

Chapter 10

Marker-Assisted Breeding for Economic Traits in Common Bean



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Abstract The common bean (*Phaseolus vulgaris* L.) is the most widely grown grain legume species that is consumed directly by humans. The crop is grown from the northern regions of Canada to the temperate regions in the Southern Hemisphere including highland tropical regions of Latin America and East Africa where a wide diversity of seed types and growth habits are produced. Local adaptation is critical, and consumers are very selective in the seed types they grow and consume. Despite its broad adaptation, common bean productivity is low compared to cereal crops and is constrained by a wide range of biotic and abiotic stresses. In addition, grower and consumer preferences for specific growth habits, maturity classes, seed types, and quality traits limit improvement to specific regions and seed types. Breeders are challenged with having to maintain separate breeding programs where outcomes are limited to specific seed types. As a community, many of the biotic stresses are similar, and the genetic tools to control them can be shared. The broad area of marker technologies linked to economic traits is one area where the bean community has shared benefits. This chapter summarizes some of the broad advances in marker technologies as they have been applied to improve economic traits controlling both productivity and quality characteristics of common bean.

Keywords Disease resistance · Dry bean · Molecular markers · Marker-assisted selection · MAS · *Phaseolus vulgaris* · Plant breeding · Quality traits · Quantitative trait loci · QTL · Quality traits

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10.1 Introduction

The common bean (*Phaseolus vulgaris* L.) community has been utilizing marker-assisted breeding (MAB) for the last 25 years (Miklas et al. 2006). Early work started in the 1990s with RAPD markers linked to major disease resistance traits, and the tool was deployed in many labs (Kelly 1995; Kelly and Miklas 1998). To expand their versatility, many of these markers were converted to sequence-characterized amplified region (SCAR) markers, and this further expanded their utility throughout the community. A number of these SCAR markers are still being used in breeding programs decades later (Melotto et al. 1996). In addition, linked markers enabled more detailed fine mapping of major resistance gene loci (Melotto and Kelly 2001). As quantitative trait loci (QTL) analysis tools were developed, work focused on mapping quantitative traits as most traits of economic importance are genetically complex (Kelly et al. 2003; Kelly and Vallejo 2005). The focus of the research expanded beyond disease resistance traits to identify QTL linked to canning quality (Posa-Macalincag et al. 2002; Walters et al. 1997; Wright and Kelly 2011), root traits (Cichy et al. 2009a), drought tolerance (Mukeshimana et al. 2014), insect pest resistance (Brisco et al. 2014), and N-fixation (Heilig et al. 2017). Improved genomic tools finally led to the development of SNP markers and whole genome sequencing of *P. vulgaris* (Schmutz et al. 2014). The development of the BARCBean6K_3 BeadChip with 5389 SNPs (Song et al. 2015) expanded research activities to a whole range of genome-wide association studies (GWAS) focused on an array of agronomic traits (Kamfwa et al. 2015a; Moghaddam et al. 2016) including some related to drought tolerance (Hoyos-Villegas et al. 2016). This work was facilitated by the development of diversity panels, the most notable being the Andean diversity panel assembled by Cichy et al. (2015a). GWAS studies in turn led to candidate gene discoveries for disease resistance traits (Zuiderveen et al. 2016), symbiotic N-fixation (Kamfwa et al. 2015b), and the phytochrome A associated with *ppd* photoperiod gene for flowering on chromosome Pv01 (Kamfwa et al. 2015a). As a community, bean breeders have widely adopted marker-assisted selection despite the absence of detailed genetic maps and the extensive genomic tools available in many of the major grain and oilseed crops. However, the recent genomic sequencing of beans has led to a wide array of genetic studies focused on the origin and domestication, gene synteny within related legume species, identification of resistance gene clusters, and fine mapping of specific economic traits. These studies are discussed in detail below.

Common bean is a diploid member of the *Phaseoleae* tribe with $2n = 22$ chromosomes. The cultivated species are classified into two major horticulture types, one cultivated for dry seeds (commercial bean types typified by pinto or kidney beans; Fig. 10.1) and the other as a vegetable consumed as fresh pods (typified as garden, green, snap, haricot, or string beans). The species *Phaseolus vulgaris* is a self-pollinated annual legume, the most important among the 5 cultivated species with the *Phaseolus* genus that has over 50 recorded species (Freytag and Debouck 2002). Multiple lines of evidence summarized by Mamidi



Fig. 10.1 Diversity in seed size, shape, and color within *Phaseolus vulgaris*. Similar levels of diversity exist for growth habit, performance, and quality traits within common bean

et al. (2013) have shown that common bean is organized in two geographically isolated and genetically distinct gene pools known as Middle American (hereafter referred to as Mesoamerican) and Andean. The wild species was originally considered to be Andean in origin based on rare phaseolin alleles present in wild species found in Peru (Kami et al. 1995). With the advent of genomic research, the actual origin has recently been shown to be in Southern Mexico (Bitocchi et al. 2012). Sequence data of five gene loci support the Mesoamerican origin of the species and the presence of a major bottleneck in the Andean gene pool that predates domestication (Bitocchi et al. 2012). A further study of 102 wild and 112 domesticated bean accessions suggests that domestication occurred independently in the Oaxaca Valley in Mexico, adjacent to the location of maize domestication, and in southern Bolivia and northern Argentina (Bitocchi et al. 2013). Schmutz et al. (2014) estimated that the wild Andean gene pool diverged from the wild Mesoamerican gene pool approximately 165,000 years ago, with a small founding population and a strong bottleneck that lasted approximately 76,000 years. This bottleneck has continued to challenge bean breeders as progress made in breeding in the Mesoamerican gene pool has not been directly transferable to the larger-seeded Andean beans due to lack of genetic diversity (Vandemark et al. 2014).

The bean genome is relatively small, 587 Mb in total across 11 chromosomes named Pv01 to Pv11. Chromosomes were originally numbered by size (Freyre et al.

1998), but a new alignment was made by Pedrosa-Harand et al. (2008) to standardize the nomenclature based on the extensive genetic mapping. The first bean genotype to be sequenced was the Andean landrace, Chaucha Chuga accession number, G19833 from Peru (Schmutz et al. 2014). Aside from opening the floodgates for detailed genetic and genomic studies to proceed, the bean genome sequence described by Schmutz et al. (2014) showed remarkable synteny with the 40 chromosomes of soybean (*Glycine max*). The data support the previous phylogeny of economically important *Phaseoleae* legumes where *P. vulgaris* diverged from soybean some 18 million years ago (MYA) and from cowpea (*Vigna unguiculata*) 4.9 MYA (McClellan et al. 2010). The recent publication of the cowpea genome underscores the remarkable synteny between these two species. Six cowpea linkage groups are largely collinear with six common bean chromosomes, while the rest have synteny mainly with two common bean chromosomes (Muñoz-Amatriaín et al. 2016). Based on extensive synteny, the *Vigna* research community has considered renumbering the 11 *Vigna* chromosomes to align directly with those of *P. vulgaris* (Muñoz-Amatriaín, personal communication).

