IDENTIFYING DRY BEAN GENOTYPES AND GENOMIC REGIONS ASSOCIATED WITH ROOT ROT RESISTANCE WITH EMPHASIS ON \textit{Fusarium solani} \textit{F. sp. Phaseoli}

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DOCTOR OF PHILOSOPHY

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Common bean (*Phaseolus vulgaris* L.) is the most produced legume in the U.S. and worldwide. Fusarium root rot (FRR) is a widespread soil-borne diseases causing up to 86% yield reduction in beans. Large-seeded cultivars are usually susceptible to root rot. Finding FRR resistant genotypes under naturally infected soil and mapping genomic regions involved in its resistance were the main objectives in this research. In addition, halo blight, days to flower, growth habit, plant survival, seed weight, and seed yield were studied. Fusarium root rot and halo blight diseases were highly epidemic during the research period. The objectives were accomplished through two consecutive steps. First, phenotyping a set of genotypes from Andean diversity panel (ADP) under field conditions during three years starting with 310 genotypes in 2013. A Randomized Incomplete Block Design with two replications was used as the experimental design. From three years phenotypic data, ADP462-PI527540B, ADP48-W6_6534, ADP624-Dolly, ADP68-Soya, and ADP438-46_1 genotypes were resistant to FRR and ADP73-Masusu, ADP601-Camelot, ADP636-Montcalm, and ADP511-Canario were susceptible. In addition, ADP84-Kablanketi-defu, ADP55-Kabuku, ADP122-Kranskop, ADP454-INIAP429, and ADP50-Salunde were among the most resistant to halo blight and ADP638-Redhawk, ADP676-CELRK, ADP677-Etna, ADP242-G9013, and ADP269-G13092 were among the most susceptible. Genotypes ADP48-W6_6534, ADP624-Dolly, ADP438-46_1, and VAX3 (check) were resistant to both diseases. These genotypes can be used as parents in the bean breeding programs. Second, for GWAS, 3525 filtered single nucleotide polymorphism (SNP) markers of 246 Andean genotypes were used to find significant (*P*≤0.001) trait-marker associations. After correcting for population structure and relatedness, genomic regions on three chromosomes were associated with five traits. The study provided insights into the genetic architecture for FRR, halo blight, days to flower, growth habit and plant survival. Resistant genotypes can be used in the breeding programs, genomic regions should be validated before using as molecular markers to accelerate the breeding process.
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DEDICATION

To my mom, dad, and Adriana, wherever they are, who taught me how to surmount difficulties and pursue challenges with joy. Nonetheless to my wife Alicia, my sons Alex and Santiago who always are by my side and for whom I do my best.
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LIST OF ABBREVIATIONS

ADP ......................................................... Andean diversity panel
AFLP ....................................................... Amplified fragment length polymorphism
AM ........................................................... Association mapping
ANOVA .................................................... Analysis of variance
DNA ......................................................... Deoxyribonucleic acid
EMMA ...................................................... Efficient mixed linear model association
FRR ......................................................... Fusarium root rot
Fsp .......................................................... *Fusarium solani f. sp. phaseolicola*
GWAS ..................................................... Genome-wide association study
LD ............................................................ Linkage disequilibrium
MAF ......................................................... Minor allele frequency
MAS ......................................................... Marker assisted selection
MM .......................................................... Mixed model
PC ........................................................... Principal component
PCA ......................................................... Principal component analysis
Psp .......................................................... *Pseudomonas syringae pv. phaseolicola*
Pv ............................................................ *Phaseolus vulgaris* L.
QTL .......................................................... Quantitative trait loci
RFLP ....................................................... Restriction fragment length polymorphism
RAPD ....................................................... Random amplified polymorphic DNA
SSR .......................................................... Simple sequence repeat
SNP .......................................................... Single nucleotide polymorphisms
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INTRODUCTION

Recent studies suggest that common bean (*Phaseolus vulgaris* L.) originated in Central America (Bitocchi et al., 2013; 2012) and confirmed the two centers of domestication (Mesoamerican and Andean) previously characterized by Singh et al. (1991) with well-defined races within each gene pool. Common bean is the most important grain legume in America, Africa, and Europe (Akibode and Maredia, 2011). It is cooked and consumed in a range of ways, as dry grain, fresh (threshed manually at physiological maturity), or as tender pods (snap or green beans). Dry bean production region in North Dakota and Minnesota produces more dry beans than any other area in the U.S. (43%). Within this region, a number of different market classes are produced, including pinto, navy, black, small red, great northern, and kidney (Knodel et al. 2016).

