



# Conventional and Molecular Approaches towards Breeding for Disease Resistance and Tolerance in the Common Bean (*Phaseolus vulgaris* L.)

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## ABSTRACT

As poverty limits access to animal protein in developing countries, people in developing countries turn to common bean, as a protein source. Disease and pests can cause significant losses to common bean production. Control of these biotic constraints using agrochemicals can increase production costs and create the potential for contamination of the environment. Thus, resistance/tolerance represents a valuable disease and pest management tool for sustainable production of beans. Therefore, the development of cultivars with greater levels of disease and pest resistance has always been a primary objective of most common bean breeding programs. The development of cultivars with enhanced levels of disease and pest resistance has been hailed as one of the milestone achievements of breeding for bean improvement so far. Hence, this review paper is initiated with the objective of documenting the most important achievements of common bean breeding for disease resistance/tolerance using conventional and molecular breeding approaches and fetching (an important piece of knowledge and database for agricultural researchers and academicians in research and higher learning institutions and other stakeholders. With this end in mind, it starts with identifying major diseases of common bean (from the African and global perspective); describe each disease (the pathogen, mode of virulence, etc.); document resistance genes and resistant cultivars; and document molecular and conventional breeding approaches used international thus far, and associated results. Accordingly, such pieces of information have been presented section-by-section for common bean diseases: anthracnose, angular leaf spot, common bacterial blight, bean common mosaic (necrotic) virus (BCMV/BCNMV), and bean rust. The information reviewed here is believed to be useful in the areas of common bean improvement and breeding. The achievements garnered thus far, though immense, have not been utilized uniformly throughout the world. Besides, the pathogenic epidemiology, virulence, sources of host resistance, etc. have not been sufficiently studied and documented. Similar review papers are recommended for major insect pests and nematodes attacking the crop.

## 1. Introduction

The common bean (*Phaseolus vulgaris* L.) (2n=22) is the most widely distributed and consumed legume species of the genus *Phaseolus*, a genus comprised of some 70 species (Freytag and Debouck, 2002). Moreover, the genus has contributed to human welfare with five cultigens domesticated in pre-Columbian times: the common bean (*P. vulgaris*), the year bean (*Phaseolus dumosus* M.), the runner bean (*Phaseolus coccineus* L.), the tepary bean (*Phaseolus acutifolius* A. Gray), and the lima bean (*Phaseolus lunatus* L.) (Delgado-Salinas, 1985). The genus originated in the American continent and a large number of its species is found in Mesoamerica (Delgado, 1985; Freytag and Debouck, 2002).

Common bean is a critical component of diets for many of the developing countries in the world, along with maize and cassava. It is an important source of family income and a critical component of the daily diet in African countries where the population is projected to double by 2020 (Fisseha et al., 2018). It is the most important edible food legume in the world's diet. Moreover, it represents 50% of the grain legumes consumed worldwide, and its production is nearly twice that of chickpeas, the second most consumed food legume (Stacey et al., 2018). It is assumed that common bean was introduced to Ethiopia in the 16<sup>th</sup> century by the Portuguese (Imru, 1985; Fisseha et al., 2016). It is an important component of the human diet in Ethiopia, and is among the most important food legumes produced in Ethiopia, which has been cultivated as a field crop for a very more than 5 decades (Abebe, 1987; Fisseha et al., 2016). Because poverty limits access to animal protein in developing countries, people in developing countries turn to common bean as one of the protein sources (Burle et al., 2011; Stacey et al., 2018).

Disease (such as, anthracnose, angular leaf spot, common bacterial blight, etc) and pests (bean weevil, etc) can cause significant losses to common bean production (Wortmann, 1998; Coyne et al., 2003; Schwartz et al., 2005). Control of these biotic constraints using agrochemicals can

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increase production costs and create the potential for contamination of the environment (Agrios, 2005). Thus, resistance/tolerance represents a valuable disease and pest management tool for sustainable production of beans. Therefore, the development of cultivars with greater levels of disease and pest resistance/tolerance has always been a primary objective of most conventional bean breeding programs. The development of cultivars with enhanced levels of disease and pest resistance has been hailed as one of the milestone achievements of breeding for bean improvement so far (Miklas et al., 2006c).

Despite the crop's importance in the daily lives of the poor farmers, its productivity is highly constrained by a number of factors, such as the large number of diseases and insect pests; low yield potential of existing varieties; and the less number of improved varieties (Habtu, 1990; FAO, 2005; Fisseha et al., 2018). Moreover, research on common bean and other pulses began later as compared to cereals. Little progress has been made to improve the lower yields of common bean varieties under cultivation presently in Ethiopia, which, on average, is only about 600 Kg/ha (Zelalem, 2005; Ferris and Kaganzi, 2008; Fisseha et al., 2018).

In stark contradiction with the aforementioned opportunities and threats the bean crop has, little has been done so far in doing the tedious, albeit, necessary job of documenting the achievements of conventional and molecular approaches toward breeding for disease resistance in common bean. Limited have been the efforts made in relation to availing well-documented information on major achievements and challenges of conventional and molecular breeding programs. These kinds of information can tremendously benefit national and international efforts to reduce effects of diseases affecting common bean.

Hence, this review paper is initiated with the following objectives.

### Objectives

- Document the most important achievements of common bean breeding for disease resistance using conventional and molecular breeding approaches in common bean;
- Organize an important piece of knowledge and database for agricultural researchers and academicians in research and higher Learning institutions; and other stakeholders.
- Synthesize the available information in a way to show the gap and indicate for possible future research directions

## 2. Review Methodologies

This review article has used relevant research publications that are pertinent to the title. In addition, personal communications and field observations have been utilized, when needs arise. As much as possible, citations have been paraphrased, before use, in such a way they do not lose their

original implications. In so doing, all the cited authors have been duly acknowledged.

