Biology and Breeding of Food Legumes

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19 Trait Mapping and Molecular Breeding

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19.1 Introduction

The role of legumes in agricultural development has been that of providing long-term stability to agricultural systems. Legumes and cereals have co-evolved since ancient times. They have acted as a major contributory factor in sustaining agricultural production throughout the millennia. Grain and forage legumes are grown on ~190 million ha, and their production is about 300 million metric t worldwide (ICRISAT, 2009). Unfortunately, yield improvements in legume crops have not kept pace with those of cereals.

The majority of legumes, apart from soybean, have literally been termed 'orphan crops' in the sense that they are devoid of a well-developed infrastructure (both knowledge and physical capacity) for genetic and genomic analysis or molecular breeding. This lack of infrastructure has restricted the biotechnological crop improvement strategies available for these crops. In this context, there is a need to increase the availability of genomic data and resources in key species and also to decrease the barriers that limit the adoption of complex genomic data sets by crop improvement specialists. Part of the solution lies in training the next generation of scientists to navigate both basic and applied plant science. This in turn, will improve the capacity for the uptake of new biotechnologies and reduce the 'gap' between genomics and traditional versus modern molecular breeding. This chapter provides general concepts of trait mapping and molecular breeding in food legumes, citing the examples of soybean, common bean and chickpea where development and use of genetic and genomic resources are at an advanced stage.

19.2 Challenges in Legume Production

Legume production is greatly challenged by numerous biotic and abiotic stresses, which result in severe losses to agricultural production on a yearly basis. Most legume crops are affected by common insect pests, diseases and a range of abiotic stresses, including adaptation to acid, saline or low-fertility soils as well as adverse weather conditions such as drought, cold temperature or heat stress. However, the occurrence and severity of biotic and abiotic stresses differ from crop to crop, and by pathogen and the environmental conditions to which the crop is exposed, requiring crop-specific breeding approaches and management practices. These stresses are discussed in detail in Chapters 15 and 16.

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The interaction between biotic and abiotic stresses is likely to be especially complex and damaging to legume crops in arid and semi-arid regions of the world, and de-convoluting such interactions is an important long-term challenge for legume improvement and molecular/physiological research. Although several breeding strategies ranging from classical breeding to more directed physiological and molecular genetic approaches have been implemented to cope with the threats of these stresses, a better understanding of the mechanisms underlying specific stresses will make molecular breeding truly feasible. The availability of tolerant and resistant cultivars to biotic and abiotic stresses is one of the most effective management practices when irrigated under a comprehensive integrated management approach, resulting in cost savings (i.e. insecticides, pesticides) and environmental protection.

Biotechnological approaches, such as marker-assisted breeding, tissue culture, *in vitro* mutagenesis and genetic engineering, can contribute to the speeding up of classical breeding and in overcoming major problems, such as lack of natural sources of genetic resistance to biotic and abiotic stresses and sexual incompatibility (Cook and Varshney, 2010). In the near future, great success in crop improvement will be possible by combining genomic tools with rational selection of germplasm and precise phenotyping for traits of interest, an approach termed 'genomics-assisted breeding' (Varshney *et al.*, 2005).

Improvement in agronomic/phenological traits of legumes is crucial in order to improve their use as human food, especially in developed countries. In the current scenario, legumes have become an increasingly important concern in marketing and profitability. Therefore, different quality characteristics of legumes such as seed size, mass and shape, storability, etc. are receiving greater attention in regard to genetic improvement. There is also an increasing interest in improving nutritional characteristics of legumes with enhanced contents of beta carotene, leutin, isoflavones and other nutraceuticals.

19.3 Molecular Breeding Approaches

The use of molecular markers for improving breeding efficiencies in plant breeding was first suggested in 1989 (Tanksley *et al.*, 1989; Melchinger, 1990). Today, plant breeding is rapidly evolving as more molecular genetic tools are being applied to commonly accepted field techniques (Kulwal *et al.*, 2010); recent advances in genomics have allowed identification of molecular markers associated with traits of interest to breeders. In this context, initially a linkage between a gene responsible for a trait of interest and a molecular marker is established and confirmed, validated using breeders' materials and subsequently used in DNA diagnostic tests to guide plant-breeding selection efforts (Morgante and Salamini, 2003; Gupta and Varshney, 2004) (Fig. 19.1). The process of indirect selection in crop improvement can be expedited by using molecular markers, which help in alleviating several time-/cost-consuming and labour-intensive aspects of direct screening under greenhouse and field conditions.

