-gatherer economies. *J. Archaeol. Res.* **23**, 169.

Muylle H., Baert J., Van Bockstaele E., Pertijs J. and Roldan-Ruiz I. 2005 Four QTLs determine crown rust (*Puccinia coronata* f. sp lolii) resistance in a perennial ryegrass (*Lolium perenne*) population. *Heredity* **95**, 348–357.

Nadeem M. A., Nawaz M. A., Shahid M. Q., Doğan Y., Comertpay G., Yıldız M. *et al.* 2018 DNA molecular markers in plant breeding: current status and recent advancements in genomic selection and genome editing. *Biotechnol. Biotech. Eq.* **32**, 261–285.

Nadeem S. M., Naveed M., Zahir Z. A. and Asghar H. N. 2013 Plant–microbe interactions for sustainable agriculture: fundamentals and recent advances. In *Plant microbe symbiosis: fundamentals and advances* (ed. N. K. Arora), pp. 51–103. , Springer India, New Delhi.

Nakedde T., Ibarra-Perez F. J., Mukankusi C., Waines J. G. and Kelly J. D. 2016 Mapping of QTL associated with Fusarium root rot resistance and root architecture traits in black beans. *Euphytica* **212**, 51–63.

Naresh P., Lin S.-W., Lin C-Y., Wang Y-W., Schafleitner R., Kilian A. *et al.* 2018 Molecular markers associated to two non-allelic genic male sterility genes in peppers (*Capsicum annuum* L.). *Front. Plant Sci.* **9**,1343.

Nei M. 1973 Analysis of gene diversity in subdivided populations. *Proc. Natl. Acad Sci. USA* **70**, 3321–3323.

Nguyen T. C. T., Abrams S. R., Friedt W. and Snowdon R. J. 2018 Quantitative trait locus analysis of seed germination, seedling vigour and seedling-regulated hormones in *Brassica napus*. *Plant Breed.* **137**, 388–401.

Niu L., Shi F., Feng H. and Zhang Y. 2019 Efficient doubled haploid production in microspore culture of Zengcheng flowering Chinese cabbage (*Brassica campestris* L. ssp. chinensis [L.] Makino var. utilis Tsen et Lee). *Sci. Hortic.* **245**, 57–64.

Nogue F., Mara K., Collonnier C. and Casacuberta J. M. 2016 Genome engineering and plant breeding: impact on trait discovery and development. *Plant Cell Rep.* **35**, 1475–1486.

Obi VI., Barriuso J. J., Usall J. and Gogorcena Y. 2019 Breeding strategies for identifying superior peach genotypes resistant to brown rot. *Sci. Hortic.* **246**, 1028–1036.

Omoigui L. O., Danmaigona C. C., Kamara A. Y., Ekefan E. J. and Timko M. P. 2018 Genetic analysis of Fusarium wilt resistance in cowpea (*Vigna unguiculata* Walp.). *Plant Breed.* **137**, 773–781.

Parker T. A., Berny Mier y Teran J. C., Palkovic A., Jernstedt J. and Gepts P. 2019 Genetic control of pod dehiscence in domesticated common bean: associations with range expansion and local aridity conditions. (bioRxiv 517516).

Pascual L., Desplat N., Huang B. E., Desgroux A., Bruguier L., Bouchet J. P. *et al.* 2015 Potential of a tomato MAGIC population to decipher the genetic control of quantitative traits and detect causal variants in the resequencing era. *Plant Biotechnol. J.* **13**, 565–577.

Pathirana R. 2011 Plant mutation breeding in agriculture. *CAB Rev.: Perspect. Agric., Vet. Sci., Nutr. Nat. Resou.* **6**, 1–20.

Pen S., Nath U. K., Song S., Goswami G., Lee J.-H. and Jung H.-J. *et al.* 2018 Developmental stage and shape of embryo determine the efficacy of embryo rescue in introgressing orange/yellow color and anthocyanin genes of Brassica species. *Plants* **7**, 99.