## 3. Major Common Bean Diseases

Common bean production is often limited by more than one biotic constraint which pose a challenge for plant breeders, who must develop cultivars having multiple disease or pest resistance (Kelly et al., 1998; Ferris and Kaganzi, 2008; Fisseha et al., 2018). Beaver and Osorno (2009) warned, however, that an over-emphasis on breeding for disease or pest resistance may reduce genetic variability and limit progress in breeding for increased seed yield. The endeavor of mitigating production losses to diseases is being accompanied by Marker Assisted Selection (MAS) and genomic (linkage) maps.

The bean crop may be attacked by a wide range of insect pests, diseases and nematodes (Hillocks et al., 2017). Table 1 illustrates the major bean diseases from averaged data taken from major bean producing areas in the world. Anthracnose, angular leaf spot, and bean rust are the first three ranking diseases in terms of associated production losses (Table 1). Many of these are a major cause of yield loss in East Africa (Hillocks et al., 2017). According to the same, of the large number of diseases that can affect beans in the tropics, the most important in East Africa are angular leaf spot (ALS) (*Phaeoisariopsis griseola*); anthracnose (*Colletotrichum lindemuthianum*); common bacterial blight (CBB) (*Xanthomonas campestris pv. phaseoli*); Bean common mosaic virus (BCMV); and rust (*Uromyces phaseoli*) holding the first five ranks.

Hence, the subsequent sub-sections are devoted to giving an introductory remark on each one of the aforementioned major diseases of common bean.

### 3.1. Anthracnose (*Colletotrichum lindemuthianum* (Sacc. & Magnus) Lams.-Scrib.)

Anthracnose, caused by the fungus, *Colletotrichum lindemuthianum*, is one of the most destructive diseases affecting common bean (*Phaseolus vulgaris* L.) in tropical and subtropical areas of Latin America and Central and Eastern Africa (Corrales, 1985; Beaver and Osorno, 2009). In such areas, a complete yield loss can occur with susceptible cultivars, when contaminated seeds are used and the environmental conditions are favorable for the pathogen development (Peloso, 1992). According to Schwartz et al., (1991), it causes losses of up to 100% when contaminated seed is planted or when prolonged favorable conditions for disease development occur during the growing cycle. The disease pathogen is distributed worldwide, wherever common bean is cultivated (Beebe, 1991; Beaver and Osorno, 2009). According to Gonçalves-Vidigal (1994), it is a seed-borne disease that can cause serious losses where (or when) humid weather with comparatively low temperature prevails. Co-evolution is known to have occurred between fungal pathotypes and the common bean's two gene pools so that Andean races of the fungus usually attack Andean bean

genotypes and Mesoamerican races attack Mesoamerican genotypes (Melotto et al., 2000). Congruent with this co-evolution, the best sources of resistance for breeding programs are often found in complementary gene pools and genes for resistance usually must be introgressed through backcrossing, especially of Mesoamerican genes into Andean backgrounds (Miklas et al., 2006c).

Méndez-Vigo et al. (2015) noted that although anthracnose is especially harmful in tropical and subtropical areas, where common bean is the major source of protein for human consumption, it is not restricted to such areas. It can also cause considerable yield losses in temperate areas, as in Northern Spain, where appreciated dry bean landraces are grown. High genetic variability of *C. lindemuthianum* has been observed in different parts of the world (Balardin et al., 1997; Fisseha et al., 2018).

Currently, the different *C. lindemuthianum* races are characterized based on phenotypic reaction on a universal set of 12 differential cultivars and named based on a binary nomenclature system (Beaver and Osorno, 2009; Fisseha et al., 2018). Up to 10 genes (Co-1 to Co-10) that confer dominant resistance (except co-8) to different sets of pathogenic races have been described (Miklas and Singh, 2007).

### 3.2. Angular Leaf Spot (*Phaeoisariopsis griseola*)

(Singh, 2015) reported that angular leaf spot, caused by the fungus, (*Phaeoisariopsis griseola*), stands one among the three most-important and widely distributed fungal diseases that cause severe yield losses in Latin America, Africa, and other parts of the world. Similarly, Méndez-Vigo et al. (2015) reported that in East Africa, angular leaf spot (ALS) is the most widespread and economically important disease of the common bean. In conformity with both authors, Hillocks et al. (2017) discussed that the disease is the first most-important disease in Eastern and Southern parts of Africa. They further reported that production losses attributed to ALS in Southern Africa are estimated at 93,500 tons/year. In Africa, pest and disease problems are the second biggest constraint to bean productivity, with an estimated annual yield loss of 2,288,000 Mg, of which 348,000 Mg (17%) is due to the angular leaf spot disease (Beaver and Osorno, 2009). Angular leaf spot is currently the most economically important disease that reduces dry bean yields by as much as 50 to 80%, when susceptible varieties are planted (de Jesus Jr et al., 2018). The development and use of resistance cultivars is the most effective, economical, and environmentally sound strategy for disease control. However, the pathogenic variability of *P. griseola* and the occurrences of newly evolving virulent pathotypes complicate the development and limit the lifetime of resistant cultivars (Miklas and Singh, 2007). The same authors argued that bean cultivars with higher genetic resistance are needed to effectively control ALS. However, the success of these resistant cultivars can be marred by the virulence diversity of *P. griseola*. This pathogen has many races that often vary from one location or year to another. In line with this, (Singh,

2015) dictated that available resistance is inadequate for angular leaf spot. Beaver and Osorno (2009) discussed that the degree of virulence among isolates *P. griseola* can also vary between regions and over time.

(Teixeira Caixeta et al., 2004) reported that there are four dominant genes for resistance to angular leaf spot (Phg-2, Phg-3, Phg-4 and Phg-5), with multiple alleles (Phg-22, Phg-32, Phg-42 and Phg-52). Once specific genes have been cloned, Michelmore and Meyers (1998) suggested, the different disease resistance genes could be pyramided and introduced as cassettes into transgenic plants.