There are many foliage and root diseases of beans throughout the world (Miklas et al., 2006) and some occur in ND/MN region. Among foliage disease are White Mold (Knodel et al., 2016), caused by *Sclerotinia sclerotiorum* (Lib.) de Bar] and bacterial blights (Markell and Pasche, 2014), caused by *Xanthomonas axonopodis pv. phaseoli* (Smith) Dye, *Pseudomonas syringae pv. phaseolicola* (Burkholder) Young et al. (Psp), and *Pseudomonas syringae pv. syringae* van Hall. Among root diseases are FRR, caused by *Fusarium solani* (Mart.) f. sp. *phaseoli* (Burkholder) Snyder and Hansen; Fusarium wilt, caused by *F. oxysporum* Schlech. f. sp. *phaseoli* Kendrick & Snyder] (Fsp), and Rizoctonia root rot, caused by *Rhizoctonia solani* Kuhn [(telemorph *Thanatephorus cucumeris* (Frank)) Dark]. Fusarium root rot is major yield-limiting root disease of dry bean in this region (Estevez de Jensen, 2000, Bilgi et al., 2008).

Few sources of partial resistance to FRR rot are available within *P. vulgaris* species. Most commercial cultivars grown in Minnesota are susceptible to FRR. Cultivars within the red kidney bean market class have been suffering more losses due to FRR than some of the other market classes grown in the region (Bilgi, 2008) due to Andean origin. Cultivars and landraces from Andean gene pool are more susceptible than from Mesoamerican gene pool (Beebe el al., 1981).

Searching for useful germplasm for a breeding program is indispensable for sustained crop improvement. Improving breeding strategies and efficiencies on a continuous basis is also equally important. Thus, plant breeders typically look for germplasm that has favorable alleles that are lacking in
their own breeding programs. Breeders usually introduce new genes using conventional and new techniques and technologies to improve the breeding process.

It is a longstanding goal to identify genotypes or germplasm that can be used to improve disease resistance in Andean cultivars. The cultivars derived from the Nueva Granada race, such as Montcalm (http://bean.css.msu.edu/100Years.cfm), Redhawk (Kelly et al., 1998a), and others, are extensively used in Minnesota but are very susceptible to root pathogens.

Traditionally, traits have been mapped to chromosomes through bi-parental population use. More recently, association mapping (AM) has been used to map quantitative trait loci (QTL) in naturally collected genotypes without parent-derived off-springs. Association mapping takes advantage of linkage disequilibrium (LD) to detect non-random marker-marker or trait-marker associations. Genome-wide association study is a variant of AM to detect trait-marker association utilizing phenotypic and genotypic data. The current study utilizes the GWAS approach to identify FRR resistant loci across a set of germplasm from Andean Diversity Panel (ADP). In addition to FRR, days to flower, determinacy growth habit, halo blight, plant survival, seed weight, and seed yield were studied.

The BARCBean 6K_3 SNP chip (Song et al., 2015) is utilized to localize markers in populations of common bean. Therefore, it could be used in finding significant markers associated with FRR and identifying potential candidate genes that control this trait. Identification of highly diagnostic markers within the Andean gene pool (mainly Nueva Granada race) could provide an opportunity to develop improved cultivars in a more efficient manner when incorporated into the breeding program. This will help the breeders in enhancement of genetic diversity, whereas maintaining commercially desired phenotypic characteristics of common bean.

Andean diversity panel field experiments were conducted at Perham, MN and screened mainly for FRR, the prevalent root disease in the area. An initial collection of 310 genotypes from the Andean diversity panel was phenotyped to identify genomic regions associated with it and other traits through GWAS.
LITERATURE REVIEW

Common bean is an important cash crop with high nutritional value and is produced on about 693,000 ha in the U.S. (USDA-NASS, 2015). The average harvested area in the U.S. was 605,000 ha during 2009-2013 period. The three leading commercial classes produced during this period were: Pinto (39%), navy (15%), and black (13%). Moreover, red kidney (6%), great northern (5%), and others (20%, including garbanzo) were produced in lower amounts. North Dakota and Minnesota produced 517,000 (43%) out of total 1.2 million metric tons leading bean production is the U.S. (Zahniser and Farah, 2014).

The region spanning across North Dakota and Minnesota, is the largest dry bean producing area in the U.S. The most important commercial classes are pinto, navy, and black bean in North Dakota, whereas kidney, navy, black, pinto and are in Minnesota. In addition, great northern and small red classes are grown on limited areas (Knodel et al., 2016). The growth type of the most modern cultivars is upright (determinate and indeterminate bush) with a life cycle 85 to 105 days from planting to harvest date. The seed yield average is 2100 kg ha\(^{-1}\) (Zahniser and Farah, 2014).

There are abiotic (excess of rainfall, drought) and biotic constraints (pathogens, weeds) present in the ND/MN region. During the 2014 growing season, excess of rainfall was ranked as the first production problem in the region and diseases as the second. White mold (Knodel et al., 2016) was the main foliar disease followed by bacterial blights (Markell and Pasche, 2014), however, FRR was the most significant problem in Minnesota (Estevez de Jensen, 2000).