Trait mapping

Molecular breeding includes the identification of genotypically and phenotypically polymorphic plant genotypes, development of segregating mapping populations, genotyping of the mapping population, phenotyping of trait(s) of interest and marker–trait association analysis. Subsequently, mapped gene(s) or quantitative trait loci (QTL) can be introgressed individually or combined (pyramided) in an improved cultivar (Gupta *et al.*, 2010a). Two main approaches can be used to identify marker–trait associations: (i) linkage mapping; and (ii) association mapping (Fig. 19.1).

In general, linkage mapping-based gene/QTL studies involve: (i) development of an appropriate mapping population from contrasting parental genotypes for the trait of interest; (ii) identification of polymorphic markers; (iii) genotyping of the mapping population with polymorphic markers;

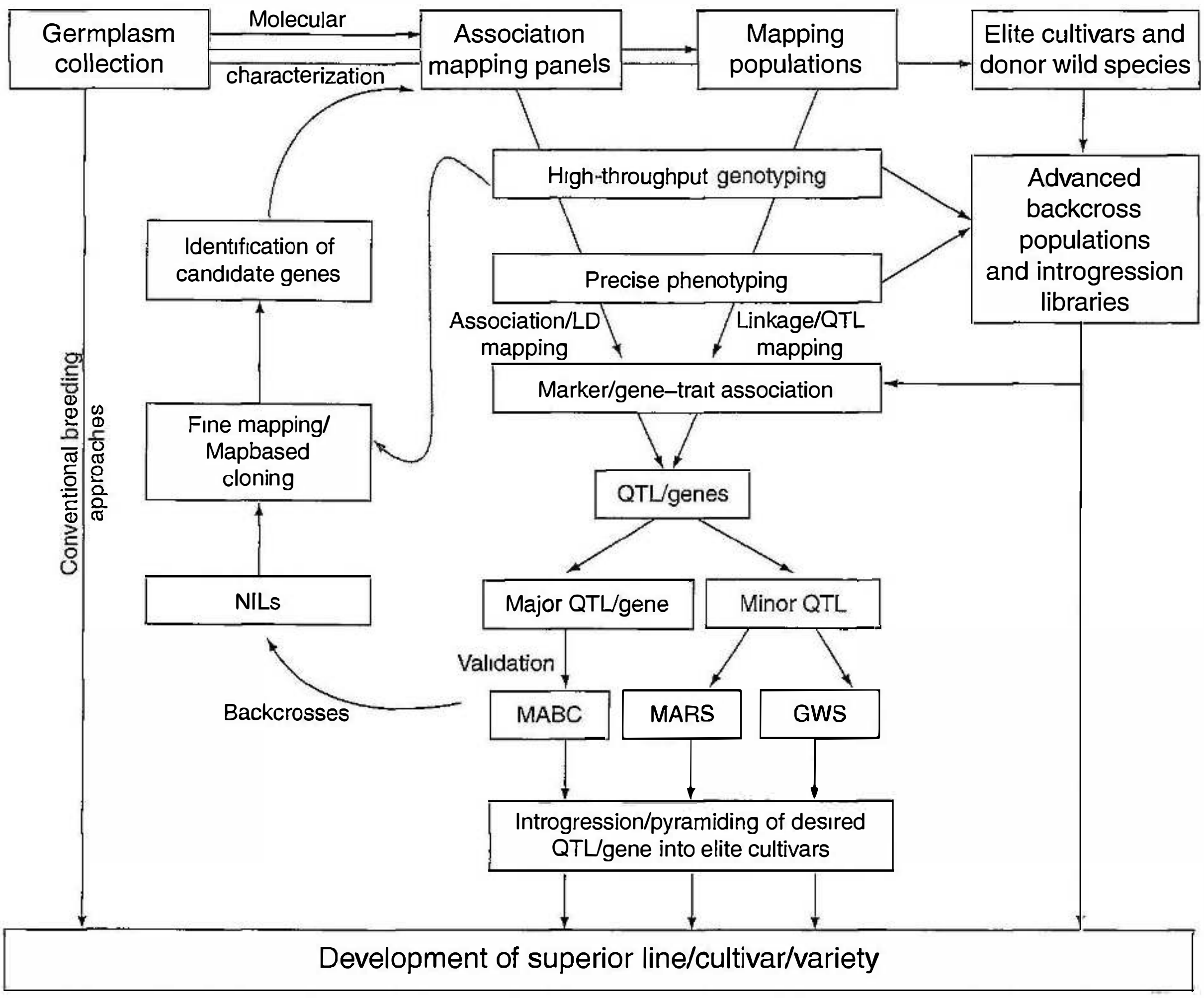

Fig. 19.1. A scheme showing integration of modern genetics and breeding approaches (trait mapping and molecular breeding) in crop improvement programmes. GWS, genome-wide selection; LD, linkage disequilibrium; MABC, marker-assisted backcrossing; MARS, marker-assisted recurrent selection; NILs, near-isogenic lines; QTL, quantitative trait loci.