### 3.3. Common Bacterial Blight (*Xanthomonas campestris* pv. *phaseoli*)

Common bacterial blight (CBB) (*Xanthomonas campestris* pv. *phaseoli*) is one of the most serious production problems of common bean (*Phaseolus vulgaris*) worldwide (Tar'An et al., 2017). According to Singh (2005), common bacterial blight is a widespread problem from tropical to temperate dry-bean-growing environments. Similarly, Hillocks et al. (2017) reported that CBB is the third most-important disease causing huge production loss on beans in Eastern Africa. The same authors mentioned that damage on bean production, due to common bacterial blight (CBB) (*Xanthomonas campestris* pv. *phaseoli*), gets substantial in warmer regions of East Africa. In another line, Kelly and Copeland (1996) reported that the seed-borne nature of CBB is a major constraint in commercial bean production and one that has greatly influenced the location of the common bean seed production industry in the United States. Further on the line, Miklas and Singh (2007) revealed that CBB causes 20 to 60% yield losses on susceptible cultivars, especially under relatively humid and warm growing conditions. Moreover, severe CBB epidemic adversely affects seed quality, including size, shape, color, and germination. Thus, the marketability of infected seed and its distribution out of the production region can be limited and seed production may be heavily hampered (Kelly and Copeland, 1996).

### 3.4. Bean Common Mosaic Virus (BCMV) and Bean Common Necrotic Mosaic Virus (BCNMV)

Bean Common Mosaic Virus (BCMV) is a seed-borne virus of dry and snap beans. The virus is transmitted by several aphid species and result in yield losses and delay in maturity in susceptible bean varieties grown for seed or green pod production. Previously, BCMV and another virus called, Bean Common Necrotic Mosaic Virus (BCNMV) had been considered to be the same virus, but recent research has shown that the two viruses are distinct and different (Miklas et al., 2006b).

BCMV, which originated in the Americas, is one of the earliest reported virus diseases of plants in the world. BCNMV originated later in Eastern Africa (Miklas and Singh, 2007). The same authors noted that this may probably be due to the recombination of BCMV strains, after beans were introduced into the East African region in the 1600s.

BCNMV spread from Eastern Africa via seeds of susceptible bean varieties shipped to other countries. Singh (2015) explained that both viruses are naturally transmitted by aphids in a non-persistent manner and by seed, which explains their worldwide distribution. Field infections by BCMV have been reported as high as 100 percent in susceptible bean varieties (Beaver and Osorno, 2009). According to the same, yield losses may vary, depending on varieties, environment and time of infection, and whether the disease originates as a seed-borne infection or is carried in later by aphids.

According to Hillocks et al. (2017), the typical symptoms of BCMV are a light green or yellow and dark green mosaic pattern on leaves, usually accompanied by puckering, distortion and rolling of the leaves. Other symptoms seen on susceptible hosts include mottling, curling and malformation of leaves, as well as general stunting of the plant. Plants infected early in the growing season or grown from infected seed may suffer a delay in maturity and have fewer pods and fewer seeds per pod than healthy plants. Moreover, Hillocks et al. (2017) discussed two syndromes: mosaic and systemic necrosis (“black root”) can be induced by these pathogens depending on the host genotype-virus combination.

### 3.5. Bean Rust (*Uromyces appendiculatus* (Pers.) Unger)

Bean rust, caused by *Uromyces appendiculatus*, is an important disease in both temperate and tropical bean production regions. Ideal conditions for rust are cool to moderate temperatures, concurrent with high humidity (>95%) for periods of at least 7-8 h, interspersed with dryer, windy periods that favor dispersal (Hillocks et al., 2017). According to Singh (2015), rust is considered as one among the three most widely distributed fungal diseases that cause severe yield losses in Latin America, Africa, and other parts of the world. Araya et al. (2004) reported that *U. appendiculatus*, cause of bean rust, has been reported to have Andean-specific and non-specific pathotypes (using virulence and RAPD fingerprints). Jochua et al. (2015) noted that one of the major constraints for snap and dry bean production in Mozambique was rust, caused by *U. appendiculatus*. Furthermore, they noted that the successive cultivation of beans usually makes the inoculum of the rust fungus available throughout the year, resulting in high incidence and severity of rust.

Possible strategies for bean rust management include fungicides, cultural practices and disease resistance. However, in most developing countries, fungicides are expensive or not available and cultural practice modifications do not fit the cropping systems used. Hence, disease resistance is the most effective and least expensive strategy for poor bean farmers in developing countries (Jochua et al., 2015). On the other hand, (Park et al., 2013) argued that a recommended strategy to obtain durable rust resistance is to use molecular markers linked to rust resistant genes for pyramiding monogenic resistant genes in to a single bean cultivar.

The dominant alleles conferring specific resistance to rust namely: Ur-3 (Nemchinova and Stavely, 1998), Ur-4 (Miklas et al., 1993; Mienie et al., 2005), Ur-5 (Haley et al., 1993; Melotto and Kelly, 1998), Ur-6 and Ur-7 (Park et al., 2013), Ur-9 (Jung et al., 1996), Ur-11 (Queiroz et al., 2006), and Ur-13 (Mienie et al., 2005) were tagged using RAPD markers with many eventually converted to SCAR and placed on the bean linkage map.

## 4. Achievements of Conventional and Molecular Approaches toward Breeding for Disease Resistance in Common Bean

Common bean (*Phaseolus vulgaris* L.) improvement programs have been successful at accomplishing wide arrays of important objectives via employing conventional and molecular breeding methods (Beaver and Osorno, 2009; Fisseha et al., 2018). Specific achievements include: the extension of range of adaptation of the crop; the development of cultivars with enhanced levels of disease and pest resistance; and breeding lines that possess greater tolerance to drought. The most effective breeding method depends on the expression and inheritance of the trait to be selected and the target environment (Beaver and Osorno, 2009; Fisseha et al., 2018). Disease resistance has been one of the top-most priority breeding priorities in common bean, ever since the commencement of bean breeding (Miklas and Singh, 2007; Fisseha et al., 2018).