**Fusarium root rot**

Fusarium root rot is one of the most common dry bean root diseases distributed worldwide. Under stress conditions, it can reduce bean yield up to 86% (Abawi and Pastor-Corrales, 1990). Large-seeded kidney beans cultivated are most affected (Beebe et al., 1981). This pathogen has been consistently isolated from areas of intensive bean cropping.

Initial symptoms appear as longitudinal narrow, reddish lesions on the hypocotyl and primary roots about one or two weeks after seedling emergence. As infection progresses, lesions become numerous, coalesce, and the entire underground stem and root systems may become covered with reddish brown external and internal lesions. There are no pronounced wilting symptoms although severely infected plants are stunted, chlorotic, and exhibit premature defoliation (Abawi, 1989).
Most isolates of *F. solani* produce appressed mycelia growth (pseudopinnotes) on artificial agar media. Fungal colonies are usually blue to blue-green, but occasionally are white to buff in color. Three types of asexually spores are produced by all isolates: microconidia, macroconidia, and chlamydospores. Microconidia are usually produced on simple short conidiophores. Macroconidia are sickle shaped, multisepate and usually produced on sporodochia. The dark and thick chlamydospores are produced abundantly on or in infected host tissues and are long-term survival structures.

The pathogen survives in soil or in the infected decaying tissue primarily as thick-walled resting spores called chlamydospores. These overwintering spores germinate readily in response to plant root exudates and infect plants through stomata and wounds (Abawi, 1989). The pathogen is disseminated into the bean field by multiple means such as movement of infected soil, infected host tissues, colonized debris, irrigation water, and contaminated seed. Once into the field, the pathogen becomes uniformly distributed at high densities after two or three cycles of common bean cropping.

Fusarium root rot reaction is a complex inherited trait controlled by many different genes with low heritability, consequently difficult to manipulate by cross breeding (Mukankusi et al., 2011). Limited attempts to transfer resistant genes found in Middle American gene pool into Andean bean cultivars have been made. Genetic resistance has been identified in Mesoamerican common bean varieties such as PI 203958 (N203) (Boomstra and Bliss, 1977); Puebla 152, Porrillo Sintetico, ICA-Pijao (Beebe et al., 1981), T-39, VAX 3, Rojo chiquito (Bilgi et al., 2008), and G40001 (tepary bean, P. acutifolius A. Gray) (Mejia-Jimenez et al., 1994). However, it is still a challenge to find Andean germplasm with high levels of resistance since the genetic base is narrow.

**Phenotyping**

Collection of high-quality phenotypic data is essential in genome-wide association studies. Newly discovered candidate genes in mapping studies can only be tested if we have existing robust and accurate phenotypic data, which is usually collected over years in multiple locations (Flint-Garcia et al., 2005). To increase the mapping power, when screening large number of genotypes, it is necessary to consider efficient field designs such as incomplete block designs (e.g., α-lattice), and appropriate statistical methods (Eskridge, 2003).
Fusarium root rot and halo blight are the two main biotic constraints at Perham, MN under field conditions. Although screening for FRR was the main objective of the project, halo blight and other agronomic traits of economic importance were also studied.

Halo blight was epidemic during the three consecutive years as had been reported by Markell and Pasche (2014), and Vasquez et al. (2015b). Susceptible genotypes from the ADP were severely attacked under field conditions. The high winds and rains created wounds in the plant tissue, providing an entry for this pathogen. Early symptoms begin as small greasy spots on plant tissue, eventually surrounded by a yellow halo. Infection is favored by plant wounding and rainfall. Optimal temperatures range from the high 20 °C to low 15 °C (Markell and Pasche, 2014). Halo blight can reduce seed yield up to 45%. Nine races have been identified. Resistant cultivars, among others, are Chase (under field conditions), US14, CAL143 and PI150414. Early inheritance studies observed both monogenic and polygenic resistance (Singh and Schwartz, 2010). Monogenic resistance can be dominant or recessive (Duncan et al., 2014). Resistant genes have been named Pse-1, Pse-2, Pse-3, Pse-4, and Pse5. In addition, Miklas et al. (2014) found another major resistant gene named Pse-6 conferring specific resistance to Races 1, 5, 7, and 9 on Pv04 by using 76 F9–derived lines from cross BelNeb-RR-1/A55. On the other hand, Duncan et al. (2014) reported another cultivar, US14HBR6, with specific recessive resistance to Race 6.