(iv) construction of the genetic map based on genotyping data; (v) precise phenotyping of the mapping population in different environments; and (vi) marker–trait association using suitable genetic linkage and QTL analysis programmes (Varshney *et al.* 2009b). In legume species, linkage mapping-based approaches have been extensively used for mapping genes/QTL for resistance to diseases, nematodes and insects and for tolerance to abiotic stresses and several agronomic traits (Table 19.1).

Association mapping (also known as linkage disequilibrium mapping) has also been used in plant species for trait mapping. It has several advantages over conventional linkage mapping approach: (i) it takes less time as there is no need to develop a specialized mapping population – rather, an existing natural population is used; (ii) it is less expensive as the same association mapping panel and genotyping data generated can be used for mapping of different traits; (iii) resolution of mapping is high because of the use of a natural population that has several meiotic recombinants, unlike the few in mapping populations; and (iv) as compared with linkage mapping where a maximum of two alleles are obtained, a higher numbers of alleles are obtained to find trait associations.

Association mapping comprises the following two broad categories based on the scale and goal of a particular study: candidate gene-based association mapping and whole-genome association mapping. The former relates to

Table 19.1. Examples of gene/QTL mapping in soybean, common bean and chickpea.

Crop	Trait	Gene/QTL	Marker type(s)	Reference(s) and related reference(s) cited
Disease resistance				
Soybean	Sclerotinia stem rot	16 QTL	SSRs	Guo *et al.* (2008); Vuong *et al.* (2008); Huynh *et al.* (2010)
	Phytophthora root rot	3–8 QTL/genes	AFLPs, SSRs, RAPDs, SCARs	Han *et al.* (2008); Li, X. *et al.* (2010); Wang *et al.* (2010)
	Brown stem rot	4 QTL/genes	RFLPs, AFLPs, SSRs	Patzoldt *et al.* (2005)
	Asian soybean rust	5 loci/QTL	SSRs, SNPs	Garcia *et al.* (2008); Silva *et al.* (2008); Chakraborty *et al.* (2009); Hyten *et al.* (2009)
	Soybean mosaic virus	Rsv1, Rsv3	SSRs	Shi *et al.* (2008)
	Sudden death syndrome	4 QTL	SSRs	Kazi *et al.* (2008)
Common bean	Anthracnose	Co-genes	RAPDs, AFLPs	Rodríguez-Suárez *et al.* (2007)
	Halo blight	Pse-1	SCARs	Miklas *et al.* (2009)
	Charcoal rot	1 QTL	AFLP	Hernández-Delgado *et al.* (2009)
	Fusarium wilt	PvPR2, PvPR1	RAPDs	Schneider *et al.* (2001)
	White mould	Fin, Phs	RAPD, SSR	Kolkman and Kelly (2003)
	Rust	UR-6, UR-13	SCAR	Mienie *et al.* (2005)
	Common bacterial blight	6 QTL	SSRs, STSs, SCARs	Liu *et al.* (2008); Vandemark *et al.* (2008)
	Bacterial brown spot	2 QTL	RAPDs	Jung *et al.* (2003)
	Bean common mosaic virus	bc-3; I	RAPD; SCAR	Johnson *et al.* (1997)
	Bean golden yellow mosaic geminivirus	bgm-1	SCAR	Blair *et al.* (2007b)
Chickpea	Ascochyta blight	AR2, ar1, ar1a, ar1b, ar2a, ar2b, Ar19	SSRs, RAPDs, DAF	Cho *et al.* (2004)
		QTL_{AR1}, QTL_{AR2}	SCARs, SSRs, RAPDs	Iruela *et al.* (2006, 2007)
		13 QTL	SSRs, RAPDs	Kottapalli *et al.* (2009)
	Fusarium wilt	foc-0, foc-1, foc-2, foc-3, foc-4, foc-5	SSRs, STSs, RAPDs	Cobos *et al.* (2005); Iruela *et al.* (2007)
	Rust	1 QTL	SSR	Madrid *et al.* (2008)
Nematode and insect resistance				
Soybean	Corn earworm	3 QTL	RFLPs	Rector *et al.* (1998)
	Cyst nematode	rhg1, rhg4	SSRs, SCARs, SNPs	Wu *et al.* (2009); Vuong *et al.* (2010)
Common bean	Leaf hopper	1 QTL	SSR, RFLP	Murray *et al.* (2004)
	Thrips	Tpr6.1	SSRs	Frei *et al.* (2005)