### 4.1. Conventional Breeding toward Disease Resistance in Common Bean

Resistance represents a valuable disease and pest management tool for organic production of beans. Therefore, the development of cultivars with greater levels of disease and pest resistance is a primary objective of most bean breeding programs (Beaver and Osorno, 2009; Fisseha et al., 2018).

Much remains to be achieved in order to ensure sustainable resistance in common bean to all economically important diseases. To exemplify this argument, Singh et al. (2003) reported that great northern, pinto, pink and small red beans produced in the Western U.S. were generally susceptible to diseases, such as common bacterial blight caused by *Xanthomonas axonopodis* pv. *Phaseoli*; halo blight caused by *Pseudomonas syringae* pv. *Phaseolicola*; bacterial brown spot caused by *Pseudomonas syringae* pv. *syringae* van Hall, anthracnose caused by *Colletotrichum lindemuthianum* (Sacc. & Magnus), rust caused by *Uromyces appendiculatus* (Pers.) Unger, wilt caused by *Fusarium oxysporum* f. sp. *phaseoli*, and white mold caused by *Sclerotinia sclerotiorum* (Lib.) de Bary. This lack of resistance limited the range of adaptation of these cultivars (Fisseha et al., 2018)(Singh et al., 2007).

Sources of resistance to many important bean diseases have been identified and used in cultivar development programs (Beaver et al., 2003; Miklas et al., 2006b; Fisseha et al., 2018). However, breeders also need information from plant pathologists concerning the virulence patterns of the

**Table 1:** Recent Releases of Bean Cultivars and Germplasm with Unique or Valuable Combinations of Traits that are the Results of Conventional Plant Breeding Techniques (*Sources: Beaver and Osorno (2009); Fisseha et al. (2018)*)

S/N	Trait(s)	Description (seed type)	Reference
1.	Angular Leaf spot		Mahuku et al. (2004)
2.	Angular Leaf Spot and Anthracnose Resistance		Singh et al. (2003)
3.	Anthracnose Resistance	Co-1, Co-2 (Black bean)	Kelly et al. (2001)
		Co-1, Co-2 (Dark red kidney bean)	Kelly et al. (1998)
		Co-6 (Small red bean)	Young and Kelly (1996)
		Co-42 (Pinto bean)	Miklas et al. (2003)
4.	BCMV and BCNMV	I, bc3 (black bean)	Kelly et al. (1994)
		I, bc3 (kidney bean)	Miklas and Kelly (2002)
		I, bc-12 (great northern)	Stewart-Williams et al. (2003)
		bc-12 (small red)	Hosfield et al. (2004)
5.	Common Bacterial Blight	bc-12 (pinto)	Brick et al. (2001)
		Higher levels of resistance derived from tepary bean ( <i>Phaseolus acutifolius</i> L.)	Singh et al. (2001)
		Higher levels of resistance derived from scarlet runner bean ( <i>Phaseolus coccineus</i> L.)	Zapata et al. (2004)
6.	Halo Blight Resistance	???	Coyne et al. (2000)

pathogens in order to most effectively deploy disease resistance genes (Coyne et al., 2003; Fisseha et al., 2016).

Improved germplasm and cultivars with resistance genes for major bean diseases had been developed using recurrent backcrossing (Pompeu, 1982), pedigree (Kelly et al., 1994), and mass-pedigree (Singh et al., 1989) methods and their modifications. Congruity backcrossing (Mejía-Jiménez et al., 2004; Urrea and Singh, 1995), single-seed descent (SSD) (Kelly et al., 1989; Urrea and Singh, 1994), recurrent (Kelly and Adams, 1987; Beaver and Kelly, 1994; Singh et al., 1999), and gamete (Singh, 1994; Singh et al., 1998) selection methods have been used more recently. On the other hand, favorable alleles and QTLs have been introgressed from the tepary bean (*P. acutifolius* A. Gray) for common bacterial blight (caused by *Xanthomonas campestris* pv. *phaseoli* (Smith) Dye) resistance (Singh and Munoz, 1999; Fisseha et al., 2018), from runner bean (*P. coccineus* L.) for common bacterial blight (Miklas et al., 1994; Okii et al., 2014) and white mold (caused by *Sclerotinia sclerotiorum* (Lib.) de Bary) resistance (Miklas et al., 1998; Singh and Munoz, 1999; Burle et al., 2011), while introgressing common bacterial blight resistance from the tepary bean (VAX 1 and VAX 2), were also pyramided the highest level of common bacterial blight resistance to develop breeding lines VAX 3 to VAX 6. Nonetheless, most breeding has largely utilized favorable alleles and QTLs available between and within cultivated common bean market classes, races, and gene pools (Miklas and Singh, 2007; Fisseha et al., 2018).

### 1. Characterization of Pathogens using Differential Cultivars

In regards to development of resistance against the anthracnose pathogen (*Colletotrichum lindemuthianum*);

- two independent genes conditioning resistance to race-73 of *C. lindemuthianum*, one dominant and another recessive, were identified using six differential cultivars (Alzate-Marín et al., 1997; Fisseha et al., 2016) (Asfaw et al., 2009);

- higher genetic variability in bean genotypes belonging to both Andean and Meso-American origins, regarding resistance against anthracnose, were observed (Vidigal Filho et al., 2004; Burle et al., 2011);
- differential cultivars carrying the gene CO4, which is one of the resistance genes against anthracnose, along with its alleles, and genes CO5 and CO6, individually or in association with other genes, conferred the highest anthracnose resistance (Alzate-Marín and Sartorato, 2004; Fisseha et al., 2018);
- A single dominant gene was hypothesized to be the source of resistance against *C. lindemuthianum* (Gonçalves-Vidigal et al., 2009; Okii et al., 2014).