Genotyping

Traditional family-based linkage mapping uses bi-parental mapping populations like F2, doubled haploids, recombinant inbred lines, near isogenic lines, and inbred backcross lines. Mostly RAPD markers along with composite interval mapping approach have been used to localize markers associated with FRR (Hagerty et al., 2015). Traditional mapping has also been called QTL mapping. Navarro et al. (2008) found polymorphism for root rot complex employing RAPDs, cosegregates S18.1500 and AD9.950 on linkage group Pv06 in recombinant inbred lines derived from cross Eagle/Puebla 152. The marker AD9.950 was genotyped in root rot resistant Puebla 152 accession and S18.1500 was genotyped in the susceptible cultivar Eagle. Contrastingly, Roman-Aviles and Kelly (2005) found RAPD markers associated with FRR resistance on linkage groups Pv02 and Pv05 of the integrated bean map. These authors used two inbred backcross lines derived from Red Hawk//Negro San Luis and C97407//Negro San Luis. Redhawk and C97407 are susceptible recurrent parents from Andean origin, whereas Negro San Luis is
resistant non-recurrent parent from Mesoamerican origin. These results are similar to findings made from Schneider et al. (2001). These authors found, using RAPDs, a marker P7 associated with FRR on linkage group Pv02 using F4-derived recombinant inbred lines from a cross made among susceptible Montcalm and Isles with resistant FR266. Bi-parental population approach has some advantages, however, Mamidi et al. (2011) concluded that the loci discovered are often specific to those populations. In addition, Al-Maskri et al. (2012) stated that, bi-parental approach is very costly, has low resolution due to lower number of recombination events, and evaluates few alleles simultaneously in a relatively longer time scale.

Song et al. (2015) developed a SNP BARCBean6K_3 Beadchip. The BeadChip captured polymorphism of 5352 SNP markers in 502 Phaseolus genotypes, approximately 3 SNPs/kb. All SNPs are distributed across the 11 chromosomes of cultivars and landraces. The BeadChip is a useful tool for genetics and genomics research and it is widely used by common bean breeders and geneticists in the U.S. and abroad.

The availability of SNP BARCBean6K_3 BeadChip has created an opportunity to dissect FRR and other agronomical, physiological and nutritional traits, with enhanced resolution because of the smaller LD blocks in an association panel than in bi-parental mapping populations (Myles et al., 2009). The smaller LD blocks result from historical diverse panel, as opposed to bi-parental mapping populations where the LD blocks are longer because short-lived recombination resulting from the few generation-recombinations (Zhu et al., 2008).

Single nucleotide polymorphic markers (SNPs) are currently known as valuable markers for genotyping, due to their abundance, stability, and simplicity (Shi et al., 2011). SNPs represent most frequent polymorphisms (Cho et al., 1999). SNP markers in common bean reflect dual domestication events and inter gene pool hybridization in both gene pools. SNPs allowed the identification of three Andean and three Mesoamerican clusters corresponding to races (Cortes et al., 2011; Schmutz et al., 2014). Due to greater polymorphism and race structure, Mesoamerican gene pool shows higher genetic diversity with SNPs than the Andean (Cortes, 2013; Cichy et al., 2015).

Using SNP markers to map FRR resistance in a snap bean RIL population, Hagerty et al. (2015) found QTLs FRR3.1 on chromosome Pv03 and FRR7.1 on chromosome Pv07 highly associated with
FRR resistance in RR138 F6-derived population from RR6950/OSU5446 cross. RR6950 is highly FRR resistant, small seeded black indeterminate type IIIA accession of unknown origin, whereas OSU5446 is a highly FRR susceptible determinate type I Blue Lake 4-sieve breeding line. Previously, Bello et al. (2014), using an F5-derived recombinant inbred population (RR138, n=168) from the same cross, found a reliable association between FRR trait and the QTL genomic region on chromosomes Pv01, Pv04, Pv09, and Pv11. It should be pointed out that the population was evaluated at the F6 generation in the field, whereas the F5 generation was under greenhouse conditions.

Genome-wide association, identify loci by examining the significant trait-marker associations that can be attributed to the strength of LD between markers and functional polymorphisms across a set of diverse germplasm. In association mapping, a natural population is surveyed to determine trait-marker associations using LD (Flint-Garcia et al., 2005). Gupta et al. (2005) make a difference among AM and LD. Linkage disequilibrium refers to non-random association between: a) two markers, b) two genes, or c) between a gene and a marker locus. Association mapping refers to significant association of molecular markers with a phenotypic trait, usually performed through GWAS. Association mapping takes advantage of LD to find trait-marker associations. Association mapping is the most effective approach to utilize natural variation in the form of ex situ conserved crop genetic resources to discover trait-marker association (Al-Maskri et al., 2012).

The general approach of GWAS includes six steps. (i) a collection of diverse genotypes that may include, landraces, elite cultivars, wild relatives and exotic accessions, (ii) a comprehensive and precise phenotyping is performed over the traits of interest in multiple repeats and years/environments, (iii) the genotypes are then scanned with suitable molecular markers (AFLP, SSRs, SNPs), (iv) population structure and kinship are determined to avoid false positives followed by (v) quantification of LD extend using different statistics like $D$, $D'$, or $r^2$. Finally, (vi) genotypic and phenotyping data are correlated using appropriate statistical software allowing tagging of molecular marker positioned in close proximity of gene(s) underlying a specific trait (Al-Maskri et al., 2012).