Continued

Table 19.1. Continued

Crop	Trait	Gene/QTL (*n*)	Marker type(s)	Reference(s) and related reference(s) cited
	Bean pod weevil	4 QTL	SSRs, SCARs	Blair *et al.* (2006, 2007a)
	Bruchids	Arc gene	SSRs	Blair *et al.* (2010b, c)
Abiotic stress tolerance traits				
Soybean	Waterlogging	6 QTL	SSRs, RFLPs	Githiri *et al.* (2006)
	Chilling tolerance in seed yield	3 QTL	SSRs	Funatsuki *et al.* (2005)
	Salt stress	1 QTL/gene	SSR	Lee *et al.* (2009); Tuyen *et al.* (2010)
	Manganese toxicity	3 QTL	SSRs, RAPDs	Kassem *et al.* (2004)
	Phosphorus deficiency	fsw1, fsw2, rp1, fsw3, rp2, lp1, lp2	SSRs, RFLPs	Li *et al.* (2005)
	Iron deficiency chlorosis	3–19 QTL	SSRs, RFLPs	Lin *et al.* (2000)
	Aluminum tolerance	11 QTL	RFLPs	Qi *et al.* (2008)
	Sulphur-containing amino acids	7 QTL	SSRs	Panthee *et al.* (2006)
Common bean	Drought	2 QTL	RAPDs	Schneider *et al* (1997)
	Phosphorus uptake	Pup4.1, 10.1 and 2.1	RAPDs	Beebe *et al.* (2006)
Agronomic/phenological traits				
Soybean	Specific leaf weight, leaf size	3–6 QTL	RFLPs	Mian *et al.* (1998)
	Seed weight	15 QTL	SSRs	Csanadi *et al.* (2001)
	Flowering time	4–9 QTL	SSRs	Su *et al* (2010)
	Sprout yield	4 QTL	RFLPs	Lee *et al* (2001)
	Seed isoflavones (genistein, daidzein, glycitein)	35 QTL	SSRs	Zeng *et al* (2009); Gutierrez-Gonzalez *et al.* (2010)
	Seed size	7 QTL	SSRs	Hyten *et al.* (2004)
	Seed flooding tolerance	4 QTL	–	Sayama *et al.* (2009)
	Ability, frequency and efficiency of somatic embryogenesis	5 QTL	SSRs, AFLPs	Choi *et al.* (2010); Song *et al.* (2010)
	Early maturity	E_8	SSRs	Cober *et al.* (2010)
	Oligosaccharides and sucrose	6 QTL	SSRs	Kim *et al.* (2006)
	Vitamin E content	21 QTL	SSRs	Li, H. *et al.* (2010)
	Chlorophyll *a* fluorescence parameter	4–13 QTL	–	Yin *et al.* (2010)
	Developmental behaviour	15 QTL	SSRs	Sun *et al.* (2006)
	Browning in soybean seed coat	5 QTL	AFLPs, SSRs	Githiri *et al.* (2007)
	Domestication	2 QTL	SSRs	Liu *et al.* (2007)
	Seed composition	52 QTL	SSRs	Li *et al.* (2007)
	Seed shape	19 QTL	SSRs	Salas *et al.* (2006)
	Photoperiod insensitivity	2 QTL	SSRs	Liu and Abe (2010)
	Net-like cracking of seed coat	2 QTL	SSRs	Oyoo *et al.* (2010)
	Cleistogamy	4 QTL	SSRs, AFLPs	Khan *et al* (2008)

Continued

Table 19.1. Continued.

Crop	Trait	Gene/QTL (*n*)	Marker type(s)	Reference(s) and related reference(s) cited
Bean	Seed mass, calcium, iron, zinc, tannin content	3–26 QTL	AFLPs	Guzman-Maldonado *et al.* (2003)
	Plant height, climbing ability, internode length, branch number	1–9 QTL	SSRs, RAPDs, SCARs	Checa and Blair (2008)
	Phenological traits, seed size traits, seed quality traits	31 QTL	SSRs, AFLPs, SCARs, ISSRs	Pérez-Vega *et al.* (2010)
	Nutritional traits (iron, zinc, tannins, phytate)	3–26 QTL	SSRs, RAPDs, AFLPs	Blair *et al.* (2009a, b, 2010a), Caldas and Blair (2009); Cichy *et al.* (2009)
	Nodulation number	4 QTL	RFLP	Nodari *et al.* (1993)
Chickpea	Seed size traits	2 QTL	SSRs	Hossain *et al.* (2010)
	Double podding	s	SSRs	Rajesh *et al.* (2002)
	Time to flowering	2 QTL	SSRs	Lichtenzveig *et al.* (2006)
	Beta carotene, leutin, seed weight	1–4 QTL	SSRs	Abbo *et al.* (2005)
	Flower colour	B/b	SSR	Cobos *et al.* (2005)

polymorphisms in selected candidate genes that appear to have roles in controlling phenotypic variation for specific traits, while the latter surveys genetic variation in the whole genome to find marker–trait associations for various complex traits (Zhu *et al.*, 2008). In taking the decision as to which is the method of choice, one has to consider the extent of linkage disequilibrium (LD) in the organism of interest.