Peng T., Sun X. and Mumm R. H. 2014 Optimized breeding strategies for multiple trait integration: I. Minimizing linkage drag in single event introgression molecular breeding : new strategies in plant improvement. *Mol. Breed.* **33**, 89–104.

Pereira L., Ruggieri V., Pérez S., Alexiou K. G., Fernández M., Jahrmann T. *et al.* 2018 QTL mapping of melon fruit quality traits using a high-density GBS-based genetic map. *BMC Plant Biol.* **18**, 324.

Popovsky-Sarid S., Borovsky Y., Faigenboim A., Parsons E. P., Lohrey G. T., Alkalai-Tuvia S. *et al.* 2017 Genetic and biochemical analysis reveals linked QTLs determining natural variation for fruit post-harvest water loss in pepper (Capsicum). *Theor. Appl. Genet.* **130**, 445–459.

Pradhan D., Mathew D., Mathew S. K. and Nazeem P. A. 2018 Identifying the markers and tagging a leucine-rich repeat receptor-like kinase gene for resistance to anthracnose disease in vegetable cowpea (*Vigna unguiculata* (L.) Walp.). *J. Hortic. Sci. Biotech.* **9**3, 225–231.

Qaim M. 2016 Plant breeding and agricultural Development. In *Genetically modified crops and agricultural development*, pp. 15–38. Palgrave Macmillan US, New York.

Qian W., Fan G. Y., Liu D. D., Zhang H. L., Wang X. W., Wu J. *et al.* 2017 Construction of a high-density genetic map and the X/Y sex-determining gene mapping in spinach based on large-scale markers developed by specific-locus amplified fragment sequencing (SLAF-seq). *BMC Genomics* **18**, 276.

Rambla J. L., Medina A., Fernandez-del-Carmen A., Barrantes W., Grandillo S., Cammareri M. *et al.* 2017 Identification, introgression, and validation of fruit volatile QTLs from a red-fruited wild tomato species. *J. Exp. Bot.* **68**, 429–442.

Ravi M. and Chan S. W. L. 2010 Haploid plants produced by centromere-mediated genome elimination. *Nature* **464**, 615.

Ren J. J., Wu P. H., Trampe B., Tian X. L., Lubberstedt T., Chen S. J. 2017 Novel technologies in doubled haploid line development. *Plant Biotechnol. J.* **15**, 1361–1370.

Ripoll J., Urban L. and Bertin N. 2016 The potential of the MAGIC TOM parental accessions to explore the genetic variability in Tomato Acclimation to Repeated cycles of water deficit and recovery. *Front Plant Sci.* **6**, 1172.

Rong F., Chen F., Huang L., Zhang J., Zhang C., Hou D. *et al.* 2019 A mutation in class III homeodomain-leucine zipper (HD-ZIP III) transcription factor results in curly leaf (cul) in cucumber (*Cucumis sativus* L.). *Theor. Appl. Genet.* **132**, 113–123.

Rubinstein M., Katzenellenbogen M., Eshed R., Rozen A., Katzir N., Colle M. *et al.* 2015 Ultrahigh-Density linkage map for cultivated cucumber (*Cucumis sativus* L.) using a single-nucleotide polymorphism genotyping array. *PLoS One* **10**, e0124101.

Saba Rahim M., Sharma H., Parveen A. and Roy J. K. 2018 Trait mapping approaches through association analysis in plants. In *Plant Genetics and Molecular Biology* (ed. R. K. Varshney, M. K. Pandey and A. Chitikineni), pp. 83–108. Springer International Publishing, Cham.

Sai C. B., Nagarajan P., Raveendran M., Rabindran R., Bapu J. R. K. and Senthil N. 2017 Understanding the inheritance of mungbean yellow mosaic virus (MYMV) resistance in mungbean (*Vigna radiata* L. Wilczek). *Mol. Breed.* **37**, 63.