Finding markers associated with root rot complex with emphasis in FRR in common bean of Andean diversity gene pool will facilitate breeding through identification of outstanding resistant parents. GWAS method is used to find the differences in DNA (genetic variation) that explain the natural
phenotypic variation. Advances in high-throughput technologies have markedly reduced the cost per data point of molecular markers, particularly single nucleotide polymorphism (Zhu et al., 2008). GWAS links phenotypes to genotypes through adequate regression models (Yu et al., 2006). Association detection depends on genetic architecture, accurate phenotypic evaluation, and genotyping (Balding, 2006).

GWAS is a practical approach for common bean wild, domesticated and advanced populations (Chiti, 2014). It does not need any previous information on candidate genes and can test large number of markers associated with complex traits. Due to the complex population structure present in common bean and lack of information about candidate genes associated with agronomic traits, GWAS is the best approach that could be applied to study agronomic traits. The population structure and relatedness that exist in bean can lead to identify false positives.

Yu et al. (2006) and Zhang et al. (2010) developed mixed linear regression models to control population structure and relatedness. These models are flexible to deal with big amounts of data available from phenotypic family-based or population-based genotypes. Mixed linear models represent methods of choice that deals with unbalanced data across multiple trials. It shows reliable inference through the explicit modeling of correlations induced by genetic and environmental causes. Genome association and prediction integrated tool (GAPIT) package integrates principal component analysis (PCA), efficient mixed model analysis (EMMA), and mixed model (MM=PCA+EMMA) and other powerful, accurate, and computationally efficient regression models into a single R statistical package (Lipka et al., 2012). Kamfwa et al. (2015) and Cichy et al. (2015) found significant SNP markers associated with days to flower and determinacy growth habit, respectively. On the other hand, Moghaddam (2015) found SNP markers associated with seed size through GWAS.

The objectives were: 1) Identify dry bean genotypes with resistance to root rot complex in the field. 2) Find out genomic regions associated with genetic resistance to root rot using GWAS.
MATERIALS AND METHODS

Plant Material

A group of 310 genotypes was initially assembled into a panel to facilitate FRR screening. These genotypes are a subset of the ADP (Cichy et al., 2015). They were screened during the 2013 cropping season at Perham, MN, where all of them germinated, 302 flowered and 280 completed the production cycle. Therefore, FRR and halo blight were evaluated in 310 genotypes, days to flower in 302 genotypes, and plant survival, seed weight, and seed yield in 280 genotypes. During the 2014 season, 265 genotypes were selected from the previous year, based mostly on seed availability and adaptation, and planted again at Perham, MN. The 265 genotypes were split into two groups based on the results obtained the previous year: early flowering group (144 genotypes) and late flowering group (121 in genotypes). To confirm previous data, in each early and late flowering groups, 22 low scored genotypes and 22 high scored genotypes were selected, based on the FRR response and then screened again in the same location in 2015 season.

During all three seasons, five checks were used: VAX3 (Singh et al., 2001) as resistant FRR check; GTS106 (Gen-Tec Seed Co) as FRR susceptible check, Dynasty (Kuropatwa, 2013), Cabernet (Seminis/Monsanto), and Talon (Osorno et al., 2016) as FRR intermediate checks. Based on least square means (LSmeans) across the three years, a sub panel of 92 genotypes was assembled for a combined analysis of variance (ANOVA), including the five checks. Likewise, based on two years LSmeans, a sub panel of 246 genotypes was assembled for GWAS. The checks were excluded from GWAS because they have not been genotyped yet.

The 246 sub panel for GWAS included 110 landraces from Africa, 15 accessions from the CIAT Germplasm Bank, 6 accessions from the U.S. National Plant Germplasm Collection, 14 lines from Puerto Rico, one landrace from Ecuador, 15 U.S. accessions from East Africa, 8 landraces from Angola, and 77 lines and cultivars from U.S. bean breeding programs (Cychy et al., 201; USDA-FtF, 2016)

Statistical procedures

Incomplete Block Designs were used throughout the three years period. All experiments were analyzed as one-way for ANOVA using PROC MIXED and PROC GLM procedures. Replications were considered as random and genotypes as fixed effects. Fusarium root rot, halo blight, days to flower, plant
survival, seed weight, and seed yield were used in ANOVA, whereas growth habit was included in the simple linear correlation analysis among the phenotypical traits, since growth habit is a discrete trait. ANOVA tables using PROC GLM are reported in as Appendix Tables. During the 2013 season, the 310 genotypes, including five) checks were planted in 32 x 10 alpha design with two replications. Bean seeds were planted in two-row plots, 2.13 m long, 1.52 m wide (3.25 m² net area). In each plot, 96 seeds (230,769 seeds ha⁻¹) were planted. Higher seed density was sowed to assure seedling emergence in order to increase seed for the following years.