More recently, a second bean genotype BAT 93 from the Mesoamerican gene pool has been sequenced by a multination consortium (Vlasova et al. 2016). Support for the expected gene synteny between the two genomes is displayed by 25,991 protein-coding genes (PCG) mapped in BAT93, where 20,617 were uniquely mapped to 20,618 PCGs in the Andean genome, G19833 (Vlasova et al. 2016). The authors report that 234 of the 852 putative resistance genes identified in the BAT93 genome belonged to the cytoplasmic NBS-LRR class. This compares with 316 NBS-LRR class genes in G19833 that could be mapped to 220 genes in BAT93. However, Vlasova et al. (2016) were unable to find resistance gene clusters that were specific to either of the two genotypes. They suggest that the genomic clustering of resistance genes predates the split of both gene pools and suggest that the differences in pathogen susceptibility might be due to polymorphisms in these loci, rather than a gene presence-absence effect (Vlasova et al. 2016). The full genome sequence of a third bean genotype, OAC-Rex with introgression from the tepary bean (*P. acutifolius*), was recently reported in Canada (Perry et al. 2013). With the decreasing costs for DNA sequencing, a wider array of bean genotypes are expected to be sequenced in the near future and expand the knowledge of the genomic basis of economically important traits of common bean.

10.2 Candidate Gene Clusters

The tagging and mapping of resistance genes in *P. vulgaris* have expanded greatly with the sequencing of the bean genome (Schmutz et al. 2014). The identification of physical positions for individual genes has generated a map with major resistance gene clusters on eight bean chromosomes. Details of the individual clusters are shown in Table 10.1 where genes controlling fungal (*Co*-genes for anthracnose, *Phg*-genes for angular leaf spot, *Ur*-genes for rust), bacterial (*Pse*-genes for halo

Table 10.1 R gene clusters in *Phaseolus vulgaris*

Chromosome	Position (Mb)	Genes	Pathogen	Reference
Pv01	50.16–50.30	<i>Co-1</i>	Anthraco-nose	Zuiderveen et al. (2016)
Pv01	49.81–50.51	<i>Co-x</i>	Anthraco-nose	Richard et al. (2014)
Pv01	ND	<i>Co-w</i>	Anthraco-nose	Geffroy et al. (2008)
Pv01	50.26–50.34	<i>Co-1^{HY}</i>	Anthraco-nose	Chen et al. (2017)
Pv01	50.16–50.55	<i>Co-Pa</i>	Anthraco-nose	De Lima Castro et al. (2017)
Pv01	48.45–50.30	<i>Co-AC</i>	Anthraco-nose	Gilio et al. (2016)
Pv01	50.5	<i>Co-1²</i>	Anthraco-nose	Vazin et al. (2014)
Pv01	50.51	<i>Co-14</i>	Anthraco-nose	Gonçalves-Vidigal et al. (2016)
Pv01	50.51	<i>Co-1⁴</i>	Anthraco-nose	Gonçalves-Vidigal et al. (2011)
Pv01	50.51	<i>Phg-1</i>	ALS	Gonçalves-Vidigal et al. (2011)
Pv01	ND	<i>Ur-9</i>	Rust	Kelly et al. (2003)
Pv02	ND	<i>Co-u</i>	Anthraco-nose	Geffroy et al. (2008)
Pv02	40.39–40.44	<i>Co-u</i>	Anthraco-nose	Trabanco et al. 2015
Pv02	48.6	<i>NN</i>	Anthraco-nose	Zuiderveen et al. (2016)
Pv02	48.18–48.27	<i>Pse-3</i>	Halo blight	Miklas et al. (2014)
Pv02	48.18–48.27	<i>I</i>	BCMV	Bello et al. (2014)
Pv03	ND	<i>Co-13</i>	Anthraco-nose	Lacanal-lo and Gonçalves-Vidigal (2015)
Pv03	<0.044	<i>Co-17</i>	Anthraco-nose	Trabanco et al. (2015)
Pv03	0.36–0.39	<i>bc-1²</i>	BCMV	Meziadi et al. (2016)
Pv03	0.36–0.39	<i>bc-u</i>	BCMV	Meziadi et al. (2016)
Pv04	0.59	<i>Pse-6</i>	Halo blight	Miklas et al. (2014)
Pv04	ND	<i>Ur-5</i>	Rust	Wright et al. (2008)
Pv04	ND	<i>Ur-D^a</i>	Rust	Miklas et al. (2002)
Pv04	1.23–1.26	<i>Ur-14</i>	Rust	Valentini et al. (2017)
Pv04	41.88–45.45	<i>Phg-4</i>	ALS	Souza et al. (2016)
Pv04	0.49–0.58	<i>Phg-3</i>	ALS	Valentini et al. (2017)
Pv04	0.49–0.58	<i>Co-3⁴</i>	Anthraco-nose	Valentini et al. (2017)
Pv04	9.08	<i>Co-15</i>	Anthraco-nose	Sousa et al. (2015)
Pv04	1.43	<i>Co-16</i>	Anthraco-nose	Coimbra-Gonçalves et al. (2016)
Pv04	3.36	<i>Co-3</i>	Anthraco-nose	Coimbra-Gonçalves et al. (2016)
Pv04	3.36	<i>Co-3³</i>	Anthraco-nose	Coimbra-Gonçalves et al. (2016)
Pv04	3.36	<i>Co-10</i>	Anthraco-nose	Gonçalves-Vidigal et al. (2013)
Pv04	ND	<i>Co-y</i>	Anthraco-nose	Geffroy et al. 2008
Pv04	ND	<i>Co-z</i>	Anthraco-nose	Geffroy et al. (2008)
Pv07	6.85	<i>Co-5²</i>	Anthraco-nose	Sousa et al. (2014)
Pv07	ND	<i>Co-6</i>	Anthraco-nose	Kelly et al. (2003)
Pv08	2.38–2.48	<i>Co-4²</i>	Anthraco-nose	Oblessuc et al. (2015)
Pv08	ND	<i>Ur-13</i>	Rust	Mienie et al. (2005)
Pv08	57.82–58.53	<i>Phg-2</i>	ALS	Souza et al. (2016)
Pv10	11.18	<i>Pse-1</i>	Halo blight	Miklas et al. (2014)

(continued)