With regards to development of resistance against the angular leaf spot pathogen (*Phaeoisariopsis griseola*), the following milestone works can be mentioned:

- Bean differential cultivars from the Andean gene pool had higher resistance against various races of *P. griseola* in South and East Africa (Pastor-Corrales et al., 2007);
- Most elite bean differential lines from Brazil were susceptible, or marginally resistant only to few of *P. griseola* pathotypes, which was attributed for the wide genetic variability of the fungus (Melo et al., 2005);
- Greater genetic diversity, virulence and non-virulence-specificity were observed in Meso-American *P. griseola* pathotypes (Cayasso and Fernández, 2005);
- Based on the set of differential cultivars they infected, *P. griseola* isolates were divided into three virulence groups: Andean, Afro-Andean and Meso-American (Wagara et al., 2006).

### 2. Mode of Inheritance and Introgression of Disease Resistance in Released Cultivars

- A single dominant gene conferring resistance to *C. lindemuthianum* races 65; 73; 453 and an Andean race (race 7) was identified in released bean cultivars (Gonçalves-Vidigal and Kelly, 2004).

- On the other hand, inoculation of parents; F1, F2, and backcross derived released bean varieties with race 63-63 of *P.griseola* indicated that a single dominant gene conditioned angular leaf resistance in a resistant bean accession family, G-10474 (Mahuku et al., 2004).
- Ernest and Kelly (2004) introduced CO-42, a gene which confers resistance against 33 out of 34 different races of *C.lindemuthianum*, in to four bush bean varieties through backcrossing.

### 3. Inter-specific Hybridization Targeted towards Introgressing Disease Resistance from Tertiary Gene Pools to Cultivated Bean Varieties

Inter-specific hybridizations between the common bean and the scarlet runner bean (*Phaseolus coccineus* L.) and the tepary bean (*Phaseolus acutifolius* L.) have been conducted since the middle of the 19<sup>th</sup> century (Debouck, 1991; Beaver and Osorno, 2009). The scarlet runner bean was originally considered to be a variety of common bean which may have encouraged scientists to make hybridizations (Debouck, 1999). Successive pollinations are required to produce inter-specific F1 seed and this seed may require special treatment to produce plants (Debouck, 1991, 1999; Freytag and Debouck, 2002; Beaver and Osorno, 2009). Embryo rescue techniques are often needed to ensure the survival of inter-specific F1 hybrids (Mejía-Jiménez et al., 2004; Beaver and Osorno, 2009). In addition, the choice of the common bean parent can affect the rate of success of the inter-specific crosses. Cultivars such as 'ICA Pijao' that are double recessive for the dl1 and dl2 dwarf lethal genes (Singh and Ariel Gutiérrez, 1984; Beaver and Osorno, 2009) proved to be most useful for inter-specific crosses. Broughton et al. (2003) suggested that molecular markers could be used to help reduce or remove barriers to inter-specific hybridization. Mejía-Jiménez et al. (2004) reported that recurrent and congruity back crossing improved the rate of success of inter-specific crosses between common and tepary beans.

Bean breeders have been able to identify only moderate levels of resistance to CBB in common bean (Coyne and Schuster, 1974; Yoshii et al., 1978; Blair et al., 2010a), whereas high levels of resistance has been identified in some tepary bean lines (Urrea et al., 1999; Singh and Munoz, 1999; Blair et al., 2010b). Results from inheritance studies suggested that common bacterial blight resistance in tepary bean lines was controlled by few genes (Urrea et al., 1999; Beaver and Osorno, 2009). In 1989, CIAT scientists initiated an effort to introgress tepary bean resistance into common bean (Singh and Munoz, 1999; Blair et al., 2010a). After the inter-specific (*P.vulgaris* x *P.acutifolius*) populations were developed, breeding lines were screened in the field in Colombia for several generations during a five-year period in order to identify breeding lines with high levels of resistance to common bacterial blight. Some of the lines with the highest levels of CBB resistance such as VAX 3, VAX 4, and VAX 6 pyramid resistance genes from tepary and

common beans (Singh and Munoz, 1999). These authors noted that one of the biggest problems with breeding for CBB resistance derived from tepary beans is the instability of the expression of resistance (Okii et al., 2014).

According to Singh (2005), resistance for CBB found in common bean is controlled by one major QTL, whereas CBB resistance introgressed from tepary bean is determined by two major QTL. The same author discussed that, in addition to the above, five to eight QTL with small effects determine inheritance of common bacterial blight resistance (Nodari et al., 1993) were identified in common bean. Although resistance found in scarlet runner bean (Freytag et al., 1982; Fisseha et al., 2018) has been introgressed, its inheritance and complementation to the common or tepary bean resistance has not been known.

On top of everything, the quantitative nature of resistance against CBB has greatly jeopardized possible achievements of conventional breeding thrusts targeted towards ensuring sustainable resistance against the CBB causal pathogen (Beaver and Osorno, 2009; Fisseha et al., 2018). Then what possible solution can bridge this gap?

O'Boyle et al. (2007) explained that the substantial progress made in molecular marker technology for the common bean holds considerable promise for breeding genetic resistance to CBB.

### 4.2. Molecular Breeding toward Disease Resistance in Common Bean

The essential nature of the gene in all biological systems means that this unit of heredity has become one of the major focal points for attempts to enhance the productivity and sustainability of agricultural production (McCouch and Xiao, 2019). Molecular markers, therefore, contribute to our understanding of where genes are located along the chromosomes, its contribution to phenotype, and how they interact with each other and the environment. Furthermore, they noted that molecular markers also provide a strategy for identifying and isolating genes of interest, offering a toolbox of creative opportunities for optimizing productivity and environmental adaptation of improved germplasm. This has created a lot of excitement about MAS with expectations to speed up the development of crop varieties with desirable traits. Nonetheless, some contended that although DNA markers hold great promise, realizing that promise remains elusive (Dale Young, 1999; Burle et al., 2011).