Sallam A. and Martsch R. 2015 Association mapping for frost tolerance using multi-parent advanced generation inter-cross (MAGIC) population in faba bean (*Vicia faba* L.). *Genetica* **143**, 501–514.

Sanetomo R., Habe I. and Hosaka K. 2019 Sexual introgression of the late blight resistance gene Rpi-blb3 from a Mexican wild diploid species Solanum pinnatisectum Dunal into potato varieties. *Mol. Breed.* **39**, 13.

Sannemann W., Lisker A., Maurer A., Léon J., Kazman E., Cöster H. *et al.* 2018 Adaptive selection of founder segments and epistatic control of plant height in the MAGIC winter wheat population WM-800. *BMC Genomics* **19**, 559.

Santamaria L., Ernest E. G., Gregory N. F. and Evans T. A. 2018 Inheritance of resistance in Lima Bean to Phytophthora phaseoli, the causal agent of downy mildew of lima bean. *Hort. Sci.* **53**, 777–781.

Sapkota S., Chen L.-L., Yang S., Hyma K. E., Cadle-Davidson L. and Hwang C.-F. 2019 Construction of a high-density linkage map and QTL detection of downy mildew resistance in Vitis aestivalis-derived 'Norton'. *Theor. Appl. Genet.* **132**, 137–147.

Schneider K. 2005 Mapping populations and principles of genetic mapping. In *The handbook of plant genome mapping* (ed. K. Meksem and G. Kahl). Wiley-VCH Verlag, Weinheim.

Scott K., Balk C., Veney D., McHale L. K. and Dorrance A. E. 2019 Quantitative disease resistance loci towards Phytophthora sojae and three species of pythium in six soybean nested association mapping populations. *Crop Sci.* S9, 605–623.

Segui-Simarro J. M. 2015 Doubled haploidy in model and recalcitrant species. *Front. Plant Sci.* **6**. 1175.

Semagn K., Bjornstad A. and Ndjiondjop M. N. 2006 Principles, requirements and prospects of genetic mapping in plants. *Afr. J. Biotechnol.* **5**, 2569–2587.

Seo J.-H., Kim K.-S., Ko J.-M., Choi M.-S., Kang B.-K., Kwon S.-W. *et al.* 2019 Quantitative trait locus analysis for soybean (*Glycine max*) seed protein and oil concentrations using selected breeding populations. *Plant Breed.* **138**, 95–104.

Seymour D. K., Filiault D. L., Henry I. M., Monson-Miller J., Ravi M., Pang A. D. *et al.* 2012 Rapid creation of Arabidopsis doubled haploid lines for quantitative trait locus mapping. *Proc. Natl. Acad. Sci. USA* **109**, 4227–4232.

Shivakumar M., Gireesh C. and Talukdar A. 2016 Efficiency and utility of pollination without emasculation (PWE) method in intra- and inter-specific hybridization in soybean. *Indian J. Genet. Plant Breed.* **76**, 98–100.

Sidhu G. K., Warzecha T. and Pawlowski W. P. 2017 Evolution of meiotic recombination genes in maize and teosinte. *BMC Genomics* **18**, 106.

Singh R. K., Rai N., Lima J. M., Singh M., Singh S. N. and Kumar S. 2015 Genetic and molecular characterisations of Tomato leaf curl virus resistance in tomato (*Solanum lycopersicum* L). *J. Hortic. Sci. Biotech.* **90**, 503–510.

Singh S., Bhatia R., Kumar R., Sharma K., Dash S. and Dey S. S. 2018 Cytoplasmic male sterile and doubled haploid lines with desirable combining ability enhances the concentration of important antioxidant attributes in *Brassica oleracea*. *Euphytica* **214**, 207.

Slavin J. L. and Lloyd B. 2012 Health benefits of fruits and vegetables. *Adv. Nut.* **3**, 506–516.

Sleper J. A. and Bernardo R. 2016 Recombination and genetic variance among maize doubled haploids induced from F-1 and F-2 plants. *Theor. Appl. Genet.* **129**, 2429–2436.