Although the association mapping approach has been used recently in several cereals like maize, barley, wheat, etc. (Ersoz *et al.*, 2007), only a few examples have become available in legume species. The candidate gene-based approach has been successfully used to map different loci for iron deficiency chlorosis in soybean (Wang *et al.*, 2008). Similarly, several candidate genes implicated in oleate biosynthesis were mapped and their co-segregation with oleate and linoleate QTL investigated (Bachlava *et al.*, 2009). Other examples of trait mapping are shown in Table 19.1.

Next-generation sequencing and high-throughput genotyping technologies are becoming popular in legumes such as chickpea, common bean and soybean (Varshney *et al.*, 2009a, c, 2010b), accelerating their use in association mapping. For example, a high-throughput SNP genotyping platform (Illumina GoldenGate assay) developed in soybean (Hyten *et al.*, 2008) has been used for mapping soybean rust resistance (*Rpp3*) (Hyten *et al.*, 2009), SCN (soybean cyst nematode) (Vuong *et al.*, 2010), flooding and fatty acids (Vuong *et al.*, unpublished data).

Molecular breeding

Once markers are identified for a trait, they can be used for a variety of applications such as enhancing biological knowledge of the inheritance and genetic architecture of the trait, in addition to their use in breeding programmes. When molecular markers are used in breeding programmes, it is important to take into account the statistical power to identify QTL numbers, QTL effect, percentage of phenotypic variation explained, major and minor QTL through use of appropriate marker density on the genetic map and reasonable population sample size. Furthermore, markers identified in one population need to be validated in other population/germplasm collections, and closely linked markers flanking the QTL should be used for indirect selection of the trait.

Figure 19.1 shows a few molecular breeding approaches commonly used in breeding programmes, which are discussed in the following sections. Soybean is the legume crop in which these approaches have been most successful, and where the use of markers in breeding programmes is routine. Several improved lines/varieties for resistance to different SCN races (also known as HG types) (Concibido *et al.*, 1996; Cahill and Schmidt, 2004; Arelli and Young, 2009); phytophthora root rot and brown stem rot (Cahill and Schmidt, 2004); insect resistance (Narvel *et al.*, 2001; Walker *et al.*, 2002; Warrington *et al.*, 2008); low linolenic acid content (Sauer *et al.*, 2008); yield (Concibido *et al.*, 2003); and mosaic virus (Saghai Maroof *et al.*, 2008; Shi *et al.*, 2009) have been developed and released. In the case of common bean the use of molecular markers in breeding programmes is intermediate between that of soybean and chickpea, and marker-assisted selection (MAS) has been used principally to deploy single genes in large-scale programmes at CIAT for resistance to quarantined viruses (Miklas *et al.*, 2006a, b; Blair *et al.*, 2007a). More specifically, MAS has been successfully used for enhanced resistance to anthracnose in the bean cultivar Perola in Brazil (Raganin *et al.*, 2003), pinto beans in the USA (Miklas *et al.*, 2003a) and Andean climbing bean in Mexico/Colombia (Garzon *et al.*, 2008). On the other hand, molecular breeding activities have only just been initiated in chickpea. Several successful examples targeting the development of superior lines or released cultivars through molecular breeding are listed in Table 19.2.

Marker-assisted backcrossing

Marker-assisted backcrossing (MABC) is the simplest and most widely used molecular breeding approach in plant breeding. MABC has become a fast-track approach for increasing the genetic gain of plants, resulting in the development of improved varieties with better yield potential, improved quality and resistance against insects, pests and diseases (Collard and Mackill, 2008; Moose and Mumm, 2008; Ribaut *et al.*, 2010). Basically, this approach incorporates desirable major genes/QTL from an agronomically inferior source (the donor parent) into an elite cultivar or breeding line (the recurrent parent) without transfer of undesirable or deleterious genes from the donor (linkage drag).

The desired outcome of MABC is a line/cultivar containing only the major genes/QTL from the donor parent, while retaining the whole genome of the recurrent parent (Hospital and Charcosset, 1997; Varshney and Dubey, 2009; Varshney *et al.*, 2009b, Gupta *et al.*, 2010a). Three types of selection

Table 19.2. Examples of development/release of improved lines/cultivars in soybean and common bean using molecular breeding approaches.