Table 10.1 (continued)

Chromosome	Position (Mb)	Genes	Pathogen	Reference
Pv10	3.49	<i>Pse-2</i>	Halo blight	Miklas et al. (2014)
Pv10	39.58	<i>Pse-4</i>	Halo blight	Miklas et al. (2014)
Pv10	3.82–8.78	<i>Phg-5</i>	ALS	Souza et al. (2016)
Pv11	46.96–47.01	<i>Ur-3</i>	Rust	Hurtado-Gonzales et al. (2017)
Pv11	51.93	<i>Ur-11</i>	Rust	McClellan p.c.
Pv11	ND	<i>Ur-6</i>	Rust	Park et al. (2004)
Pv11	ND	<i>Ur-D</i> ^b	Rust	Miklas et al. (2002)
Pv11	ND	<i>Co-2</i>	Anthracnose	Adam-Blondon et al. (1994)

ND not determined, NN not named, ALS angular leaf spot, BCMV bean common mosaic virus

^aUr-Dorado 108

^bUr-Dorado 53 (Miklas et al. 2002)

blight), and viral (*I* and *bc*-genes for *bean common mosaic virus*) pathogens co-localize. The resistance gene codes are named to ally with the pathogen name *Co* for *Colletotrichum*. An excellent graphic of these resistance gene clusters in *P. vulgaris* is also provided by Meziadi et al. (2016), and the implications for bean breeders will be discussed further. Aside from the physical mapping, genetic studies have confirmed the absolute co-segregation of gene pairs on Pv01, Pv02, and Pv04. The *Co-1*⁴ and *Phg-1* genes co-segregate at 50.51 Mb on Pv01 (Gonçalves-Vidigal et al. 2011), the *Pse-3* and *I* genes co-segregate at 48.2 Mb on Pv02 (Miklas et al. 2014), and the *Co-3*⁴ and *Phg-3* genes co-segregate at 0.5 Mb on Pv04 (Valentini et al. 2017). Examples of other genes that co-segregate are forthcoming, as additional mapping data is needed to confirm these associations.

Within the *Phaseolus* research community, a genetics committee of the Bean Improvement Cooperative approves all new gene symbols based on genetic and allelism studies and maps positions to ensure that the new gene is unique and provides a real service to breeders worldwide. Identifying alleles is critical so that breeders can choose the most effective allele for a particular pathogenic race or isolate that exists in their region. Not all researchers have chosen to follow the convention, but the physical mapping of genes is now permitting a clearer identification of resistance genes, alleles, and loci that should aid in MAB. All named genes have a number following the symbol that identifies the trait or pathogen, and those without numbers have not received full approval from the genetics committee.

10.3 Chromosome Pv01

The major resistance locus on Pv01 is the *Co-1* locus controlling bean anthracnose. Five alleles have been identified at this locus (Ferreira et al. 2013). The *Co-1*² allele has been mapped to a 50.1–50.3 Mb region on Pv01 (Zuiderveen et al. 2016), and Vazin et al. (2014) mapped the *Co-1*² allele to the region of 50.2–50.5 Mb in the cultivar bolt. Three other genes coded *Co-1*^{HY}, *Co-Pa*, and *Co-AC* essentially map to

the same location as the Co-1 locus (Table 10.1). A new gene, *Co-14* in the cultivar Pitanga, was mapped to the same region as the *Co-1⁴* allele using the same CV 542014 marker (Gonçalves-Vidigal et al. 2016) that Richard et al. (2014) had mapped at 50.51 Mb. Likewise, the *Co-x* gene first described by Geffroy et al. (2008) has been mapped to the same general region (49.8–50.5 Mb) on Pv01 by Richard et al. (2014). It would appear that these genes are either new or existing alleles at the Co-1 locus, but in the absence of thorough allelism studies, breeders are left with no clear choice as to which gene or allele to use. To assist breeders, an InDel marker, NDSU_IND_1_50.2219, was developed that was linked with *Co-1²* at 3.2 cM (Zuiderveen et al. 2016). The InDel marker (50.22 Mb) was present in genotypes possessing different resistant alleles except *Co-1⁵* (Widusa) at the Co-1 locus including the *Co-x* in Jalo EEP558 (Vallejo et al. 2003). The InDel marker should be useful for breeders in third world countries as it can be utilized to integrate the most effective resistance allele at the Co-1 locus using MAB in labs with limited resources. The *Co-1⁴* allele has been shown to co-segregate with the *Phg-1* gene, which conditions resistance to specific races of angular leaf spot (Gonçalves-Vidigal et al. 2011). Other resistance genes of interest on Pv01 are the *Ur-9* rust avoidance gene from the Andean cultivar Pompadour Checa (Kelly et al. 2003). No physical position has been assigned to this gene, but it is linked to the Bng 122 SSR marker at the distal end of Pv01 (Pedrosa-Harand et al. 2008). Interestingly, all the *Co-1* alleles and the other reported genes including the *Ur-9* gene are found in Andean cultivars, suggesting that this region of Pv01 is strongly Andean in origin.

10.4 Chromosome Pv02

The *I* gene is the most widely deployed and best recognized resistance gene in common bean and resides on the proximal region of Pv02 (Table 10.1). The *I* gene conditions resistance to BCMV through a hypersensitive resistance response to strains of BCMV and was mapped to 48.18–48.27 Mb region of Pv02 (Bello et al. 2014). The *Pse-3* gene that conditions resistance to strains of halo blight co-segregates with the *I* gene (Miklas et al. 2014). The *Co-u* gene first described by Geffroy et al. (2008) was reported to be in close proximity to the *I* gene. Recently Trabanco et al. (2015) mapped *Co-uto* a 40.4 Mb region of Pv02 where prior work had identified a quantitative resistance locus (QRL) for anthracnose resistance in this region (Oblessuc et al. 2014). It is unclear that Trabanco et al. (2015) studied the actual *Co-u* gene as Zuiderveen et al. (2016) identified a genomic region at 48.6 Mb on Pv02 that conditioned resistance to anthracnose in an Andean diversity panel. This region adjacent to the *I* and *Pse-3* genes is a more likely the location of *Co-u* as the SW13 marker linked to the *I* gene (Melotto et al. 1996) co-segregated with the anthracnose resistance gene (not yet named) in a segregating population within the 48.2 to 48.6 Mb interval (Kelly, personal communication). Resistance genes effective against three different pathogens appear to co-localize in this region.

