



ACHIEVEMENTS AND PROSPECTS OF COMMON BEAN (*PHASEOLUS VULGARIS L.*) BREEDING FOR DISEASE RESISTANCE: A REVIEW

Afework Legesse*

Crop Research Department, Jimma Agriculture Research Center, Jimma, Ethiopia

*Corresponding author

ABSTRACT

Common bean (*Phaseolus vulgaris L.*) is an important legume crop that provides a significant source of protein and nutrients to a large part of the world's population. However the yield and qualities of common bean are often compromised by various diseases caused by pathogens such as fungi, bacteria and viruses. Breeding for disease resistance is a sustainable and cost effective approach to mitigate the impact of these diseases. This review paper aims to discuss the achievements and prospects of common bean breeding for disease resistance, including the identification of resistance source, and future prospects. The importance of incorporating diverse resistance genes and the utilization of modern breeding techniques to enhance disease resistance in common bean varieties highlighted.

Keywords: Common bean, gene pyramiding, genetic diversity, host-pathogen interaction, plant resistance

INTRODUCTION

The common bean (*Phaseolus vulgaris L.*) is the most important legume directly used for human consumption globally. It is consumed worldwide for its edible seeds and pods. It is the most important source of proteins for nearly five hundred million people in Africa, Latin America and the Caribbean particularly for low income earning households. Among the five domesticated and grown species of the genus *Phaseolus*, a genus comprised of some 70 species (Freytag & Debouck, 2002), *P. vulgaris* accounts for more than 90% of the cultivated crop in the world (Singh *et al.*, 2001). The immediate ancestors of the cultivated common bean ($2n = 2x = 22$) are wild populations distributed from northern Mexico to northern Argentina (Gepts, 1998; Koenig *et al.*, 1990). There are two types of common bean: those used for the dry and green-shelled seed and green, garden, snap, or string less bean in which pods are consumed (Myers and Baggett, 1999; Singh, 1992).

Production Constraints

Abiotic Constraints

Abiotic stress is the major constraint to bean productivity in most tropical countries. Abiotic factor such as extreme limited water stress (drought) cause yield loss in Mexico, Brazil, Central America, and Eastern and Southern Africa. Heat stress adversely affects the cultivation of beans in Central and Southern America and Africa (Beebe *et al.*, 2011). Nutrient deficiencies of phosphorous (P) and nitrogen (N) also reduces yield, while Aluminum and Manganese toxicity associated with acid soil, as well as low Calcium availability, cause significant common bean yield loss (Table 1).

Table 1. A schematic comparison of different bean production limitation, classified for their frequency, likely intensity, and risk to farmers.

Limitation	Frequency	Intensity	Risk
Pest and diseases	high	High	Very high
Drought	low	Very high	
Low soil fertility	Very high	High	Very low
High temperature	Very high	High	Very low

Source: Adapted from Beebe *et al.*, 2006.

Biotic Constraints

Biotic stresses such as diseases and pests are universal constraints to common bean production, especially fungal pathogens. Several bacterial, fungal, and viral diseases attack aerial and underground parts of common bean (Schwartz *et al.*, 2005). Under favorable disease conditions, fungal pathogens cause significant yield losses. Yield losses also occur due to insect damage (Table 2).

Anthrachnose, rust, and angular leaf spot are widely distributed, while rhizoctonia web blight and ascochyta blight can be locally intense in warm-moist environments, respectively. In recent years, root rots have emerged as a significant problem for common bean production, especially those caused by *Pythium* spp. and *Fusarium* spp. Insects are occasional problems. In Central America the bean pod weevil, *Apion godmani* and *A. aurichalceum*, is the most important pest, while in East Africa the bean stem maggot, aphids, and pod borers cause the most serious problems.

Table 2. Summary of major diseases attacking common bean, yield loss potential, and seed transmissibility and survival

Common Name	Organism	Yield loss potential	Transmission and survival
Angular leaf spot	Phaeoisariopsis griseola	80%	Seed, wind, plant debris
Anthracnose	Colletotrichum lindemuthianum	100%	Seed, wind, plant debris
Bacterial brown spot	Pseudomonas syringae pv. Syringae	25%	Seed, wind, water, plant debris
BCMV	Bean common mosaic virus	100%	Seed, plant debris, aphid
BCMNV	Bean common mosaic necrosis virus	100%	Seed, plant debris, aphid
BCTV	Beet curly top virus	100%	Leafhopper (Circulifer tenellus)
BGMV	Bean golden mosaic virus	100%	Whitefly (Bemisia spp.)
BGYMV	Bean golden yellow mosaic virus	100%	Whitefly (Bemisia spp.)
Common bacterial blight	Xanthomonas campestris (axonopodis) pv. Phaseoli	45%	Seed, wind, water, plant debris
Halo blight	Pseudomonas syringae pv. Phaseolicola	45%	Seed, wind, water, plant debris
Root rots	Aphanomyces, Fusarium, Pythium, Rhizoctonia, Thielaviopsis species	100%	Seed, wind, water, plant debris
Rust	Uromyces appendiculatus	50%	Wind, plant debris
Web blight	Thanatephorus cucumeris	100%	Seed, wind, water, plant debris
White mold	Sclerotinia sclerotiorum	90%	Seed, wind, water, soil, plant debris