Crop	Cultivar/breeding line	Trait	Country and year of release	Reference
Soybean	JTN-5503	Disease resistance	USA, 2005	Arelli *et al.* (2006)
	JTN-5303	Disease resistance	USA, 2005	Arelli *et al.* (2007)
	JTN-5109	Soybean cyst nematode resistance	USA, 2009	Arelli and Young (2009)
	DS-880	Soybean cyst nematode resistance	USA, 2010	Smith *et al.* (2010)
Bean	USPT-ANT-1	Disease resistance	USA, 2004	Miklas *et al* (2003b)
	ABCP-8	Disease resistance	USA, 2005	Mutlu *et al.* (2005)
	ABC-Weihing	Disease resistance	USA, 2006	Mutlu *et al.* (2008)

can be exercised in MABC: foreground, recombinant and background. Foreground selection involves the selection of target genes/QTL on the carrier chromosome with the help of two flanking markers (Hospital and Charcosset, 1997). It can be used to select for laborious or time-consuming traits and it allows selection of heterozygous plants at the seedling stage and therefore identifies plants desirable for backcrossing. Furthermore, recessive alleles can be identified and selected, which is difficult to perform using conventional methods.

Recombination events between the target locus and linked flanking markers can also be identified in backcross (BC) progeny. This can be used to reduce linkage drag, which is difficult to overcome through the use of conventional backcrossing (Frisch *et al.*, 1999b). For this purpose, Hospital and Decoux (2002) have developed a statistical programme called 'Popmin' (http://moulon.inra.fr/~fred/programs/popmin) for calculating the minimum population size.

Background selection involves selection of BC progeny with highest proportion of recurrent parent (RP) genome, using unlinked markers present on 'non-carrier' chromosomes (Hospital and Charcosset, 1997; Frisch *et al.*, 1999b). The use of background selection during MABC to accelerate the development of a RP genome with additional genes has been referred to as complete line conversion (Ribaut *et al.*, 2002). While conventional backcrossing takes a minimum of six BC generations to recover the RP genome, the use of markers enables the similar degree of progress in two BC generations (Visscher *et al.*, 1996; Hospital and Charcosset, 1997; Frisch *et al.*, 1999a, b; Varshney and Dubey, 2009). Studies have also shown that the use of a limited number of markers on non-carrier chromosomes can be sufficient to recover more than 95% of the recurrent parent genome in three BC generations (Visscher *et al.*, 1996; Kumar *et al.*, 2010).

The MABC approach has also been used to construct near-isogenic lines (NILs) or chromosome segment substitution lines (CSSLs), which are often used for genetic analysis of genes/QTL (Peleman and van der Voort, 2003; Lorieux, 2005; Varshney *et al.*, 2010b). NILs are developed in the same way as advanced backcross (AB) lines by crossing a donor parent with a recurrent parent. After several generations of backcrossing, the advanced backcross lines are expected to contain all of the recurrent parent genome except for the chromosomal region containing a gene or QTL of interest. NILs have been utilized for validation of QTL, for fine mapping and can also be used directly in breeding programmes (Stuber *et al.*, 1999). NILs containing different genes affecting the same trait are very useful for comparing the effectiveness of these genes in different locations or environments (Fig. 19.1).

Another use of MABC is to pyramid various genes for multiple traits within the same cultivar (Koebner and Summers, 2003; Sharma *et al.*, 2004; Saghai Maroof *et al.*, 2008; Li, X. *et al.*, 2010). Several excellent reviews have documented the use of MABC for pyramiding genes/QTL resulting in the development of superior lines/varieties/hybrids in crop plants (Gupta *et al.*, 2010a, b; Kumar *et al.*, 2010; Varshney *et al.*, 2010a), and examples in soybean and common bean are presented in Table 19.2. However, the use of MABC has now been initiated in elite lines of chickpea at ICRISAT, in collaboration with its partners, for the introgression of QTL/genes for drought-related traits and resistance to diseases (fusarium wilt and ascochyta blight). In addition, the introgression of root trait QTL is in progress in collaboration with the Indian Institute of Pulses Research (IIPR) and the India and Ethiopia Institute of Agricultural Research (EIAR), Ethiopia. Molecular breeding for development of superior lines with enhanced resistance to fusarium wilt and ascochyta blight has been initiated recently in collaboration with several Indian partners, including IIPR, Jawaharlal Nehru Krishi Vishwavidyalaya, Mahatma Phule Krishi Vidyapeeth and the Agricultural Research Station, Gulburga.

Marker-assisted recurrent selection

One of the limitations of MABC is that only a limited number of desirable alleles can be introgressed at a time. To overcome this limitation, particularly in the case of complex traits like drought tolerance, the marker-assisted recurrent selection (MARS) approach has been proposed for transferring/pyramiding of superior QTL/gene alleles for trait(s) of interest in one genetic background (Bernardo and Charcosset, 2006; Varshney and Dubey, 2009; Gupta *et al.*, 2010a, b; Ribaut *et al.*, 2010). The genetic gain feasible through MARS has been estimated as being higher than that via MABC (Bernardo and Charcosset, 2006).