During the 2014 season, 144 genotypes from the early flowering group were planted in 12 x 12 square alpha lattice and 121 genotypes from the late flowering group were planted in 11 x 11 square alpha lattice. In both trials similar five checks were included. In the 2015 season, both the 49 early and 49 from late flowering groups were planted in 7 x 7 square alpha lattice, including five checks in both trials. The experimental plots in 2014 and 2015 were 3.66 m long, 1.52 m wide (5.57 m²). In each plot 75 seeds (172,352 seeds ha⁻¹) were planted.

Individual ANOVA for each year were analyzed considering blocks and replications as random effects and genotypes as fixed effects. From the ANOVA table, statistical differences were considered at \( P \leq 0.05 \) level of significance. Coefficient of variation (CV%) was calculated using PROC GLM procedure.

Before doing the combined ANOVA and Pearson linear correlations, the homogeneity of variances test called “10x rule” was carried out. To do so, the highest residual value from the PROC MIXED covariance parameters was divided by the lowest residual value for each trait after computing from the five individual trials. If the difference was less than 10-fold, trials were considered homogeneous and therefore, combined analysis was performed (Patterson and Silvey, 1980).

Based on the three years LSmeans, a panel of 92 common genotypes was selected for a combined ANOVA. Years were considered as random effects and genotypes as fixed effects. Moreover, the relationship among traits was determined by Pearson’s simple correlation analysis (level of probability 0.001, 0.01, and 0.05) computed from Lsmeans across years when variances were homogenous using PROC CORR. Correlations \( (r) > 0.5 \) were considered strong, correlation \( (r) < 0.49 \) were considered weak. For GWAS, based on the two years LSmeans, a panel of 246 common genotypes was selected. An ANOVA was computed considering years as random and genotypes as fixed effects.
Location, soil characteristics, and phenotyping

The study was carried out at Perham, MN (Lat: 46.45°N; Lon: 95.21°W; Elev.: 416 m), during three consecutive years 2013, 2014, and 2015 in the field. Soil samples were taken every year from the 0 to 15 cm top layer and sent to the NDSU Soil Testing Laboratory for mechanical and chemical analyses, and Agvise Laboratories, Northwood, ND, for chemical analysis (Tables A14, A15, A16). In average, the soil contained 71% sand, 22% silt and 7% being classified as sandy-loam [(name=Sandberg; family=Entic Haplydolls; order=Mollisol (USDA-NRCS, 2016)]. According to the chemical analysis, the pH ranged from 6.2 to 7.2, organic matter content from 1.6 to 2.2, nitrate-nitrogen from 28 to 38 ppm, phosphorus 28 to 50 ppm (Olsen), potassium from 280 to 300 ppm from a soil layer 0 to 15 cm depth.

The Central Minnesota area, where Perham is located, is a leading kidney bean producer in Minnesota (Osorno et al., 2016). This location is used by the NDSU Dry Bean Breeding Program to screen mainly large-seeded breeding lines and cultivars for disease resistance, adaptation, and agronomic performance.

Since FRR phenotyping was the main objective, seeds were neither treated (with the exception of 2013) nor broadcast nitrogen was applied during the growing seasons. Additional cultural practices, such as pre-planted fertilization and irrigation were done following the farmer's common practices, weeds were eliminated manually. Previous rotational crops planted by the farmer were corn (Zea mays L.) in 2012, wheat (Triticum aestivum L.) in 2013, and potato (Solanum tuberosum L.) in 2014.

Infected plant samples were collected every year and sent to NDSU Plant Pathology Laboratory. Using Koch’s postulates, the Laboratory identified F. solani f. sp. phaseoli associated with root rot in the Andean panel. No other root pathogen was found associated with it across three years.

Between days to flower (R6) and pod filling stage (R8), 4 plants from each plot were carefully removed with a shovel, cleaned of debris, and evaluated for FRR using the 1-9 scale (1 to 3= resistant, 4 to 6 intermediate, 7 to 9 susceptible) (CIAT, 1987). Description for each score is in Table 1.
Table 1. Description of visual disease rating scale used for FRR screening (CIAT 1987).

<table>
<thead>
<tr>
<th>Score</th>
<th>Phenotypic description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>No visible symptoms</td>
</tr>
<tr>
<td>3</td>
<td>Light discoloration either without necrotic lesions with approximately 10% of the hypocotyl and root tissues covered with lesions.</td>
</tr>
<tr>
<td>5</td>
<td>Approximately 25% of the hypocotyl and root tissues covered with lesions but tissues remain firm with deterioration of the root system. Heavy discoloration system may be evident.</td>
</tr>
<tr>
<td>7</td>
<td>Approximately 50% of the hypocotyl and root tissues covered with lesions combined with considerable softening, rooting, and reduction of the root system.</td>
</tr>
<tr>
<td>9</td>
<td>Approximately 75% or more of the hypocotyl and root tissues affected with advanced stages of rotting combined with a severe reduction of the root system.</td>
</tr>
</tbody>
</table>

Halo blight was rated using the same 1 to 9 CIAT (1987) scale between flowering (R6) and pod formation stage (R7). Description for each score is in Table 2. Inoculum from infected plants was isolated by the NDSU Plant Pathology Laboratory and race-typed using a set of eight differentials. Race 6 has been identified attacking beans in MN/ND area and to the Andean panel (K. Ghising, personal communication, 2016).