Source: Singh and Schwartz, 2010

Fungal Diseases

Anthracnose

Anthracnose caused by the fungal pathogen *Colletotrichum lindemuthianum* is a serious seed-borne disease of common bean and can cause devastation to farmers' fields, resulting in yield losses as high as 100% in susceptible cultivars (Singh and Schwartz, 2010). This pathogen overwinters in seed and crop residues (primary source of infection) and infects all aerial parts of the bean plant. Recent literature shows presence of more than 100 races of pathogen worldwide (Gonzalez *et al.* 2015), and 1590 isolates of *C. lindemuthianum* inoculated on 12 bean differential cultivars have resulted in the identification of 182 races worldwide. Cultivating resistant varieties is the most economical and effective approach for controlling common bean diseases and is an important goal for common bean breeders. Currently, more than 20 resistance loci are identified against anthracnose disease with a gene symbol *Co* (Coimbra-Gonçalves *et al.* 2016). Incorporating genetic resistance to anthracnose is

the area of research and development that holds the most promise for reducing the effects of the pathogen in common bean. Careful selection of genes providing resistance to races producing anthracnose disease is required. The varieties carrying resistance genes provide a short-lasting control over the disease lasting only until new strains of fungus emerge. The major difficulty with the process of compiling the resistance genes is that detection of the resistant plants takes time since it requires systematic inoculation with different strains of the fungus. A literature review indicates that in other countries where cultivation is common, strains of the common fungi have been identified, and the varieties resistant to the identified strains have been developed. MAS have been used successfully to breed for enhanced resistance to anthracnose in the cultivar Perola in Brazil (Ragagnin *et al.* 2003) and in pinto beans in the United States (Miklas *et al.* 2003b). Genchev *et al.* (2010) developed anthracnose resistance source using several physiological races of anthracnose identified in Bulgaria which was performed from F1 to F5 generation. The line DG 2-36-58-3 was identified as the most promising by quality complex of growth habit type, vegetation period, type of seeds, yield and presence of *Co-1* and *Co-4* genes that confer resistance to 74 out of 78 worldwide recognized anthracnose races. Achieving durable anthracnose resistance poses a challenge to bean breeders. Due to the high degree of pathogen variability and the continual emergence of new races, single-gene deployment is not an effective strategy to control bean anthracnose. The pyramiding of resistance genes which have complementary spectra of resistance has been suggested as a strategy to circumvent the problem of pathogen variability.

Angular Leaf Spot (ALS)

Angular leaf spot (ALS) disease caused by *Pseudocercospora griseola* (Sacc.) is a major disease of common beans in the tropics and subtropics (Stenglein *et al.*, 2003). Studies on the variability of *P. griseola* isolates revealed the existence of two major groups of the pathogen, Andean and Mesoamerican, which correspond to and have co-evolved with the Andean and Mesoamerican gene pools of common bean (Crous *et al.*, 2006). Mesoamerican strains of this pathogen are considered more virulent as compared to Andean strains, and they tend to affect both Mesoamerican and Andean beans, while Andean strains are less virulent, affecting mostly Andean genotypes. The disease is of great economic importance in Eastern and Central African countries of Uganda, Kenya, Tanzania, Ethiopia, Rwanda, Burundi and Kivu Province of the Democratic Republic of Congo (Pastor-Corrales *et al.*, 1998). According to Stenglein *et al.* (2003), every 10% increase in ALS severity results in 7.9% yield loss. ALS disease is spread within and among fields by wind-blown particles of infested soil and wind-blown and rain-splashed spores. However, the primary source of infection is considered to be infested seed. Resistance to ALS in common bean is controlled by single dominant (Correa *et al.*, 2001; Namayanja *et al.*, 2006) as well as recessive genes (Correa *et al.*, 2001). As the best form of disease control includes using resistant cultivars, the genetic characterization of resistance sources is very important for the genetic improvement of the crop. In the case of ALS, two dominant resistance genes have been described so far. The first, called *Phg-1*, was identified in the AND 277 variety. While, the second, called *Phg-2*, was identified in the Mexico 54 varieties (Sartorato *et al.*, 2000) linked to SCAR OPN02 and RAPDOPE04 markers. Apart from these two genes, dominant monogenic inheritance for resistance to ALS has also been described in the Ouro Negro (Correa *et al.*, 2001) and G10474 varieties. But the relationship of these genes with *Phg-1* and *Phg-2* remains unknown. In addition to qualitative resistance genes, there are also reports of QTLs controlling resistance to ALS. Five QTLs were mapped on linkage group B04,