10.5 Chromosome Pv03

Two anthracnose genes and two recessive virus genes are located on Pv03. The *bc-l²* and *bc-u* genes that condition resistance to strains of BCMV are loosely linked (Strausbaugh et al. 1999) and, based on the map of Meziadi et al. (2016), are located around 0.4 Mb in the proximal end of Pv03. However, the SCAR marker SBD5 linked to the *bc-l²* gene allows for direct selection of this allele alone (Miklas et al. 2000b). The *Co-17* gene in the bean accession, SEL1308 that conditions resistance to anthracnose races 3 and 7, was mapped at the extreme proximal end of Pv03 in a region bordered by the InDel marker NDSU_IND_3_00441 at 441 kb (Trabanco et al. 2015). A second anthracnose gene designated *Co-13* and derived from the landrace cultivar Jalo Listras Pretas from Brazil has not been physically mapped (Lacanallo and Gonçalves-Vidigal 2015), but the gene may reside in the same teleomorphic region as *Co-17*.

10.6 Chromosome Pv04

This chromosome is home to the largest number of resistance genes and gene clusters. The major Co-3 locus with 5 alleles is located on Pv04: *Co-3* (Mexico1), *Co-3²* (Mexico 227, extinct), *Co-3³* (*Co-9*), *Co-3⁴* (*Co-10*), *Co-3⁵* (*Co-7*), in addition the *Co-15*, *Co-16*, *Co-y*, and *Co-x* genes. At least 3 rust-resistant genes, *Ur-5*, *Ur-14*, and *Ur-Dorado* resistant to race 108 (Miklas et al. 2002), the *Pse-6* gene for halo blight, and *Phg-3* gene for angular leaf spot (ALS) that co-segregates with the *Co-3⁴* allele, are also located on Pv04 (Table 10.1). The majority of the *Co-3* alleles including the *Co-10* gene was tagged with the g2303 marker located at 3.36 Mb (Coimbra-Gonçalves et al. 2016). The same group working with the resistant Ouro Negro cultivar showed co-segregation between the *Phg-3* and *Co-3⁴* genes, the later formerly named *Co-10* (Gonçalves-Vidigal et al. 2013). These *Phg-3* and *Co-3⁴* genes were recently mapped to a region 0.49–0.58 Mb (Valentini et al. 2017) on Pv04 quite distant from the original Co-3 locus at 3.36 Mb, so the rationale for renaming *Co-10* gene is unclear. Meziadi et al. (2016) shows a similar clear separation of the *Co-3* and *Co-10* genes based on sequence data of 376 NB-LRR families (see Fig. 10.1). In addition, Souza et al. (2016) previously mapped the *Phg-3* gene with the g2303 marker at 3.36 Mb. A second ALS gene *Phg-4* was mapped to a region 41.88–45.45 Mb toward the distal end of Pv04 (Souza et al. 2016). The *Co-16* gene in Crioulo 159 was mapped at 1.43 Mb (Coimbra-Gonçalves et al. 2016) well within the region the same authors claim that the Co-3 locus resides. A third gene *Co-15* was mapped at 9.1 Mb outside this region suggesting independence from the *Co-3* and *Co-16* genes (Sousa et al. 2015). The *Pse-6* gene also appears to reside within the *Co-3⁴/Phg-3* cluster on Pv04 (Miklas et al. 2014). Two rust resistance genes, *Ur-5* and *Ur-Dorado108* (Miklas et al. 2000a), were never physically mapped, but *Ur-14* from Ouro Negro was mapped to 1.23–1.26 Mb region (Valentini

et al. 2017) adjacent to the *Co-16* gene. That conclusion seems more likely than that drawn by Valentini et al. (2017) where they associate the *Ur-14* gene with the *Co-3⁴/Phg-3* cluster. Other small pustule rust resistance sources have been mapped to Pv04, but their physical positions were not reported (Wright et al. 2008). The type of resistance reported on Pv04 stands in contrast to the hypersensitive resistance typified by the *Ur-3* and *Ur-11* genes on Pv11. Further work must be done to elucidate the actual number of resistance alleles and resistance genes co-localized at the Co-3 locus.

10.7 Chromosome Pv07

Two anthracnose genes *Co-5* and *Co-6* are located on Pv07. The *Co-5²* allele present in bean accession G2333 was mapped to 6.85 Mb (Sousa et al. 2014) and is clearly distinct from the *Co-6* gene based on numerous genetic studies supporting independent loci (Kelly and Vallejo, 2004). The *Co-6* gene has not been physically mapped, but it appears to localize in a region of Pv07 flanked by the *Phs* (phaseolin) genes at 5.1 Mb and the *P* locus (basic color gene) at 40.47 Mb (Moghaddam et al. 2014).

10.8 Chromosome Pv08

The major Co-4 anthracnose resistance locus resides on Pv08. The *Co-4²* allele is one of the most studied given the broad-based resistance conferred by this allele (Melotto and Kelly 2001; Burt et al. 2015). The complex [*C R Prp*] color locus is linked to the Co-4 locus, which has three known alleles (Kelly and Vallejo 2004). The Co-4 locus occupies a 325 kb region (2.38–2.48 Mb) on Pv08 and contains a unique cluster of 18 *COK-4* genes (Oblessuc et al. 2015). Two other genes have been mapped to the distal end of Pv08 (Meziadi et al. 2016). These include the rust resistance gene *Ur-13* in the cultivar Kranskop (Mienie et al. 2005) and the *Phg-2* gene for angular leaf spot that was mapped to the region of 57.82–58.53 Mb (Souza et al. 2016).

10.9 Chromosome Pv10

Three genes controlling resistant reaction to different races of halo blight were mapped to Pv10 (Miklas et al. 2014). The genes map to different regions of Pv10 suggested independence; however, allelism test has not yet been conducted. The race structure of the pathogen is defined on a set of differential host genotypes and individual resistance genes (*Pse-1*, *Pse-2*, *Pse-4*) control either by single or multiple races of the pathogen depending on the breadth of resistance spectrum they possess.

For example, *Pse-2* conditions resistance against 7/9 races when tested, whereas *Pse-4* conditions resistance to single race 5 (Miklas et al. 2014). The *Phg-5* gene is also mapped to a region 3.82–8.78 Mb in the vicinity of the *Pse-2* gene. More refined mapping is needed to better localize the *Phg-5* gene.