In addition to these diseases, the following agronomic traits were measured: days to flower was rated since planting date up to 50% of the plants in a plot have at least one opened flower (CIAT, 1987); growth habit 1=determinate with the main stem ending in a terminal flower bud, and 2=indeterminate, where the flower bud was not terminal (NDSU, 2013); percentage of plant survival was calculated dividing number of harvested plants by number of planted seed then multiplied by hundred; 100-seed weight, seeds were chosen randomly, weighted in grams with approximately 14% humidity; and seed yield in kg pet plot and transformed to kg ha⁻¹.
Table 2. Description of visual disease rating scale used for halo blight screening (CIAT 1987).

<table>
<thead>
<tr>
<th>Score</th>
<th>Phenotypic description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>No visible symptoms.</td>
</tr>
<tr>
<td>3</td>
<td>Approximately 2% of the leaf or pod surface area covered with round lesions. Very slight systemic chlorosis may be evident.</td>
</tr>
<tr>
<td>5</td>
<td>Approximately 5% of the leaf or pod surface area covered with round lesions of about 5 mm in diameter. Limited system chlorosis may be present on growing points.</td>
</tr>
<tr>
<td>7</td>
<td>Approximately 10% of the leaf tissues affected either by lesions or by resulting chlorosis. Limited leaf distortion is present and the pods generally show a bacterial exudation on coalescing lesions that can be about 10 mm in diameter.</td>
</tr>
<tr>
<td>9</td>
<td>Twenty-five percent or more of the leaf tissues affected by lesions and chlorosis. Severe leaf distortion and coalescing lesions covering large areas on pods cause deformation and empty pods.</td>
</tr>
</tbody>
</table>

Genotyping

A set of 5352 SNPs were obtained from the Illumina iSelect 6K Gene Chip (BARCBean6K_3; Song et al., 2015). Based on the phenotypic field data and genotypic data, 246 accessions were used for genotyping. After filtering for markers with more than 50% SNPs missing, missing data was imputed using fastPHASE 1.3 (Scheet and Stephens, 2006) and 5188 SNPs remained. Finally, the panel was filtered for minor allele frequency (5%) and monomorphic markers, resulting in 3525 SNPs for GWAS.

Population structure and trait-SNP marker association test

GWAS was done using the GAPIT package in R (Lipka et al. 2012). Multiple statistical models were tested: Naïve, PCA, MM and EMMA (Table 3). Principal component analysis was used to control for population structure; identity-by-state kinship matrix [EMMA, (Kang et al. 2008)] was used to control for family relatedness. The purpose of these models is to minimize the number of false positives which could be generated in structured populations by using genotypic information of all the markers in the genome. EMMA model (Kang et al. 2008) that controlled for both population structure and family relatedness was chosen because it most effectively reduced the number of false positives. For each trait, significant SNP
markers ($p = 1 \times 10^{-4}$) were selected from the selected best models. Manhattan plots were constructed by GAPIT package using $-\log_{10}$ of $P$-values against chromosome location to represent position of these markers.

Table 3. Statistical models used to test for trait-marker associations through genome association and prediction integrated tool (GAPIT) package in R (Mamidi et al., 2011).

<table>
<thead>
<tr>
<th>Model</th>
<th>Linear regression equation</th>
<th>Information captured in the model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Naïve</td>
<td>$y = X\alpha + \epsilon^\dagger$</td>
<td>$y$ is related to $X$, without correction for structure</td>
</tr>
<tr>
<td>PCA</td>
<td>$y = X\alpha + P\beta + \epsilon$</td>
<td>$y$ is related to $X$, with correction for structure</td>
</tr>
<tr>
<td>EMMA</td>
<td>$y = X\alpha + Ku + \epsilon$</td>
<td>$y$ is related to $X$, with correction for kinship</td>
</tr>
<tr>
<td>MM</td>
<td>$y = X\alpha + P\beta + Ku + \epsilon$</td>
<td>$y$ is related to $X$, with correction structure and kinship</td>
</tr>
</tbody>
</table>

$^\dagger y$ is phenotype, $X$ is the fixed effect of the SNP; $P$ is the fixed effect of the structure (from PCA matrix); $K$ is the random effect of kinship; and $\epsilon$ is the error term.
RESULTS AND DISCUSSION

Phenotypic analysis by year and across years

Fusarium root rot

In 2013, the genotypic effect was not significant (Table 4). FRR severity averaged 4, ranging from 1 to 9, with a standard deviation of 1. In 2014, the genotypic effect was significant \((P<0.01)\) for early genotypes but not significant for late genotypes (Table 4). FRR severity averaged 5, ranging from 1 to 9, with a standard deviation of 2 in both trials. From the early genotypes VAX3 (check) ranked first with LSmeans of 2 (resistant) and GTS106 ranked last with 8 (susceptible) (Table A9).