one on B08, one on B09 and three on linkage group B10 (Lopez *et al.*, 2003; Mahuku *et al.*, 2009; Mahuku *et al.*, 2011). The Mesoamerican ALS resistance locus, *Phg-3*, mapped in accession Ouro Negro, is linked to marker G2303 at a distance of 0 cM (Gonçalves-Vidigal *et al.*, 2013).

Singh *et al.* (2003) developed ALS resistant dry bean breeding lines including A 339, MAR 1, MAR 2 and MAR 3 from interracial populations between the Middle American common bean races. Mahuku *et al.* (2003) identified 78 interspecific dry bean lines with resistance putatively transferred from the secondary gene pool, which represents important germplasm for future utilization. Traditional breeding at CIAT involving hybridization among resistance sources in single or multiple interracial crosses followed by selection under disease pressure in field nurseries and greenhouse screening trials has resulted in development of germplasm lines MAR1, MAR 2, MAR 3, AND 277 and CAL 143 with improved broad-based resistance to angular leaf spot (Singh *et al.*, 2003; Aggarwal *et al.*, 2004). Pyramiding resistance genes into a single genotype is one of the practical approaches through which durable resistance can be achieved. There are several *Phg* genes that have been identified as sources of resistance to *P. griseola* from landraces, secondary and tertiary genes pools. However, utilization of these genes in a breeding programme will depend on the mode of inheritance and the background of the cultivar carrying them. Landrace varieties might be excellent sources for resistance breeding against ALS. Landraces are readily available, adapted to the environments and have been kept by farmers because of their desired traits. In this regard, breeding against multi-races of ALS disease is an overriding consideration which requires gene pyramiding that involves several parents. Therefore, appropriate mating design and genetic analysis that will provide information of the best parent in a combination and best selection methods to identifying superior progenies is important.

Powdery Mildew

Powdery mildew is a serious disease for many crops worldwide including common bean. Common bean powdery mildew causal agent has been frequently ascribed to *Erysiphe polygoni* DC. But recent studies suggest that it is closer to *Erysiphe diffusa* (Cooke and Peck) U. Braun and S. Takam, formerly *Microsphaera diffusa* Cke. and Pk. (Almeida *et al.*, 2008). Limited information about sources of resistance to the fungus and the nature and inheritance of resistance are available to bean breeders and plant pathologist. A few sources of resistance to powdery mildew have been described (Schwartz *et al.*, 1981), and a qualitative nature of resistance has been suggested (Ferreira *et al.*, 2001). The response of common bean to powdery mildew was previously reported to be governed by a single dominant gene (Dundas 1936), by one dominant and other recessive resistance genes (Bett and Michaels 1995) or by two complementary dominant genes. Sources of resistance to PWM have also been described (Schwartz *et al.* 1981) including “Cornell 49, 242, Porrillo Sintetico, Negro San Luis and ESAL 686” cultivars (Rezende *et al.*, 1999; Trabanco *et al.*, 2012; Perez-Vega *et al.*, 2013). Much of these sources are characterized by possessing a few genes involved in the trait with different patterns of action. The genetic positions of resistance genes were first investigated in Xana/Cornell 49,242 recombinant inbred line population. Results showed that the resistance in the genotype Cornell 49,242 was conferred by two independent and epistatic genes: *Pm1*, located in linkage group (LG) Pv11 conferring total resistance in which there is no visible disease symptoms, and *Pm2*, located in LG Pv04, conferring intermediate resistance with a very limited disease development

(Perez-Vega *et al.*, 2013). From a breeding perspective, molecular-genetic maps and QTL mapping are tools that allow the localization of some genomic regions that control both single and complex inheritance. This information could be used in breeding programmes for producing new cultivars for resistance to powdery mildew.