10.10 Chromosome Pv11

A major cluster of rust resistance genes have been mapped to Pv11. The *Ur-3* and *Ur-11* genes on Pv11 have long been recognized as being linked based on genetic studies using different races of the pathogen, and earlier reports considered them to be allelic differing in number of races they controlled (Stavely 1998). Recent detailed fine mapping of *Ur-3* located the gene at 47 Mb (Hurtado-Gonzales et al. 2017) and *Ur-11* at 51.93 Mb (McClellan, personal communication). The close proximity of the two genes underscores the linkage previously reported in traditional genetic studies (Miklas et al. 2002). A KASP marker has been developed for the *Ur-3* gene to facilitate its use in MAB (Hurtado-Gonzales et al. 2017). Other rust-resistant genes, *Ur-6* and *Ur-Dorado* resistant to race 53 (Miklas et al. 2000a), were mapped to Pv11, but no physical position has been reported (Table 10.1). The first anthracnose-resistant gene to be mapped was the *Co-2* gene on Pv11 (Adam-Blondon et al. 1994), and additional linked RAPD markers were reported by Young and Kelly (1996). One of these markers was converted to SCAR marker SQ4 that was also shown to be linked to the *Ur-11* gene (Awale et al. 2008). Further genetic studies placed the *Co-2* in closer proximity to the *Ur-11* than the *Ur-3* gene (Liebenberg et al. 2009) The *Co-2* gene provides resistance to 10 races of *C. lindemuthianum* (Campa et al. 2014) but has lost favor among bean breeders due to a breakdown of resistance to more virulent strains of the pathogen (Kelly and Vallejo 2004), so no further detailed mapping of the *Co-2* locus on Pv11 has been pursued.

10.11 Mapping QTL for White Mold Resistance

White mold, caused by *Sclerotinia sclerotiorum*, is one of the most serious production constraints of beans grown in temperate regions of North America and is particularly problematic as more intensive bean production systems are adopted in Brazil (Miklas et al. 2013). Intensive management systems such as higher plant populations, narrow row production, increased fertility rates, and supplemental irrigation can contribute to increased losses from white mold. Genetic resistance is partial, quantitative in nature, and influenced by both the environment and plant growth and architecture traits. QTL mapping for partial resistance has been

underway in beans for almost 20 years, and recently an integrated map of 79 QTL for white mold was generated by Miklas et al. (2013). These QTL can be divided into 27 for resistance, 36 for avoidance, and 16 for root traits associated with lodging resistance. Many of these QTL have no known physical position as mapping was conducted prior to the development of SNP markers for common bean. A recent meta-QTL analysis of resistance to white mold conducted on 37 QTL with a known physical distance condensed that number to 17 loci that included 12 previously identified QTL and 5 new QTL (Vasconcellos et al. 2017). Moreover, nine meta-QTL for resistance were identified and suggested as useful target regions for marker-assisted selection (MAS). In addition to shrinking the number of QTL to a more manageable and useful number, researchers have been able to significantly shrink the interval of two of these meta-QTL, WM7.1 and WM8.3, to improve the precision of MAS efficiency at these loci (Mamidi et al. 2016). Given the important role that plant architecture plays in disease avoidance, Hoyos-Villegas et al. (2015) confirmed that a major QTL WM3.1 was associated with plant architecture avoidance and validated earlier work where RAPD markers were first used to identify this region. Progress in fine mapping these regions will further improve the accuracy of selection for resistance to white mold as phenotypic selection is challenging due to the many controlling environmental factors that influence the development of this disease. Since the same pathogen attacks soybean and given the synteny between beans and soybeans (McClellan et al. 2010), future mapping studies and candidate resistance gene identification could be focused on those syntenic regions of common bean where resistance loci have been mapped in soybean.

10.12 Plant Architectural and Photoperiod Traits

Bean plant architecture has been the focus of breeding programs worldwide as the ancestral indeterminate, climbing habit limits production to smaller-scale cropping systems and is not suited to large mechanized farming systems. Four distinct growth habits have been described in beans, and breeding efforts to develop erect upright types suitable for direct harvest were reviewed by Kelly (2001). Type I growth habit is the only determinate bush type, all others are indeterminate differing in length of vine, type II is upright, type III is prostrate, and type IV includes climbing types. A more detailed genetic analysis of upright indeterminate type II genotypes suited for direct harvest revealed that four traits including canopy height, plant length, lodging, and stem diameter are highly correlated and suggests possible anatomical mechanisms responsible for upright plant types (Soltani et al. 2016). A GWAS study of architectural traits in a Middle American diversity panel revealed strong co-localized signals in a narrow genomic interval of Pv07 for three interrelated traits—growth habit, lodging, and canopy height (Moghaddam et al. 2016). The growth habit peak on Pv07 is masked by a stronger peak on Pv01 that is associated

with the *fin* gene present only in determinate plant types. Three terminal flower 1 (TFL-1) homologs associated with determinacy in *P. vulgaris* were previously mapped to Pv01, Pv04, and Pv07. One homolog co-segregated with the *fin* determinacy locus on Pv01 and a second mapped near a second determinacy locus on Pv07 (Kwak et al. 2008). Since the earlier studies were conducted prior to the publication of the bean genome sequence, no physical mapping information is available to associate these regions with the 45.0 to 48.7 Mb region on Pv07 where the main peak for lodging and canopy height is located (Moghaddam et al. 2016). However, the peak identified with determinacy at 45 Mb on Pv01 is near a TFL-1 homolog that maps to the *fin* locus (Repinski et al. 2012). Although determinacy and photoperiod response are interrelated (Kwak et al. 2008), the two traits do not appear to co-localize on Pv01. In a GWAS study of Andean beans grown in a temperate region, Kamfwa et al. (2015a) mapped the days to flower trait at 48.3 Mb on Pv01. This locus appears to be the *ppd* photoperiod gene for flowering and is associated with a phytochrome A candidate gene on Pv01. Candidate genes for flowering, determinacy, and architecture traits were proposed in these GWAS studies but remain to be experimentally validated.

10.13 Quality Traits

Prior to consumption, dry beans must undergo hydrothermal processing to soften the cotyledons and inactivate anti-nutritional factors (Van Der Poel 1990; Martínez-Manrique et al. 2011). As such, dry beans can either be domestically prepared by boiling in water or commercially prepared as a canned product. During canning, beans are soaked and blanched before a brine solution is added, and the cans are thermally sterilized (Matella et al. 2013). Boiling and canning methods both cause physicochemical changes in the beans that influence culinary quality parameters (Wassimi et al. 1990). Quality parameters like water absorption, cooking time, texture, appearance, and color vary among and within market classes (Fig. 10.1) due to both genetic and environmental effects (Hosfield et al. 1984; Hosfield and Uebersax 1990). These quality traits are distinct from agronomic traits and must be selected for accordingly to maintain industry and consumer acceptability. Many studies have focused on physical observations of dry, soaked, or cooked seeds, but fewer studies have been able to relate the actual phenotypic traits with a genetic component. Because culinary traits are typically considered to be under polygenic control, phenotypic selection is largely limited to later generations when most loci are fixed and sufficient seed is available for replicated field trials. The requisite inbreeding and phenotyping are time- and resource-intensive processes that delay germplasm improvement for these traits. Identification of molecular markers linked to quality traits will enable earlier, higher-throughput, and more precise selection. Further advances in biotechnology will facilitate the study of quality traits and their underlying genetic basis.