In principle, MARS is a forward breeding approach combining MAS (Stam, 1995) with increase in the frequency of favourable alleles/QTL at multiple loci (Edwards and Johnson, 1994; Koebner and Summers, 2003; Eathington, 2005). This involves multiple cycles of marker-based selection that include improvement of F_2 progeny by one cycle of MAS based on marker data and phenotypic data, followed by three recombination cycles of the selected progenies based on marker data only and repetition of these cycles to develop the population for multi-location phenotyping (Ribaut *et al.*, 2010; Tester and Langridge, 2010). In MARS, a selection index is used that gives weights to markers according to the relative magnitude of their estimated effects on the trait (Lande and Thompson, 1990; Edward and Johnson, 1994). For the successful use of MARS, a number of factors including heritability of the target traits, marker coverage in the genome, reliability of marker–trait associations, family size, number of families and type of population should be considered (Mayor and Bernardo, 2009). Moreover, knowledge of the quantitative traits can be very useful in enhancing the selection response through MARS with the help of candidate gene markers, or tightly linked markers, each having a relatively large effect. The response to MARS decreases as the knowledge of the number of minor QTL associated with the trait decreases (Charcosset and Moreau, 2004; Bernardo and Charcosset, 2006).

The MARS approach has been/is being used extensively in maize breeding in both the private and public sectors. For instance, it has been employed to fix six marker loci in two different F_2 populations that showed an increase in the frequency of marker alleles, from 0.50 to 0.80 (Edward and Johnson, 1994). Several multinational companies, such as Syngenta and Monsanto, are using MARS in their breeding programmes in several crops, including soybean (Ribaut *et al.*, 2010).

Recently, some international agricultural research centres (IARCs), such as ICRISAT and CIAT, in collaboration with the Generation Challenge Program (GCP), have initiated the use of MARS in chickpea and common bean, respectively, for pyramiding favourable drought-tolerant alleles. Therefore, the potential of MARS is yet to be demonstrated in legume breeding for the development of superior lines/genotypes.

Genome-wide selection

A new approach based on genome-wide marker profiling, called 'genome-wide selection (GWS)' or 'genomic selection (GS)', has been proposed for complex traits that are controlled by many genes/QTL, each of small effect. Basically, this method predicts genomic estimated breeding values (GEBVs) of progenies, which are calculated for progenies based on both phenotyping and genotyping data. These GEBVs are then used to select the superior progeny lines for advancement in the breeding cycle (Heffner *et al.*, 2009; Jannink *et al.*, 2010). Several computational tools are available or are being developed to calculate GEBVs, such as BLUPs (best linear unbiased prediction) programmes, and the geostatistical mixed model has recently been developed as a tool in GS (Robinson, 1991; Streeck and Piepho, 2010). This approach is not required to elucidate marker–trait associations by QTL mapping (Bernardo, 2010a, b; Tester and Langridge, 2010). Furthermore, it has been shown that double-haploid (DH) populations are very useful in GWS compared with F_2 populations, when many QTL control a trait (Mayor and Bernardo, 2009). Currently, however, there is little information available on the use of GWS in crop plants, although recent developments in plant genomics make it feasible to generate genome-wide marker data (using SNPs) to start GWS in breeding programmes. In the next few years GWS is expected to be used in legumes, at least in soybean.

Introgression of superior alleles from wild species

Plant breeders mostly use existing germplasm and landraces to develop new varieties for desirable agronomic traits. However, yields have remained stagnant partly because sufficient genetic diversity is missing for progress in some of the traits, due to genetic bottlenecks that occurred during the domestication process (Tanksley and McCouch, 1997; Gur and Zamir, 2004). It is well known that wild species/relatives are the reservoirs for resistance genes to many biotic and abiotic stresses. However, their transfer from wild species to elite cultivars through conventional breeding has been limited, mainly due to the associated transfer of undesired alleles (linkage drag). However, it is now feasible to recover/transfer the favourable alleles in elite germplasm left behind by the domestication process more efficiently, using innovative genomics-assisted breeding strategies such as molecular maps and integrative QTL analysis. In this context, several methods for transferring superior alleles from wild species have been suggested and some of these are discussed below.