Rust

Among the fungal diseases, one of the most a widespread and important disease of common bean is rust, caused by a highly variable basidiomycete fungus *Uromyces appendiculatus* (Pers.Pers.) unger which has a narrow host range -attacks only common bean. This disease is distributed throughout the world, but it effectively causes major production problems in humid tropical and subtropical areas and periodic severe epidemics in humid temperate regions (Pastor-Corrales 2003). Severe bean rust epidemics have been reported in Australia, China, the United States and some areas of Europe. Major losses have occurred in Burundi, Ethiopia, Kenya, Malawi, Rwanda, South Africa, Tanzania, Uganda and Zimbabwe. In Latin America, the bean rust is also a serious problem; major losses occurred in Argentina, Bolivia, Brazil, Colombia, Costa Rica, Cuba, Dominican Republic, Ecuador, El Salvador, Guatemala, Haiti, Honduras, Jamaica, Mexico, Nicaragua and Peru. Disease losses worldwide measured in greenhouse and field conditions can vary from 18 to 100%. The *U. appendiculatus* is a highly variable and is among the most pathogenically variable of all plant pathogens. It has been identified and reported in all bean production areas of the world (Stavely and Pastor-Corrales 1989) and is characterized by highly diverse virulence phenotypes (Souza *et al.*, 2005). According to Lindgren *et al.* (1995), 1% increase in bean rust severity leads to a yield loss of approximately 19 kg/ha. Resistance to bean rust is mainly controlled by major single dominant genes (Souza *et al.*, 2007). However, it can be also controlled by single recessive genes (Zaiter *et al.*, 1989), two genes (Finke *et al.*, 1986), two complementary dominant genes (Grafton *et al.*, 1985) or by many genes with minor effect (Edington *et al.*, 1994). According to Souza *et al.* (2011), 13 dominant rust resistance (RR) genes (*Ur-1* to *Ur-13*) have been identified. In addition to these genes, other important unnamed genes have been identified, such as those present in the common bean cultivars as BAC6, CNC, CSW 643, Dorado, Ouro Negro and PI 260418.

Bacterial diseases

Common Bacterial Blight (CBB)

Common bacterial blight (CBB) is a significant foliar disease of dry bean caused by the pathogen *Xanthomonas axonopodis* pv. *phaseoli*, a gram-negative bacillus with a genome of approximately 3.9 Mb. The bacteria are seed-borne, and under field conditions, dissemination can occur through wind-driven rain or mechanical transfer by insect vectors. In addition to natural methods, the bacteria can be spread by overhead sprinkler systems and the use of infected seeds (Singh and Schwartz, 2010). Studies of the genetic diversity of *X. axonopodis* pv. *phaseoli* have found that the pathogen can be grouped into four genetic lineages. Three of these groups are composed exclusively of *X. axonopodis* pv. *phaseoli*, while the last group contains the *X. fuscans* subsp. *fuscans* strains (Alavi *et al.*, 2008). Several inheritance studies have been conducted on CBB resistance, and different results were reported depending on various factors such as the pathogenic variability and the genetic background of the parental lines (Fourie *et al.*, 2011). CBB resistance is inherited quantitatively, with largely additive effects, low to moderately high heritability and transgressive segregation (Aggour and Coyne, 1989; Arnaud-Santana *et al.*,

1994). Similarly, Miklas *et al.* (2003a) reported that the inheritance of CBB resistance in Montana No. 5 was polygenic with at least one major gene effect. Likewise, Zapata *et al.* (2011) reported that CBB resistance was governed by a single dominant gene in resistant lines Wilk-2 and VAX6 and VAX4 and PR 0313-58, respectively. The identification of major quantitative trait loci (QTL) controlling resistance to CBB (Singh and Miklas, 2015) has facilitated marker-assisted breeding for higher levels of CBB resistance into better-adapted and higher-yielding dry bean lines (Miklas *et al.*, 2000a). CBB-tolerant/resistant dry bean varieties have been developed from germplasm derived from interspecific crosses by various breeding programs in North America. Singh and Muoz (1999) and developed CBB-resistant interspecific breeding lines VAX1 and VAX 2 from a multiple-parent interspecific cross between common and topiary bean G 40001. The substantial progress made in molecular marker technology for the common bean holds considerable promise for breeding genetic resistance to CBB. Molecular markers for disease resistance are powerful tools for analyzing the genome and are comprehensively applied in mapping genes and MAS (Boyle *et al.*, 2007). To date, 24 QTL conferring resistance to CBB have been identified, distributed across all 11 chromosomes of common bean (Singh and Schwartz 2010; Shi et al. 2011).

Halo Blight (HB)