According to Mohan et al. (2007), molecular markers have several advantages over the phenotypic and iso-enzyme markers, which were previously available to plant breeders. They offer great scope for improving the efficiency of conventional plant breeding by carrying out selection not directly on the trait of interest but on molecular markers linked to that trait. Besides, they are not environmentally regulated, are not affected by growing conditions, and are detectable in all stages of plant growth (Mohan et al., 2007; Fisseha et al., 2018).

The rapid development of molecular techniques has opened up sources of genes to plant breeding that were

not available previously through conventional breeding creating a lot of excitement about MAS (Allen, 1994). The opportunity to select desirable lines based on genotypes rather than phenotype has been extremely attractive to breeders; analyzing plants at the seedling stage, screening multiple traits that would normally be epistatic with one another, minimizing linkage drag, and rapidly recovering a recurrent parent's genotype were just a few of the attractions of MAS (Tanksley et al., 1989). Dale Young (1999) and Mohan et al. (2007) recognized that in cases of simple but important characters that are difficult to assay such as resistance to pathogens, insects and nematodes, tolerance to abiotic stresses, quality parameters, and quantitative traits MAS clearly has the potential to be a powerful tool for the breeder. Molecular markers have been developed for many disease resistance genes and these markers have been successfully used to develop improved common bean cultivars and germplasm (Miklas et al., 2006c). Miklas et al. (2006b) noted that marker-assisted selection has been used more for breeding for disease resistance than for other traits of economic importance, such as tolerance to abiotic stress. Molecular markers have also permitted the development of common bean lines that pyramid genes for disease resistance (Miklas and Singh, 2007). This strategy is designed to develop common bean lines with more durable resistance (McDonald and Linde, 2002). Although many molecular markers linked to disease genes have been reported, only a handful of these markers are being used routinely by common bean breeding programs. Lack of repeatability in different genetic backgrounds, weak marker-gene linkages, overestimated QTL effects (due to small population sizes used to develop the marker), and lack of economic resources can limit the use of molecular markers in a breeding program (Bernardo, 2008).

Miklas and Singh (2007) summarized disease resistance traits tagged with SCAR markers. Primarily, RAPD followed by AFLP have been used to tag disease resistance traits in common bean. Subsequently, resistance-linked RAPD and AFLP found useful for MAS were converted to allele-specific markers (SCAR) to facilitate utilization and portability, because RAPD and AFLP are notoriously difficult to reproduce across different laboratories. The *Ur-4* gene for rust resistance was the first gene specifically tagged in common bean with a DNA marker (Miklas et al., 2006b). The tagging of other genes and QTLs for resistance to bacterial, fungal and viral pathogens, among others, as described below, quickly followed. There has been a recent emphasis on tagging genes conditioning resistance to angular leaf spot, a devastating disease in Africa and the Americas. Ferreira et al. (2000) found a RAPD marker that was linked to a single dominant allele (*Phg-2*) in breeding line MAR<sub>2</sub> imparting resistance to race 63.39 of *P. griseola*. Nietsche et al. (2000) also reported RAPD and SCAR (SN<sub>02</sub>) markers linked to a dominant allele controlling resistance to race 31.17 of *P. griseola* in small back bean Cornell 49-24-2. Moreover, the same marker (SN<sub>02</sub>) was linked with the resistance found in MAR<sub>2</sub> and Mexico-54. Miklas et al. (2006b) mapped

the SN<sub>02</sub> marker to chromosome 3 of the core BJ map. Teixeira Caixeta et al. (2003) reported a dominant allele for resistance to race 61.41 of the same pathogen in dry bean breeding line BAT-332 that was linked to two RAPD markers in cis-position. The SH<sub>13</sub> SCAR linked with putative resistance gene *Phg-1* was identified in the cultivar 'AND 277' (Queiroz et al., 2006). A SCAR marker converted from an AFLP marker was linked to a single dominant gene from G 10474 (Mahuku et al., 2004). López et al., (2003) observed five QTLs for resistance to angular leaf spot located on chromosomes 8 and 10. Kelly and Vallejo (2004) reported that seven of nine major resistance genes for anthracnose have been tagged and mapped. Four of the genes, *Co-1*, *Co-2*, *Co-9*, and *Co-10*, co-segregate with rust resistance and the latter two co-segregate with halo blight resistance (Kelly and Vallejo, 2004), which is indicative of resistance gene clusters derived from ancestral genes having undergone duplication and divergence events (Michelmore and Meyers, 1998). Both recessive and dominant viral resistance genes have been tagged with molecular markers. For BCMV and BCMNV resistance, the *bc-3* (Haley et al., 1994; Johnson et al., 1997), *bc-12* (Miklas et al., 2000), and *I* genes ((Melotto et al., 1996) were tagged and mapped to chromosomes 1, 5, and 9, respectively. Urrea et al. (1999) found a RAPD marker (map location unknown) for the *bgm-1* allele imparting resistance to leaf chlorosis induced by BGMV (occurring in Brazil, Argentina, and Bolivia).

The following sections briefly summarize the status and achievements of molecular breeding pertinent to the major bean diseases.

In relation to resistance against anthracnose:

- Miklas et al. (2003) used the SCAR marker SAS-13 to develop pinto bean germplasm having the Co-42 gene for anthracnose resistance;
- Ansari et al. (2004) mapped specific genes and QTL for anthracnose resistance;
- Fine mapping of the Co-4 anthracnose resistance locus suggested development of SNPs (single nucleotide polymorphisms) markers inside the gene families harnessed the clear identification of the different alleles of Co-4 (Yang et al., 2004);
- Goncalves-Vidigal et al. (2004) reported that a RAPD marker OA181500 was linked in repulsion-phase with the dominant Co-15 gene and might be effective in providing broad resistance to anthracnose.