One approach is the construction of introgression libraries using the genetic background of elite lines by introgressing small wild species segments in a systematic manner. Introgression libraries are made up of introgression lines (ILs) that are produced by successive backcrossing (generally three to four generations) to the recurrent parent. The introgressed fragments can be monitored using molecular markers, either in each generation or at chosen stages. Fixation of the materials is obtained by either selfing or using double-haploid methodology. As a result, each line possesses one or several homozygous chromosomal fragments of the donor genotype, introgressed into a recurrent background genome. These fragments should be arranged continuously from the first to the last chromosome, either manually or using a computer software-aided process (graphical genotyping). The whole donor genome is thus represented by a set of small, contiguous overlapping fragments. This differs from the more traditional approach of introducing resistance genes from wild species into elite cultivars through genetically balanced mapping populations of progeny recombinant inbred lines (RILs) derived from an early generation (e.g. F_2 plants or families or F_1-derived doubled haploids). Such populations contain an equal proportion of exotic and elite genotypes, and deleterious effects of exotic alleles may mask the desired target gene effect. Therefore the development of introgression lines represents a significant advantage over the previously used RIL-type populations. In regard to legumes, some reports on the development of introgression libraries have become available in soybean using wild soybean species (*Glycine soja*) (Concibido *et al.*, 2003), and in groundnut from synthetic tetraploids (Fonceka *et al.*, 2009).

Another important approach used in the transfer of superior alleles from wild species into cultivated germplasm is based on the advanced-backcross QTL (AB-QTL) analysis proposed by Tanksley and Nelson (1996). This method proved effective in detecting additive, dominant, partially dominant and over-dominant QTL. This approach uses repeated backcrossing with the elite parent but decreases the number and size of the exotic introgressions, thereby reducing the burden of linkage drag. During backcrossing cycles, the transfer of desirable genes/QTL is monitored by molecular markers. The segregating BC_2F_2 or BC_2F_3 population generated during backcrossing (F_2 or F_3 stages) is then used not only for recording phenotyping data for the trait of interest, but also for genotyping with polymorphic molecular markers. These data are then used for QTL analysis, leading to simultaneous discovery of QTL and the generation of introgression lines. Once favourable QTL alleles are identified, only a few additional marker-assisted generations are required to develop full NILs that can be field tested and used for variety development.

The AB-QTL approach has been used in common bean and soybean. For instance, in the case of common bean, Blair *et al.* (2005) used a cross between a wild Colombian accession and an Andean cultivar to develop $BC_2F_{3\,5}$-derived lines for AB-QTL analysis of yield traits, and finding that segregation distortion was minimal except at a few domestication syndrome genes. Similar populations have been developed for: (i) introgression of high seed iron content from wild Mexican accessions into the Andean and Meso-American background cvs Cerinza or Tacana; and (ii) introgression of drought tolerance between the common bean gene pools from Meso-American sources to Andean cultivars as part of the Tropical Legumes project on adaptation to drought-prone marginal regions of eastern and southern Africa. Population sizes in these AB-QTL mapping populations have ranged from 157 to 300 genotypes, with various experimental designs used for analysis. In the case of soybean, for instance, Chaky *et al.* (2003) generated 296 $BC_2F_{4\,6}$ backcross introgression lines (BILs) from the cross *Glycine max* (Dunbar) × *Glycine soja* (PI 326582A). This study provided several QTL for seed yield, seed protein and oil, in addition to some late-maturing and taller BILs.

19.4 Conclusions

It is evident that several success stories on both trait mapping and molecular breeding are available in soybean. The availability of the soybean genome sequence (Schmutz *et al.*, 2010) and the establishment of high-throughput SNP genotyping platforms (Hyten *et al.*, 2008) are expected further to accelerate molecular breeding in soybean improvement.

In the case of common bean, efforts aimed at trait mapping and molecular breeding are extensive, as compared with chickpea. However, molecular breeding activities in common bean have remained focused mainly on simple inherited traits like disease resistance. In the case of chickpea, although several examples on trait mapping are available, the use of molecular breeding activities as compared with soybean and common bean is still at the preliminary stage. As both of these legume crops are very important in sub-Saharan Africa and South America (common bean) and South Asia (chickpea), CIAT and ICRISAT have initiated molecular breeding programmes in these crops to improve complex traits like drought tolerance, through the use of MABC and MARS approaches as a part of the Tropical Legume (TL-I) project of the Generation Challenge Programme (GCP) in collaboration with the Bill and Melinda Gates Foundation (BMGF) (http://www.generationcp.org/gcptli/). With the goal of sustainable crop production in these legume crops, it is essential that national agricultural research programmes in the developing countries of sub-Saharan Africa, South Asia and South America should lead or actively participate in the molecular breeding of these legumes. Shortage of appropriate human resources and physical infrastructure in developing countries, however, are challenging issues. The establishment of the Integrated Breeding Platform (IBP) as a one-stop shop for accessing genotyping services, information and data management, decision support, statistical tools and technical support will help in overcoming some of above-mentioned limitations.

In summary, due to advances in sequencing, genotyping, biometrics and bioinformatics, the future of molecular breeding in legume crops is promising, not only in soybean, common bean and chickpea but also in other crops like lentil, faba bean and pigeon pea, which are still considered 'orphan legume crops'.

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