It is an important seed-borne disease of dry beans caused by *Pseudomonas syringae* pv. *phaseolicola* (Burkh.) Dows. (*Psp*). The disease is a major constraint of dry bean production in moderately cool and wet regions of Africa, Europe, North America and South America (Taylor *et al.*, 1996; Rico *et al.*, 2003). The gene-for-gene interaction between common bean and HB pathogen races was demonstrated using molecular techniques and resistant genotypes (c). Nine races of the pathogen and five race-specific resistance genes have been previously described. However, a quantitative response to this pathogen has also been described (Yaish *et al.*, 2006). Several researchers studied genetic inheritance of HB resistance. As per the earlier findings, resistance to HB is inherited by single dominant or recessive genes (Taylor *et al.*, 1996). Taylor *et al.* (1996) screened over 1000 accessions of *Phaseolus* spp. and identified both race-specific and non-race-specific resistance to halo blight. For example, CAL 143, great northern Nebraska #1 Sel. 27, 'Jules', PI 150414 and Wis HBR 72 among others carry non-race-specific resistance. Molecular and genetic studies established that the relationship between the race specific genes and *Psp* races conformed to a gene-for-gene interaction (Jenner *et al.*, 1991). Furthermore, genetic studies have established that inheritance of halo blight resistance depends on the nature of the resistance as well as the genetic background. Chataika *et al.* (2011) also reported a single dominant resistance gene in the large seeded (40 g per 100 seeds) Andean breeding line CAL 143. On the other hand, the quantitative race non-specific resistance in PI 150414 is due to a recessive gene (Taylor *et al.*, 1996). Miklas *et al.* also mapped the dominant *Pse-2* gene, which is derived from the differential genotype ZAA 12 and confers resistance to seven *Psp* races (excluding *Psp* races 1 and 6), to linkage group Pv10. Miklas *et al.* (2009) identified six random amplification of polymorphic DNA (RAPD) markers tightly linked (0–3.3 cM) with *Pse-1* in a 'Canadian Wonder'/UI 3 dry bean population of which three completely linked markers were converted into SCAR markers SH11.800, SR13.1150 and ST8.1350. However, usefulness of these SCAR markers for marker-assisted selection would be limited to populations of large-seeded Nueva.

Significant progress has been made in developing cultivars with resistance to various diseases using conventional breeding. Some important resistance-mapping studies are summarized in Table 3. Markers associated with established resistance loci can be used for more efficient breeding to develop resistant cultivars.

Table 3. Summary of bean fungal, bacterial and viral disease distribution, transmission and resistance genes (Teshale *et al.* 2019)

Disease	Distribution	Seed	Transmission	Resistance
<i>Fungi</i>				
Anthrachnose (<i>Colletotrichum</i>)	Worldwide (cool = 14–18 °C, humid, and >1000 m in tropics)	Yes	Wind and rain; animal and insect	QTL: Pv01, Pv02, Pv04, Pv10, Co-1, Co-2
Angular leaf spot (<i>Phaeoisariopsis</i>)	Worldwide (moderate temp. 18–25 °C, high moisture)	Yes	Wind	QTL: Pv04, Pv10 (ALS10.1) Phg1, Phg2
Rust (<i>Uromyces</i>)	Worldwide	No	Wind, crop and residue	KASP SS68 marker associated with Pv11
Leaf spot (<i>Ascochyta</i>)	Tropics (high altitude: >1500 m)	Yes	Splash, contact, crop residue	Quantitative (<i>P. polyanthus</i>)
Pythium root rot	Worldwide	Yes	Crop residue, infected soil	QTL: ER3XC (LG3), SV6XC(LG6), Py-1 (LG7)
<i>Fusarium</i>	Worldwide	No	Crop residue, infected soil	QTL (<i>FRR3.1 km</i> (Pv03), LGs B2 and B3
Web blight	Worldwide (hot-humid)	Yes	Infected soil, seed	Quantitative
<i>Bacteria</i>				
Common blight (<i>Xanthomonas</i>)	Worldwide (cool to moderate temp.)	Yes	Rain, moisture	QTL: BC420 (Pv06), SU91 (Pv08), Xa11.4OV1(Pv11)
Halo blight (<i>Pseudomonas</i>)	Worldwide (cool to moderate temp.)	Yes	Rain, moisture	Quantitative: Psc-1, Psc-2, Psc-3, Psc-4, Psc-6, HB5.1 98BB, 98LFA, 96LFA, 96BBS
Bacterial brown spot (<i>Pseudomonas</i>)	Worldwide (warm- humid weather)	Yes	Seed, wind	LG02
<i>Viruses</i>				
Bean common mosaic virus and mosaic necrosis virus	Worldwide	Yes	Aphid	Qualitative: bc-1, bc-2, bc-3
Bean golden yellow mosaic virus	Central America, Caribbean	No	Whitefly	Qualitative, quantitative, Bgm-1, RNAi

CONCLUSIONS AND PROSPECTS

Breeding common bean for disease resistance is critical for enhancing its productivity and sustainability in the face of various pathogenic threats. Significant advances have been made in breeding common bean for resistance to specific diseases. Molecular marker-assisted selection is being increasingly used for bean improvement. Researchers should therefore strive to combine the best of conventional and modern molecular approaches to improve resistance to multiple diseases and other desirable traits in the shortest time possible in otherwise high yielding, high quality, and broadly adapted cultivars of different market classes of common bean. Collaboration among breeders, pathologists, and molecular biologists is essential to achieve long term success in common bean breeding for disease resistance.