Soltis D. E. and Soltis P. S. 1999 Polyploidy: recurrent formation and genome evolution. *Trends Ecol. Evol.* **14**, 348–352.

Stadlmeier M., Hartl L. and Mohler V. 2018 Usefulness of a multiparent advanced generation intercross population with a greatly reduced mating design for genetic studies in winter Wheat. *Front. Plant Sci.* **9**, 1825–1825.

Strobbe S., De Lepeleire J. and Van Der Straeten D. 2018 From in planta function to vitamin-rich food crops: the ace of biofortification. *Front. Plant Sci.* **9**, 1862.

Sugita T., Semi Y., Sawada H., Utoyama Y., Hosomi Y., Yoshimoto E. *et al.* 2013 Development of simple sequence repeat markers and construction of a high-density linkage map of *Capsicum annuum*. *Mol. Breed.* **31**, 909–920.

Sun X.-R., Liu L., Zhi X.-N., Bai J.-R., Cui Y.-N., Shu J.-S. *et al.* 2019 Genetic analysis of tomato internode length via mixed major gene plus polygene inheritance model. *Sci. Hortic.* **246**, 759–764.

Sun X., Luo S., Luo L., Wang X., Chen X., Lu Y. *et al.* 2018 Genetic analysis of Chinese cabbage reveals correlation between rosette leaf and leafy head variation. *Front. Plant Sci.* **9**, 1455.

Swarm S. A., Sun L., Wang X., Wang W., Brown P. J., Ma J. *et al.* 2019 Genetic dissection of domestication-related traits in soybean through genotyping-by-sequencing of two interspecific mapping populations. *Theor. Appl. Genet.* **135**,1195–1209.

Szała L., Cegielska-Taras T., Adamska E. and Kaczmarek Z. 2018 Assessment of genetic effects on important breeding traits in reciprocal DH populations of winter oilseed rape (*Brassica napus* L.). *J. Integr. Agri.* **17**, 76–85.

Taiz L. 2013 Agriculture, plant physiology, and human population growth: past, present, and future. *Theor. Exp. Plant Phys.* **25**, 167–181.

Takuno S., Terauchi R. and Innan H. 2012 The Power of QTL mapping with RILs. *PLoS One* **7**, 46545.

Tanhuanpaa P., Kalendar R., Schulman A. H. and Kiviharju E. 2008 The first doubled haploid linkage map for cultivated oat. *Genome* **51**, 560–569.

Thakur H., Jindal S. K., Sharma A. and Dhaliwal M. S. 2019 A. monogenic dominant resistance for leaf curl virus disease in chilli pepper (*Capsicum annuum* L.). *Crop Prot.* **116**, 115–120.

Toppino L., Barchi L., Lo Scalzo R., Palazzolo E., Francese G. and Fibiani M. *et al.* 2016 Mapping quantitative trait loci affecting biochemical and morphological fruit properties in eggplant (*Solanum melongena* L.). *Front. Plant Sci.* **7**, article ID 256.

Torkamaneh D., Boyle B. and Belzile F. 2018 Efficient genome-wide genotyping strategies and data integration in crop plants. *Theor. Appl. Genet.* **131**, 499–511.

Turcotte M. M., Araki H., Karp D. S., Poveda K. and Whitehead S. R. 2017 The eco-evolutionary impacts of domestication and agricultural practices on wild species. *Philos. Trans R. Soc. London, B Biol. Sci.* **372**, pii: 20160033.

Vallarino J. G., Pott D. M., Cruz-Rus E., Miranda L., Medina-Minguez J. J., Valpuesta V. *et al.* 2019 Identification of quantitative trait loci and candidate genes for primary metabolite content in strawberry fruit. *Hortic. Res.* **6**, 4.

van Berloo R. and Stam P. 1998 Marker-assisted selection in autogamous RIL populations: a simulation study. *Theor. Appl. Genet.* **96**, 147–154.

van de Wouw M., Kik C., van Hintum T., van Treuren R. and Visser B. 2010 Genetic erosion in crops: concept, research results and challenges. *Plant Genet. Resour.* C **8**, 1–15.