On the other hand, the following achievements were reported with respect to resistance against angular leaf spot via molecular breeding:

- Ferreira et al. (2000) found a RAPD marker that was linked to a single dominant allele (*Phg-2*) in breeding line MAR<sub>2</sub> imparting resistance to race 63.39 of *P. griseola*;
- Nietsche et al. (2000) also reported RAPD and SCAR (SN<sub>02</sub>) markers linked to a dominant allele controlling resistance to race 31.17 of *P. griseola* in small back bean Cornell 49-24-2. Moreover, the same marker

(SN02) was linked with the resistance found here MAR<sub>2</sub> and Mexico 54;

- Miklas et al. (2006b) mapped the SN<sub>02</sub> marker to chromosome 3 of the core BJ map;
- Teixeira Caixeta et al. (2003) reported a dominant allele for resistance to race 61.41 of the same pathogen in dry bean breeding line BAT332 that was linked to two RAPD markers in cis-position;
- López et al. (2003) observed five QTLs for resistance to angular leaf spot located on chromosomes 8 and 10. Nonetheless, tests of independence among the tagged genes for resistance to angular leaf spot were not conducted, and map location of the genes were not identified, with the exception of SN<sub>02</sub> (*Phg-2*) and the QTL
- A SCAR converted from an AFLP marker was linked to a single dominant gene from G 10474 Mahuku et al. (2004);
- Queiroz et al. (2006) contended that Sequence Characterized Amplified Region (SCAR) markers can serve more important roles in marker assisted common bean breeding against angular leaf spot resistance than corresponding RAPD markers, as they are highly specific RAPD-derived markers which do not have reduced reproducibility across different labs;

In the case of deploying resistance against common bacterial blight in common bean via molecular breeding, the following milestone achievements were reported:

- Beaver and Osorno (2009) noted that one of the biggest problems with breeding for CBB resistance derived from tepary beans is the instability of the expression of resistance. To this end, the authors recommended the use of molecular markers to help reduce or remove barriers to inter-specific hybridization would be the right solution;
- A SCAR marker, SU-91, was recommended in the transfer of the tepary-derived common bacterial blight resistance into different market classes of beans (Kelly et al., 2003; Miklas et al., 2006a);
- Tight linkages were reported between two SCAR markers, SU91 and BC420, and an independent common bacterial blight resistance QTL in a common bean breeding line 'XAN-159' (Singh, 2005);
- On the other hand, Kelly et al. (2003) reported that more than 80% of *P. acutifolius* cultivars were highly resistant to common bacterial blight, whereas, fewer than 25% of wild accessions possessed similar resistance. They argued that the former, therefore, might have had a narrower genetic base and the same resistance alleles and QTL might be present in multiple cultivated tepary bean lines.
- Melotto et al. (1996) developed the SCAR marker SW13, which has been widely used to screen both Andean and Mesoamerican bean breeding lines for the presence of the 'I' gene and provided broad protection against many strains of BCMV and other potyviruses, but vulnerable to the necrotic strains of BCNMV;4
- Pyramiding the dominant I gene with the recessive gene bc-3 provided resistance to all known strains of BCMV and BCNMV (Kelly et al., 2003);
- Plant breeders screened lines with the SCAR marker SW13 and with a virulent strain of BCNMV (NL-3) to develop cultivars such as 'Raven' (Kelly et al., 2003) and Middle American and Andean bean germplasm (Beaver et al., 1998; ?; ?) that combined the dominant I gene and the recessive bc-3 gene;
- Mukeshimana et al. (2005) identified a RAPD marker (OG6595), and a co-dominant AFLP marker (EACAMCGG-169/172) that was converted to the STS markers (SEACAMCGG-134/137), which were linked to the bc-3 resistance gene. These markers, according to the same, would permit indirect selection for resistance to BCNMV;
- On the other hand, Kelly et al. (2003) discussed that resistance to BCMV in bean may also be conditioned by a series of multi-allelic loci. The dominant 'I' gene, located on B2 (Gepts, 1999), is independent of three recessive bc loci that are currently mapped;
- Independence of the BCMV resistance genes provides opportunities to use gene pyramiding as a strategy in breeding for durable resistance. Bean breeders recognize that the combination of the dominant 'I' gene with recessive bc resistance genes offers durability over single gene resistance to BCMV and BCNMV, since the two types of genes have distinctly different mechanisms of resistance (Miklas and Singh, 2007);
- The dominant I gene is a resistance gene that confers a typical hypersensitive resistance, whereas the three most effective recessive genes (bc-12, bc-22, bc-3) act by restricting virus movement within the plant, probably by restricting the virus movement proteins. (Beaver and Osorno, 2009);
- The action of the dominant I gene is masked by the recessive bc-3 gene, so as efforts to incorporate the bc-3 gene into new germplasm proceed, the risk of losing the I gene in improved germplasm increases, since direct selection for the I gene is not possible (Beaver and Osorno, 2009);
- Larsen et al. (2006) Larsen et al. (2006) located significant differences in the genome of NL-3 K, a more virulent strain of NL-3 race of BCMNV discovered in Kimberly, Idaho, which may be responsible for changes in host response to the virus.

In regards to resistance against bean common mosaic (BCMV) and bean common mosaic necrotic virus (BCMNV), the following results were reported:

Concerning resistance against the common bean rust pathogen (*U. appendiculatus*), scholars reported the following research breakthroughs:

- Park et al. (2013) recommended that markers linked to the Ur-7 gene of Middle American origin identified in their study, along with other independent rust resistance genes from other germplasms, could be utilized to pyramid multiple genes into bean cultivars for more durable rust resistance;
- Park et al. (2014) reported that two RAPD markers, OBC06.300 and OAG15.300, and one SCAR marker, SOBC06.308, were present in six Andean cultivars without the Ur-6 gene;
- Mienie et al. (2005) developed a SCAR marker from the RAPD fragment, OA141100. They discovered that the SCAR marker acted co-dominantly, amplifying two different bands for the two alleles present at this locus, with a fragment of 1079 bp linked to the resistant allele (in BelMiDak-RR-9 and -RMR-11) and 800 bp linked to the susceptible allele (in Teebus and BelNeb-RR-1). The results were repeatable and easy to score. These results confirmed the finding of Miklas et al. (2006b) that the RAPD marker was only useful in a Middle-American genetic background. All cultivars of Andean origin were positive for the 1079 bp allele (resistance allele), except for KW780.