Modern biotechnological tools, such as genomics selection, gene editing, and transgenic approaches, hold great potential to expedite the development of disease resistant common bean

varieties. The application of next-generation sequencing technologies and high-throughput phenotyping can facilitate the identification and characterization of novel resistance genes and QTLs. Integration of multi-omics approaches, such as transcriptomics and metabolomics, can provide a comprehensive understanding of the plant pathogen interactions and aid in the identification of key genes involved in disease resistance.

REFERENCE

- Aggarwal VD, Marcial A, Pastor C, Rowland M, Chirwa BRA., 2004. Andean beans (*Phaseolus vulgaris* L.) with resistance to the angular leaf spot pathogen (*Phaeoisariopsis griseola*) in Southern and Eastern Africa. *Euphytica* 136:201–210
- Arnaud-Santana E, Coyne DP, Eskridge KM, Vidaver AK., 1994. Inheritance, low correlations of leaf, pod, and seed reactions to common blight disease in common beans, and implications for selection. *J Am Soc Hortic Sci* 119:116–121
- Bett KE, Michaels TE., 1995. A two-gene model for powdery mildew resistance in common bean. *Annu Rep Bean Improv Coop* 38:145–146
- Boyle PDO, Kelly JD, Kirk WW, 2007. Use of marker-assisted selection to breed for resistance to common bacterial blight in common bean. *J Am Soc Hortic Sci* 132:381–386
- Chataika BYE, Bokosi JM, Chirwa RM, Kwapata MB, 2011. Inheritance of halo blight resistance in common bean. *African Crop Sci J* 19:325–333
- Coimbra-Gonçalves GK, Gonçalves-Vidigal MC, Coelho RT, Valentini G, Vidigal Filho PS, Lacanallo GF, Sousa LL, Elias HT, 2016. Characterization and Mapping of Anthracnose Resistance Gene in Mesoamerican Common Bean Cultivar Crioulo 159. *Crop Science* 56 (6):2904–2915
- Correa RX, Pedro IV, Oliveira MLP, Nietzsche S, Moreira M, Barros EG, 2001. Heranca da resistencia a mancha angular do feijoeiro e a identificacao de marcadores moleculares fanqueando o loco de resistencia. *Fitopatol Bras* 26:27–32
- Crous PW, Liebenberg MM, Braun U, Groenewald JZ, 2006. Re-evaluating the taxonomic status of *Phaeoisariopsis griseola*, the causal agent of angular leaf spot of bean. *Stud Mycol* 55:163–173
- Dundas B., 1936. Inheritance of resistance to powdery mildew in beans. *Hilgardia* 10:243–253
- Edington BR, Shanahan PE, Rijkenberg FHJ, 1994. Breeding for partial resistance in dry beans (*Phaseolus vulgaris*) to bean rust (*Uromyces appendiculatus*). *Ann Appl Biol* 124:341–350
- Ferreira RV, Bosco dos Santos J, Patto MA, Furtado D., 2001. Agronomical characters and RAPD markers associated with the resistant allele to the *Erysiphe polygoni* in common bean. *Crop Breed Appl Biot* 1:11–21
- Finke ML, Coyne DP, Steadman JR, 1986. The inheritance and association of resistance to rust, common bacterial blight, plant habit and foliar abnormalities in *Phaseolus vulgaris* L. *Euphytica* 35:969–982
- Fourie D, Herselman L, Mienie C., 2011. Improvement of common bacterial blight resistance in South African dry bean cultivar Teebus. *Afr Crop Sci J* 19:377–386
- Freytag GF, Debouck DG, 2002. Taxonomy, distribution, and ecology of the genus *Phaseolus* (Leguminosae-Papilionoideae) in North America, Mexico and Central America. Ft. Worth TX, USA. Botanical Research Institute of Texas.
- Genchev D, Christova P, Kiryakov I, Beleva M, Batchvarova R, 2010. Breeding of common bean for resistance to the physiological races of anthracnose identified in Bulgaria. *Biotechnol Biotechnol Equip*.