Varshney R. K., Terauchi R. and McCouch S. R. 2014 Harvesting the promising fruits of genomics: applying genome sequencing technologies to crop breeding. *PLoS Biol.* **12**, e1001883.

Velmurugan J., Milbourne D., Connolly V., Heslop-Harrison J. S., Anhalt U. C. M., Lynch M. B. *et al.* 2018 An immortalized genetic mapping population for perennial ryegrass: a resource for phenotyping and complex trait mapping. *Front. Plant Sci.* **9**, 717.

Wada T., Oku K., Nagano S., Isobe S., Suzuki H., Mori M. *et al.* 2017 Development and characterization of a strawberry MAGIC population derived from crosses with six strawberry cultivars. *Breed. Sci.* **67**, 370–381.

Wahid A., Gelani S., Ashraf M. and Foolad M. R. 2007 Heat tolerance in plants: an overview. *Environ. Exp. Bot.* **61**, 199–223.

Wang C., Li H., Li Y., Meng Q., Xie F., Xu Y *et al.* 2019 Genetic characterization and fine mapping BrCER4 in involved cuticular wax formation in purple cai-tai (*Brassica rapa* L. var. purpurea). *Mol. Breed.* **39**, 12.

Wang P. Y., Wang L. R., Guo J. J., Yang W. C. and Shen H. L. 2016 Molecular mapping of a gene conferring resistance to Phytophthora capsici Leonian race 2 in pepper line PI201234 (*Capsicum annuum* L.). *Mol. Breed.* **36**, 66.

Wang Y., Zhou Q., Zhu G., Wang S., Ma Y., Miao H. *et al.* 2018 Genetic analysis and identification of a candidate gene associated with in vitro regeneration ability of cucumber. *Theor. Appl. Genet.* **131**, 2663–2675.

Wei Y., Li F., Zhang S., Zhang S., Zhang H. and Sun R. 2018 Characterization of ınterspecific hybrids between flowering Chinese cabbage and Chinese kale. *Agronomy* **8**, 258.

Welsh C. E. and McMillan L. 2012 Accelerating the inbreeding of multi-parental recombinant inbred lines generated by sibling matings. *Genes Genomes Genet.* **2**, 191–198.

Whitlock M. C and Guillaume F. 2009 Testing for spatially divergent selection: comparing Q(ST) to F-ST. *Genetics* **183**, 1055–1063.

Win K. T., Zhang C., Silva R. R., Lee J. H., Kim Y.-C. and Lee S. 2019 Identification of quantitative trait loci governing subgynoecy in cucumber. *Theor. Appl. Genet.* **132**, 1505–1521.

Win K. T., Zhang C., Song K., Lee J. H. and Lee S. 2015 Development and characterization of a co-dominant molecular marker via sequence analysis of a genomic region containing the Female (F) locus in cucumber (*Cucumis sativus* L.). *Mol. Breed.* **35**, 229–238.

Wright S. I. 2005 The effects of artificial selection on the maize genome. *Science* **310**, 54–54.

Wu X., Li G., Wang B., Hu Y., Wu X., Wang Y *et al.* 2018 Fine mapping Ruv2, a new rust resistance gene in cowpea (Vigna unguiculata), to a 193-kb region enriched with NBS-type genes. *Theor. Appl. Genet.* **131**, 2709–2718.

Xia N., Wu D. P., Zhan Y. H., Liu Y., Sun M. Y., Zhao X. *et al.* 2017 Dissection of genetic architecture for oil content in soybean seed using two backcross populations. *Plant Breed.* **136**, 365–371.

Xiao D., Shen H.-R., Zhao J.-J., Wei Y.-P., Liu D.-R., Hou X.-L. *et al.* 2019 Genetic dissection of flowering time in Brassica rapa responses to temperature and photoperiod. *Plant Sci.* **280**, 110–119.