10.13.1 Water Uptake

Soaking dry beans before thermoprocessing is commonly used to soften the cotyledons and hasten cooking time (Reyes-Moreno et al. 1993). However, there can be significant variation in water absorption due to factors like genotype, soaking solution, and storage conditions (Varriano-Marston and De Omana 1979; Jackson and Varriano-Marston 1981; Elia et al. 1997). A study by Pérez-Vega et al. (2010) was the first study to associate water absorption with genetic markers. Using a recombinant inbred line (RIL) population derived from a Xana (fabada bean market class) x Cornell 49,242 (black bean market class) hybridization, the authors detected two QTL for water absorption, both derived from Xana. The WA3 QTL on Pv03 was found in just one environment and increased water absorption, while the WA4 QTL on Pv04 was found in two environments and decreased water absorption (Pérez-Vega et al. 2010). The WA3 QTL was flanked by markers MCTAETA³⁸ and SR20, and the WA4 QTL was flanked by markers SE15 and SH15. Genetic positions of QTL and markers were not given by the authors, but BLAST queries against the *P. vulgaris* genome release V2.1 suggest physical positions for SR20 (Pv03 \approx 50.18 Mb) and SE15 (Pv04 \approx 30.6 Mb or \approx 39.8 Mb). More recently, Cichy et al. (2014) performed a QTL study on black bean canning quality and found the *Asp* locus on Pv07 conferring shiny seed coat was the closest linked marker to water uptake QTL and best explained the phenotypic variation ($R^2 = 48.9\%$). Other measured traits associated with water uptake (hydration coefficient and washed-drained weight) co-localized around the *Asp* locus. However, while some studies consider the *Asp* locus as a major determinant of water uptake (Bushey et al. 2000, 2001), there may be other factors involved (Brick et al. 2000; Konzen and Tsai 2014). In another study, Cichy et al. (2015b) performed a GWAS using a subset of 206 genotypes from the Andean diversity panel (ADP). Significant SNPs associated with water uptake were found on Pv01, Pv03, Pv06, and Pv07. Notably, the two SNPs on Pv01 (ss715639380 and ss715640804) were the most statistically significant and explained the highest amount of phenotypic variation. Also of interest, the two SNPs on Pv06 (ss715648493 and 715,645,753) explained just 8.3 and 4.6% of the phenotypic variation but had minor allele frequencies of 0.29–0.32. These findings suggest that the markers on Pv01 contribute more to water uptake, but those on Pv06 are better candidates for screening diverse germplasm. Although water uptake is essential for the hydration and cooking of dry beans, there is still limited practical application of MAS for this trait.

10.13.2 Cooking Time

Cooking time is perhaps the most important culinary trait for dry beans on a global scale. The practice of soaking beans to reduce cooking time is not universal, which further exacerbates the time and energy costs involved in cooking beans. While Elia

et al. (1997) determined genotypic differences in cooking times, Jacinto-Hernández et al. (2003) were the first to map cooking time with molecular markers. The authors developed a RIL population from a cross between the quick-cooking Bayo Mecentral (53 ± 15 min) and slow-cooking Bayo Victoria (153 ± 46 min) and evaluated cooking times of the RILs over 3 years. Distribution of cooking times among the progeny suggested that the trait was under oligogenic control. Selected RILs with the shortest and longest cooking times were screened with 14 RAPD markers polymorphic in the parents to find RAPD markers associated with cooking time. Of these markers, 3 were associated with cooking time and were used to screen 70 RILs. A RAPD marker named UNAM 16 was found to be associated with short cooking time when the 310 bp band was present. Due to the high heritability of cooking time and low marker association, the authors recommended against MAS for cooking time. In 2005, Silva and Santos used a combination of RAPD and SSR markers in a bulk segregant analysis study for cooking time. Of the 175 markers, only 1 was found to be associated with the trait. Garcia et al. (2012) used a RIL population derived from a cross between a fast-cooking EMBRAPA line CNFM 7875 and slow-cooking “Laranja” cultivar to identify QTL for cooking time. The most noteworthy QTL, ct1.1, was detected on Pv01 at one location over two generations and explained 20.3% of the phenotypic variation for cooking time. Research by Cichy et al. (2015b) identified several significant SNPs associated with cooking time on Pv02, Pv03, and Pv06. Pv02 contained 2 separate regions at 37.6–38.6 Mb and 48–48.1 Mb that added 17 min and subtracted 7 min from cooking time, respectively. The major allele for the region on Pv03 was responsible for a 21–24 min reduction in cooking time, while the SNPs in linkage disequilibrium on Pv06 were the most significant and increased cooking time by 14.5 min. Interestingly, a neighbor-joining tree analysis featured four of the five fastest-cooking lines on the same branch, suggesting that a similar genetic mechanism is responsible for reduced cooking time in these genotypes. Reducing the cooking time of dry beans will save time, labor, and resources, especially for cooking methods reliant on gathering and burning firewood. These genetic studies provide a foundation for continued research on the potential of marker-assisted selection for cooking time. Although there is general agreement that cooking time is highly heritable and controlled by just a few loci, limited progress has been made in developing useful markers for this trait.

10.13.3 Canning Traits

For many consumers, the convenience of canned beans is preferable to the long preparation time associated with soaking and cooking dry beans. As part of the industrial canning process, beans are cleaned, soaked in a salt solution, quickly heated (“blanched”), and then filled into cans where they are covered in brine or sauce before being heat-sterilized (Matella et al. 2013). These canning conditions induce dramatic physicochemical changes in the seed and may result in beans with undesirable processing characteristics (clumping, viscous broth, nonuniform

soaking/cooking) or sensory characteristics (firm/mushy texture, heavy splitting, color loss) (Wassimi et al. 1990; Hosfield et al. 1995). To meet these industry and consumer standards, dry bean breeders must evaluate elite material for canning quality in addition to yield and agronomic traits. Small-scale canning procedures (Hosfield and Uebersax 1980; Balasubramanian et al. 2000) allow small samples of beans to be processed similarly to commercial canning but require substantial time, labor, and specialized equipment. An alternative to this extensive phenotyping is to identify genetic markers associated with quality traits and implement them in earlier-generation marker-assisted selection. A study by Walters et al. (1997) evaluated three navy bean RIL populations derived from parents contrasting for canning quality. Using RAPD markers, few marker-trait associations were determined due to small population size and lack of polymorphic markers across populations.