- Gonçalves-Vidigal MC, Cruz AS, Lacanallo GF, Vidigal Filho PS, Sousa LL, 2013. Co-segregation analysis and mapping of the anthracnose Co-10 and angular leaf spot Phg-ON disease resistance genes in the common bean cultivar Ouro Negro. *Theor Appl Genet* 126:2245–2255
- Gonzalez AM, Yuste-Lisbona FJ, Rodino AP, De Ron AM, Capel C, Garcia-Alcazar M, Lozano R, Santalla M, 2015. Uncovering the genetic architecture of *Colletotrichum lindemuthianum* resistance through QTL mapping and epistatic interaction analysis in common bean. *Front Plant Sci* 6:141
- Grafton KF, Weiser GC, Littlefield LJ, Stavely JR, 1985. Inheritance of resistance to two races of leaf rust in dry edible bean. *Crop Sci* 25:537–539
- Jenner C, Hitchin E, Mansfield J, Walters K, Betteridge P, Teverson D, Taylor J, 1991. Gene-for gene interactions between *Pseudomonas syringae* pv. *phaseolicola* and *Phaseolus*. *Mol. Plant Microbe Interact* 4:553–562
- Koenig, R., S.P. Singh, and P. Gepts, 1990. Novel phaseolin types in wild and cultivated common bean (*Phaseolus vulgaris*, Fabaceae). *Econ. Bot.* 44:50–60.
- Lindgren DT, Escridge KM, Steadman JR, Schaaf DM, 1995. A model for dry bean yield loss due to rust. *Hort Technol* 5:35–37
- Lopez CE, Acosta IF, Jara C, Pedraza F, 2003. Identifying resistance gene analogs associated with resistances to different pathogens in common bean. *Phytopathology* 93:88–95
- Mahuku G, Jara C, Cajiao C, Beebe S, 2003. Sources of resistance to angular leaf spot (*Phaeoisariopsis griseola*) in common bean core collection, wild *Phaseolus vulgaris* and secondary gene pool. *Euphytica* 130:303–313
- Mahuku GS, Henriquez MA, Montoya C, Jara C, Teran H, Beebe S, 2011. Inheritance and development of molecular markers linked to angular leaf spot resistance genes in the common bean accession G10909. *Mol Breed* 28:57–71
- Mahuku GS, Iglesias AM, Jara C, 2009. Genetics of angular leaf spot resistance in the Andean common bean accession G5686 and identification of markers linked to the resistance genes. *Euphytica* 167:381–396
- Miklas PN, Coyne D, Grafton KF, Mutlu N, Reiser J, Lindgren DT, Singh SP, 2003a. A major QTL for common bacterial blight resistance derives from the common bean great northern landrace cultivar Montana No. 5. *Euphytica* 131:137–146
- Miklas PN, Fourie D, Wagner J, Larsen RC, Mienie CMS, 2009. Tagging and mapping Pse-1 gene for resistance to halo blight in common bean differential cultivar UI 3. *Crop Sci* 49:41–48
- Mink, Silbernagel (1992) Serological and biological relationships among viruses in the bean common mosaic virus subgroup. *Arch Virol Suppl* 5:397–406.
- Miklas PN, Kelly JD, Singh SP, 2003b. Registration of anthracnose-resistant pinto bean germ plasm line USPT-ANT-1. *Crop Sci* 43:1889–1890
- Miklas PN, Larsen RC, Riley R, Kelly JD, 2000. Potential marker-assisted selection for bc-1(2) resistance to bean common mosaic potyvirus in common bean. *Euphytica* 116:211–219
- Namayanja AR, Buruchara G, Mahuku P, Rubaihayo P, Kimani S, Mayanja EH, 2006. Inheritance of resistance to angular leaf spot in common bean and validation of the utility of resistance linked markers for marker assisted selection outside the mapping population. *Euphytica* 151:361–369
- Pastor-Corrales MA, 2003. Sources, genes for resistance, and pedigrees of 52 rust and mosaic resistant dry bean germplasm lines released by the USDA Beltsville Bean Project in