Xu Y., Guo S. R., Shu S., Ren Y. and Sun J. 2017 Construction of a genetic linkage map of rootstock-used pumpkin using SSR markers and QTL analysis for cold tolerance. *Sci. Hortic.* **220**, 107–113.

Yan G. J., Liu H., Wang H. B., Lu Z. Y., Wang Y. X., Mullan D. *et al.* 2017 Accelerated generation of selfed pure Lline plants for gene identification and Crop Breeding. *Front. Plant Sci.* **8**, 1786.

Yang H. Y. and Zhou C. 1982 In vitro induction of haploid plants from unpollinated ovaries and ovules. *Theor. Appl. Genet.* **63**, 97–104.

Yang S., Chen S., Zhang K., Li L., Yin Y., Gill R. A. *et al.* 2018 A high-density genetic map of an Allohexaploid brassica doubled haploid population reveals quantitative trait loci for pollen viability and fertility. *Front. Plant Sci.* **9**, 1161.

Yang Y., Lv H. and Liao H. 2019 Identification and mapping of two independent recessive loci for the root hairless mutant phenotype in soybean. *Theor. Appl. Genet.* **132**, 301–312.

Yano M., Harushima Y., Nagamura Y., Kurata N., Minobe Y. and Sasaki T. 1997 Identification of quantitative trait loci controlling heading date in rice using a high-density linkage map. *Theor. Appl. Genet.* **95**, 1025–1032.

Yu H. F., Wang J. S., Zhao Z. Q., Sheng X. G., Shen Y. S., Branca F. *et al.* 2019 Construction of a high-density genetic map and identification of loci related to hollow stem trait in broccoli (*Brassic oleracea* L. italica). *Front. Plant Sci.* **10**, 00045.

Yu J. M., Holland J. B., McMullen M. D. and Buckler E. S. 2008 Genetic design and statistical power of nested association mapping in maize. *Genetics* **178**, 539–551.

Zhang M., Montooth K. L., Wells M. T., Clark A. G. and Zhang D. 2005 Mapping multiple quantitative trait loci by Bayesian classification. *Genetics* **169**, 2305–2318.

Zhang S., Yu H., Wang K., Zheng Z., Liu L., Xu M. *et al.* 2018 Detection of major loci associated with the variation of 18 important agronomic traits between Solanum pimpinellifolium and cultivated tomatoes. *The Plant J.* **95**, 312–323.

Zhang Y.-M. 2012 F2 Designs for QTL analysis. In *Quantitative trait loci (QTL): methods and protocol*s (ed. S. A. Rifkin), pp. 17–29. Humana Press, Totowa.

Zhang Y. M. and Xu S. 2004 Mapping quantitative trait loci in F2 incorporating phenotypes of F3 progeny. *Genetics* **166**, 1981–1993.

Zhao B., Wang B., Li Z., Guo T., Zhao J. and Guan Z. *et al.* 2019 Identification and characterization of a new dwarf locus DS-4 encoding an Aux/IAA7 protein in *Brassica napus*. *Theor. Appl. Genet.* **132**, 1435–1449.

Zhao Z. D., Gu H. H., Sheng X. G., Yu H. F., Wang J. S., Huang L. *et al.* 2016 Genome-wide single-nucleotide polymorphisms discovery and high-density genetic map construction in cauliflower using specific-locus amplified fragment sequencing. *Front. Plant Sci.* **7**, 334.

Zhong Y. J., Zhou Y. Y., Li J. X., Yu T., Wu T. Q., Luo J. N. *et al.* 2017 A high-density linkage map and QTL mapping of fruit-related traits in pumpkin (*Cucurbita moschata* Duch). *Sci. Rep.* **7**, 12785.

Zhu C., Huang J and Zhang Y. M. 2007 Mapping binary trait loci in the F-2 : 3 design. *J. Hered.* **98**, 337–344.

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