Later, Posa-Macalincag et al. (2002) performed a QTL analysis on two kidney bean RIL populations resulting from crosses between acceptable and excellent canning beans. The authors estimated narrow-sense heritability for canned appearance and degree of splitting to be approximately 0.84 and found high correlation between the two traits across environments ($r = 91\text{--}0.97$). The RAPD markers previously identified by Walters et al. (1997) were not polymorphic in these populations, but others were associated with canned appearance and splitting, namely, OP15.1150 on linkage group 1 (putatively located on Pv08) and OG17.1300 on linkage group 2 (unanchored). Wright and Kelly (2011) used a black bean RIL population to map yield and quality traits using SSRs and other markers. QTL were identified for post-processing color retention (7 QTL across 5 linkage groups), canned appearance (Pv05, Pv08), texture (Pv06, Pv11), and washed-drained weight (Pv03, Pv10), although few were detected across multiple years. Most recently, Cichy et al. (2014) used SNP markers to genotype a black bean RIL population derived from crossing shiny black-seeded (*Asp*) and dull-seeded (*asp*) parents. QTL for appearance, color retention, texture, and other quality traits were detected across the genome, though several genomic regions contained clusters of quality traits. Other interesting QTL co-localizations occurred on Pv05 (anthocyanin content, L*, b*, color retention) and Pv11 (L*, a*, b*, color retention, canned appearance). A QTL for canned appearance on Pv08 previously identified by Posa-Macalincag et al. (2002) and Wright and Kelly (2011) was not detected. While MAS has not yet been utilized to improve canning quality traits, the aforementioned studies may be useful in identifying genomic regions for potential marker development.

10.13.4 Post-Harvest Traits

After harvesting, dry beans can be stored for months before being consumed or processed. Seed coat color change resulting from extended storage times, known as post-harvest darkening (PHD), is a phenomenon that is most apparent in pinto, cranberry, small red, pink, carioca, and kidney bean market classes. Consumers perceive

beans with a darker background as too old or harder to cook, which may result in fewer or discounted sales for vendors. Unlike other quality traits, there is a substantial body of research on both physical and genetic mechanisms regarding this trait. Beninger et al. (2005) isolated and quantified polyphenols in a regular-darkening and slow-darkening pinto variety and found that kaempferol levels decreased in the regular darkening bean but not the slow-darkening bean. They suggested that the oxidation of proanthocyanidins may be responsible for seed coat darkening and that a similar reaction may occur in red beans. From a genetic standpoint, at least two loci are involved in PHD: *J* (Prakken 1974; Bassett, 1996) and *sd* (Junk-Knievel et al. 2008; Elsadr et al. 2011).

The *J* locus, previously recorded as *L* (Schreiber 1940) or *mar* (Lamprecht 1951), causes seed coat after-darkening when the dominant allele is present (Prakken 1970; Bassett 2007). McClean et al. (2002) mapped the *J* locus to Pv10 and tagged it with the RAPD marker OL4₅₂₅, which they subsequently converted to an STS marker OL4S₅₀₀. Because this marker was developed using Middle American germplasm, it may be gene pool-specific; thus, further marker development is needed for screening Andean germplasm. Recently, Freixas Coutin et al. (2017) used a combined metabolomic and transcriptomic approach to isolate polyphenolic compounds and identify differentially expressed genes between darkening and non-darkening cranberry beans. Regular-darkening beans were found to have greater amounts of proanthocyanidins and increased expression of proanthocyanidin biosynthesis genes flavanone 3-hydroxylase 1, dihydroflavonol 4-reductase 1, and anthocyanin reductase 1 (*PvANRI*), among others. Further research is needed to determine if the relationships between anthocyanin biosynthesis and post-harvest darkening are similar in other market classes. While marker-assisted selection for the *J* locus is not currently feasible for all gene pools, there is certainly potential for marker development and utilization.

The other locus known to affect PHD, *sd*, confers a slow rate of seed coat darkening when homozygous recessive as described by Junk-Knievel et al. (2008). The researchers crossed slow- and regular-darkening pinto beans, evaluated them by using UV light to artificially darken the seed coats (Junk-Knievel et al. 2007), and analyzed the segregation ratios to decide on a one-gene model. Because the *J* locus exhibits recessive epistasis over the *sd* locus, all germplasms must be homozygous for the dominant *J* allele conferring darkening to discriminate regular- and slow-darkening phenotypes. Felicetti et al. (2012) genotyped slow- and regular-darkening pinto bulks from three segregating F₂ populations to detect SNPs and linked SSRs associated with the *sd* locus. Three SSRs, Pvsd-1157, Pvsd-1158, and Pvsd-0028, exhibited tight linkage with the *sd* locus and mapped to Pv07. The authors also demonstrated that these SSRs may be useful to indirectly select for slow-darkening trait in other market classes. These PCR-based markers are now being used in breeding programs for early-generation MAS to develop slow-darkening pinto genotypes.

10.14 Fe and Zn Content

Iron and zinc nutritional deficiencies affect many people around the world, yet high levels of these minerals can be obtained from dry bean seeds. Increasing the content and bioavailability of these micronutrients through biofortification of staple crops like dry beans is a major research focus. Because iron and zinc accumulation are polygenic traits (Ghandilyan et al. 2006), the underlying QTL and genes need to be characterized before marker-assisted selection can be utilized. Using Mesoamerican-derived RILs, Guzmán-Maldonado et al. (2003) mapped several QTL for zinc and iron uptake, but linkage groups were unanchored and of low resolution due to the use of AFLP markers. Blair et al. (2010) genotyped a Mesoamerican-derived RIL population with SSR markers to identify several QTL, including some that co-localized on Pv01 and Pv11. Because dry beans from the Andean gene pool are well represented in global diets, several independent studies have identified QTL for iron and zinc content in Andean germplasm. Cichy et al. (2009b) used a G19833 x AND696-derived RIL population and found co-localizing QTL on Pv01, Pv06, and Pv11, while Blair et al. (2009) used a DOR364 x G19833-derived RIL population to find co-localizing QTL on Pv07 and Pv11. Later, Blair et al. (2011) used a climbing bean RIL population and found an environmentally stable iron concentration QTL on Pv02, an iron concentration QTL near the phaseolin locus on Pv07, and a notable absence of QTL on Pv11 found in other studies. The abundance of co-localizing QTL detected across populations and gene pools suggests similar uptake, or partitioning processes are involved in zinc and iron accumulation, a phenomenon demonstrated in other plants (Frossard et al. 2000; Schroeder et al. 2013). Markers located near large-effect or co-localizing QTL are prime candidates for implementing MAS but need to be validated in the target germplasm beforehand.