- collaboration with the Michigan, Nebraska and North Dakota Agricultural Experiment Stations. *Ann Rep Bean Improv Coop* 46:235–241
- Pastor-Corrales MA, Jara C, Singh S., 1998. Pathogenic variation in, source of, and breeding for resistance to *Phaeoisariopsis griseola* causing angular leaf spot in common bean. *Euphytica* 103:161–171
- Perez-Vega E, Trabanco N, Campa A, Ferreira JJ, 2013. Genetic mapping of two genes conferring resistance to powdery mildew in common bean (*Phaseolus vulgaris* L.). *Theor Appl Genet* 126:1503–1512
- Ragagnin VA, Sanglard DA, de Souza TLPO, Moreira MA, de Barros EG, 2003. Simultaneous transfer of resistance genes for rust, anthracnose, and angular leaf spot to cultivar Perola assisted by molecular markers. *Annu Rep Bean Improv Coop* 46:159–160
- Rezende VF, Ramalho MAP, Corte HR, 1999. Genetic control of common bean (*Phaseolus vulgaris*) resistant to powdery mildew (*Erysiphe polygoni*). *Genet Mol Biol* 22:233–236
- Rico A, Lopez R, Asensio C, Aizpun MT, Asensio-S-Manzanera MC, Murillo J., 2003. Nontoxigenic strains of *Pseudomonas syringae* pv. *phaseolicola* are main cause of halo blight of beans in Spain and escape current detection methods. *Phytopathology* 93:1553–1559
- Sartorato A, Nietzsche S, Barros EG, Moreira MA, 2000. RAPD and SCAR markers linked to resistance gene to angular leaf spot in common beans. *Fitopatol Bras* 25:637–642
- Schwartz HF, Katherman MJ, Thung MDT, 1981. Yield response and resistance of dry beans to powdery mildew in Colombia. *Plant Dis* 65:737–738
- Schwartz, H.F., J.R. Steadman, R. Hall, and R.L. Forster (ed.), 2005. *Compendium of bean diseases*, 2nd ed. APS Press, St. Paul, MN.
- Shi C, Navabi A, Yu KF, 2011. Association mapping of common bacterial blight resistance QTL in Ontario bean breeding populations. *BMC Plant Biol* 11(1):52
- Shree P. Singh and Howard F. Schwartz, 2010. Breeding Common Bean for Resistance to Diseases: A Review. *CROP SCIENCE*, VOL. 50.
- Singh S, Sidhu JS, Huang N, Vikal Y, Li Z, Brar DS, Dhaliwal HS, Khush GS, 2001. Pyramiding three bacterial blight resistance genes (xa5, xa13 and Xa21) using marker-assisted selection into indica rice cultivar PR106. *Theoretical and Applied Genetics* 102:1011-1015.
- Singh SP and Muoz CG, 1999. Resistance to common bacterial blight among *Phaseolus* species and common bean improvement. *Crop Sci* 39:80–89.
- Singh SP, Miklas PN, 2015. Breeding common bean for resistance to common blight: a review. *Crop Sci* 55:971–984.
- Singh SP, Schwartz HF., 2010. Breeding common bean for resistance to diseases: a review. *Crop Sci* 50:2199–2223.
- Singh SP, Teran H, Gutierrez JA, Pastor-Corrales MA, Schwartz HF, Morales FJ, 2003. Registration of A 339, MAR 1, MAR 2, and MAR 3 angular leaf spot and anthracnose resistant common bean germplasm. *Crop Sci* 43:1886–1887
- Singh, S.P., 1992. Common bean improvement in the tropics. *Plant Breed. Rev.* 10:199–269.
- Souza TLPO, Alzate MAL, Moreira MA, Barros EG, 2005. Analise da variabilidade patogênica de *Uromyces appendiculatus* em algumas regiões brasileiras. *Fitopatol Bras* 30:143–149
- Souza TLPO, Dessaune SN, Sanglard DA, Moreira MA, Barros EG, 2007. Rust resistance gene present in common bean cultivar Ouro Negro (Ur-ON) does not correspond to Ur-3+. *Ann Rep Bean Improv Coop* 50:119–120

- Souza TLPO, Dessaune SN, Sanglard DA, Moreira MA, Barros EG, 201. Characterization of the rust resistance gene present in the common bean cultivar Ouro Negro, the main rust resistance source used in Brazil. *Plant Pathol* 60:839–845.
- Stavelly JR, Pastor-Corrales MA, 1989. Rust. In: Schwartz HF, Pastor-Corrales MA (eds) *Bean production problems in the tropics*, 2nd edn. Centro Internacional de Agricultura Tropical, Cali, CO, pp 159–164
- Stenglein S, Ploper LD, Vizgarra O, Balatti P., 2003. Angular leaf spot: a disease caused by the fungus *Phaeoisariopsis griseola* (Sacc.) Ferrarison *Phaseolus vulgaris* L. *Adv Appl Microbiol* 52:209–243.
- Taylor JD, Teverson DM, Davis JHC, 1996. Sources of resistance to *Pseudomonas syringae* pv. *phaseolicola* races in *Phaseolus vulgaris*. *Plant Pathol* 45:479–485
- Trabanco T, Perez-Vega E, Campa A, Rubiales D, Ferreira JJ, 2012. Genetic resistance to powdery mildew in common bean. *Euphytica* 186:875–882
- Yaish MWF, Daynet S, Francisco JV, Francisca V, 2006. Genetic mapping of quantitative resistance to race 5 of *Pseudomonas syringae* pv. *Phaseolicola* in common bean. *Euphytica* 152:397–404.
- Zaiter HZ, Coyne DP, Steadman JR, 1989. Inheritance of resistance to a rust isolate in beans. *Ann Rep Bean Improv Coop* 32:126–127.
- Zapata M, Beaver JS, Porch TG, 2011. Dominant gene for common bean resistance to common bacterial blight caused by *Xanthomonas axonopodis* pv. *phaseoli*. *Euphytica* 179:373–382.