#### 4.3. Pyramided Disease Resistance for Major Diseases of the Common Bean

World's crop production is facing serious threats from the occurrence of biotic and abiotic stresses which contributes around 60% of production loss during the cropping period (Beaver and Osorno, 2009). Furthermore, the same authors noted that despite concerted efforts through breeding programs aimed at developing biotic and abiotic stress tolerant crop varieties by exploiting endogenous resistance genes, the progress is very limited, because of the complex nature of resistance mechanism(s). Large amount of chemical pesticides and fungicides are being used which leads to increase in cost of production and in addition it causes environmental pollution (FAO, 2005). A key step in breeding better crops that survive under stress has been to understand the changes in cellular, biochemical and molecular processes that occur in response to stress (Stacey et al., 2018).

Gene pyramiding or simultaneous transfer of multiple genes may be helpful in conferring broad spectrum resistance against different races of pathogens or conferring resistance against different pests or pathogens or combination of stresses. Essentially gene pyramiding enable us to have simultaneous expression of more than one gene(s) associated with resistance in cultivated plant (Shelton et al., 2002). The rationale behind gene pyramiding originates from the age old philosophy of the use of insecticide mixtures to broaden the spectrum of insects controlled in one spray event. Gene pyramiding has been hailed as a lasting insect/disease resistance management strategy (Jackson et al., 2003). It is also believed that gene pyramiding strategy can be successfully deployed against combination pest and diseases and in some cases it can be successfully implemented against combination of biotic and abiotic stresses (Shelton et al., 2002).

#### Achievements of Breeding Beans for Pyramided Disease Resistance So Far

The following is a cursory summary of the major achievements of conventional and molecular breeding efforts towards pyramiding disease resistance genes in the common bean (*P. vulgaris*):

- Kelly and Vallejo (2004) developed anthracnose (caused by *C. lindemuthianum*), BCMV, BCMNV, and rust resistant black-seeded cultivar Raven, which was then used to develop Phantom with similar resistance.
- Kelly et al. (1999) combined good canning quality, BCMV resistance, and the Andean Co-1 and Middle American Co-2 alleles for anthracnose resistance in a large-seeded light red kidney bean 'Chinook-2000'.
- Both anthracnose resistance alleles were also combined with BCMV and rust resistance in small black cultivar Jaguar (Kelly et al., 2001).
- Good canning quality and resistance to anthracnose, BCMV, Beet curly top virus (BCTV, a leafhopper-vectored-gemini-virus), and rust, either singly or in various combinations, were bred into dark and light-red kidney, red mottled, white kidney, and cranberry beans for North America (Miklas and Kelly, 2002; Miklas et al., 2001) and for the tropics and subtropics (Beaver et al., 2003).
- Singh et al. (2003) developed angular leaf spot; anthracnose, BCMV, rust, and halo blight resistant breeding lines A339, MAR1, MAR2, and MAR3 from interracial populations between the three Middle American races.
- Sanchez-Valdez et al. (2004) combined resistance to angular leaf spot, anthracnose, BCMV, and rust into high-yielding 'bayo-black', 'flor de mayo', 'ojo de cabra', 'pinto', and shiny black bean cultivars for Mexican highlands.
- Mahuku et al. (2003) reported angular leaf spot resistance in some wild common bean populations that has yet to be introgressed into and pyramided with the resistance already found in Andean and Middle American cultivars.
- Yang et al. (2004) reported that two cultivars 'Envoy' and 'Morden 003' pyramided three (Co-1, Co-2 and Co-4) and two (Co-1 and Co-4) resistance genes from both gene pools, respectively, and were resistant to anthracnose races 23, 73, 89 and 1096. This combination of resistance genes would afford resistance to all the known anthracnose races in Northern America.

## 5. Conclusion and Recommendations

The aforementioned are only glimpse of what is supposed as "an ocean of infinite endeavors", targeted toward deploying sustainable host-resistance traits in bean cultivars from primary, secondary, or tertiary gene pools of the common bean (*P. vulgaris*). In so doing, emphases have been given to the most notorious and economically important diseases in common bean.

The review paper dissected in order to inform the reader about resistance genes (either from the domesticated species, *P. vulgaris*, and/or associated species from different gene pools in the genus, *Phaseolus*. In so doing, it has focused on the five major bean diseases- anthracnose, angular leaf spot, common bacterial blight, BCMV/BCMV, and bean rust. The information thus generated shall be helpful in local breeding/improvement projects, through availing sources and identities of resistant varieties (or resistance genes) for each disease, as well as, genotypes with pyramided resistance for multiple diseases.

In stark contrast, considerable gaps have been observed in the following areas.

1. The insufficiency of relevant works vis-à-vis the incorporation of research works on incorporation of resistance genes from wild relatives and gene pool species;
2. The limitedness of data on the case of plant genetic resources from Africa and Asia, which is harrowing, as both are considered secondary centers of diversity for the crop;
3. The limited access to the resistance genes, due to lack of information and/or complications arising from various national patent rights and benefits; and
4. The pathogenic epidemiology, virulence, sources of host resistance, etc. have not been sufficiently studied and documented.

In prospect, aggressive research works on neglected plant genetic resources and devising ways to ensure the free transfer of genetic materials and pertinent information should be of higher priority. Furthermore, similar review works on major insects, nematodes, etc. shall supplement the information generated in our review paper, and greatly recommended.

### Conflict of Interest

The author declares that they don't have conflict of interest.

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