Improving iron and zinc content is only one component of biofortification. Divalent cations like iron and zinc are conjugated by anti-nutrients like phytic acid or polyphenols, which lower bioavailability (Frossard et al. 2000). Compared to phytic acid, polyphenolic compounds have a less negative effect on bioavailability. Their effect on iron absorption ranges from moderately inhibitive to negligible (Petry et al. 2015), and their contribution to biochemical process and seed coat appearance may preclude efforts to reduce polyphenolic content for improving bioavailability. Conversely, phytic acid has been shown to have a broad, negative effect on iron and zinc bioavailability (Petry et al. 2015). Plants with low phytic acid tend to have reduced germination, growth, and response to stress (Raboy 2007), yet Campion et al. (2009) identified a dry bean mutant, *lpa1*(280–10), with 90% less phytic acid without the accompanying decrease in agronomic performance. This line was further studied by Panzeri et al. (2011) who identified a recessive mutation in the *PvMRP1* phytic acid transporter gene as a single base pair mutation causing an amino acid substitution. This gene and a homolog, *PvMRP2*, were found to be orthologous to known phytic acid transporters in soybean and rice (Shi et al. 2007). The authors also utilized comparative mapping with soybean (*Glycine max*) to identify linked SSR markers flanking the two genes on Pv01 and Pv07, respectively.

Fileppi et al. (2010) utilized synteny between dry bean and soybean reference genomes to identify and map genes in phytic acid biosynthesis. Extensive synteny with *Arabidopsis* and rice was also observed, reflecting high conservation of genes in this pathway. These studies demonstrate the usefulness of comparative genomics in dry bean research, especially when using the soybean genome as a guide. While genomic information continues to improve, genes involved in iron and zinc accumulation and bioavailability have been already characterized in *Arabidopsis thaliana*, rice (*Oryza sativa*), maize (*Zea mays*), and soybean (Pilu et al. 2003; Ghandilyan et al. 2006; Xu et al. 2009; Fileppi et al. 2010; Kim and Tai 2011). It is now possible to determine physical positions of orthologous genes in silico as a preliminary step toward marker development, using sequence similarity and genomic resources. Once orthologs are given a physical position in the dry bean genome, they can be compared to published QTL and surrounding markers. MAS is a promising strategy in breeding for nutrition for both increasing micronutrients and minimizing anti-nutrients. Although dry bean breeders may have indirectly selected for enhanced mineral content (McClellan et al. 2017), MAS provides additional opportunities for increasing micronutrients and/or decreasing anti-nutrients. The health benefits provided by all grain legumes including common bean are well recognized, but grain legume crops constitute a minor part of most human diets and are greatly underutilized (Foyer et al. 2016). In addition to advantages that grain legumes offer farmers in sustainable crop rotations, N-fixation, and water use efficiency, Foyer et al. (2016) state that “the current lack of coordinated focus on grain legumes has comprised human health, nutritional security and sustainable food production” worldwide.

10.15 Bean Transformation

One area where progress has been more modest is in bean transformation. Problems and progress in bean transformation were reviewed by Veltcheva et al. (2005), and the major challenges and obstacles were discussed by Hnatuszko-Konka et al. (2014). Unlike the progress made in gene transformation in related grain legumes, such as pigeon pea (*Cajanus cajan*; Varshney et al. 2012), chickpea (*Cicer arietinum*), pea (*Pisum sativum*), lentil (*Lens culinaris*), and cowpea (Popelka et al. 2006), only a single successful event has been reported in common bean (Bonfim et al. 2007). The authors used biolistic approach to insert an RNA interference construct to silence the AC1 viral gene and generate transgenic common bean plants that were highly resistant to the whitefly vectored gemini virus, *Bean golden mosaic virus* (BGMV), in Brazil. A single line (Embrapa 5.1) exhibited high levels of resistance upon inoculation at high pressure (300 viruliferous whiteflies per plant) at an early stage of plant development (Bonfim et al. 2007). Crosses and backcrosses were made to commercial carioca cultivars Perola and BRS Pontal, and homozygous near-isogenic lines were developed that exhibited resistance under high BGMV pressure in the field (Faria et al. 2014). This research is an example of the first geminivirus-resistant (bean) plant developed through genetic engineering that has

the potential to impact a large sector of family-based agricultural systems in Brazil (Aragão and Faria 2009). Despite the success, the authors were only able to transform a single genotype, pinto bean cultivar Olathe, and they transferred the transgene through conventional backcrossing into the carioca seed type. Carioca beans are widely grown and consumed in Brazil, and plans only exist to use the RNAi technology in this seed type as GM beans have not been deregulated in any other country except Brazil. Currently, a single elite high-yielding, resistant transgenic line from the backcross program has been released by the Biosafety Network of EMBRAPA after testing over 3 seasons in 31 locations and will represent the first genetically modified common bean cultivar developed in the world (Souza et al. 2018).

10.16 Conclusions

As dry bean research enters the “omics age,” adaptation of new technologies and methods will advance the selection methods further. Large-scale sequencing projects have already provided reference genomes, and falling costs are improving access to sequence data for more targeted experiments. First described by Elshire et al. (2011), genotyping by sequencing (GBS) can identify thousands of SNPs that may be used for linkage map construction or aligned to a reference genome if desired. Several GBS protocols have recently been published for dry beans with differing restriction enzymes and experimental objectives (Zou et al. 2014; Hart and Griffiths 2015; Ariani et al. 2016; Schröder et al. 2016). Another potential application of affordable sequencing is genomic selection (GS). Relying on dense marker coverage and prediction models, GS attempts to predict superior genotypes based on genomic estimated breeding values. While MAS is useful for improving large-effect, highly heritable traits, genomic selection may facilitate the improvement of polygenic traits like yield and quality characteristics. However, unlike many small grain crops, dry bean GS may be limited by the need for market-class specific training populations, cost-effectiveness, and lack of prior adaptation. Lastly, the accessibility of sequencing can improve upon current microarray genotyping technology by improving SNP coverage and density across the dry bean genome. Microarray “SNP chips” like the BARCBear6K_3 BeadChip (Song et al. 2015) represent an accessible and convenient genotyping platform but may not contain sufficient marker density or polymorphisms needed for modern genetic studies. Identification of genome-wide, polymorphic, gene-based SNPs through sequencing can create a more robust microarray capable of capturing more genetic variation within and across gene pools and market classes. Dry bean breeders and researchers have a long history of utilizing molecular markers. Applications have ranged from the study of species-wide topics like domestication and disease resistance to market class-dependent quality characteristics. As bioinformatics and sequencing technologies have improved over the past decade, the dry bean community has abundant opportunities to further advance dry bean breeding through MAB.

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