In 2015, the genotypic effect for the early and late genotypes was significant \((P<0.01, P<0.05,\) respectively) (Table 4). FRR averaged 6, ranging from 1 to 9, and the standard deviation was 2 in both trials. From early genotypes, ADP438-46_1 ranked first with LSmeans of 2 (resistant), and ADP73-Masusu ranked last with 8 (susceptible) (Table A11). From the late genotypes, VAX3 (check) ranked first with LSmeans of 2 (resistant), and GTS104 ranked last with 8 (susceptible).

All trials were homogeneous for FRR, the difference was less than 10-fold and therefore, combined ANOVA and Pearson’s simple linear correlation was performed. Genotypic effect was significant \((P<0.01)\) in the combined ANOVA (Table 4). The FRR averaged 5, ranging from 2 to 8, and the standard deviation was 2. Genotypes ADP462-I527540B, ADP48-W6_6534, ADP624-Dolly, and ADP68-Soya were the top resistant and GTS106 was the most susceptible (Table 5). The checks, VAX3 confirmed its resistance, GTS106 its susceptibility, Dynasty, Cabernet, and Talon confirmed their intermediate resistance to FRR (Table A13).

The population average for FRR was 4 in 2013, 5 in 2014, and 6 in 2015 (Table 6). The yearly increase observed could be due to infected seed planted each year. \textit{F. solani} is a seed-borne pathogen transported on the seed coat (Mahmoud et al., 2013). Seed planted in 2014 and 2015 was harvested at Perham, MN, in Fusarium infected fields.
Table 4. Population mean of five individual trials and combined analysis, range, standard deviation (SD), and P-value for six traits measured in five from Andean diversity panel grown at Perham, MN, from 2013 to 2015.

<table>
<thead>
<tr>
<th>Year</th>
<th>Genotype No.</th>
<th>Parameter (Fusarium root rot 1-9, Halo blight 1-9, Days to flower No., Plant survival %, 100-seed weight g, Seed yield kg ha⁻¹)</th>
<th>Year</th>
<th>Genotype No.</th>
<th>Parameter (Fusarium root rot 1-9, Halo blight 1-9, Days to flower No., Plant survival %, 100-seed weight g, Seed yield kg ha⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2013</td>
<td>310†</td>
<td>Mean 4 4 47 30 44 1407 Min 1 1 36 4 20 62 Max 9 9 76 59 71 3960 SD 1 2 7 11 11 818 P-value ns ** ** ** ** **</td>
<td>2014-early</td>
<td>144</td>
<td>Mean 5 6 41 70 43 974 Min 1 1 35 23 20 68 Max 9 9 48 99 64 3300 SD 2 2 4 17 9 543 P-value ** ** ** ** **</td>
</tr>
<tr>
<td>2014-late</td>
<td>121</td>
<td>Mean 5 5 49 55 39 1093 Min 1 1 42 22 23 79 Max 9 9 61 96 58 2880 SD 2 2 3 14 7 617 P-value ns ** ** ** ** **</td>
<td>2015-early</td>
<td>49</td>
<td>Mean 6 4 43 61 40 1257 Min 1 1 36 17 22 140 Max 9 9 52 90 58 2917 SD 2 2 3 13 40 537 P-value ** ** ** ns ** **</td>
</tr>
<tr>
<td>2015-late</td>
<td>49</td>
<td>Mean 6 3 48 60 32 813 Min 1 1 42 38 18 115 Max 9 9 60 91 57 3029 SD 2 2 4 11 8 522 P-value * ** ** ** ** **</td>
<td>Combined</td>
<td>92</td>
<td>Mean 5 4 45 52 42 1214 Min 2 1 36 7 20 206 Max 8 9 64 98 69 3096 SD 2 2 5 20 10 540 P-value ** ** ** ** **</td>
</tr>
</tbody>
</table>

ns=not significant; *Significant at the 0.05 probability level; **Significant at the 0.01 probability level

†310 genotypes for FRR and halo blight; 302 for days to flower; 280 for plant survival, 100-seed weight and seed yield

**Halo blight**

Along with FRR, halo blight disease was epidemic at Perham, MN during all three years and significantly affected the Andean panel during the study period. The genotypic effect was significant
Table 5. Top five and the button genotypes for six traits from 92 combined analysis from ADP grown at Perham, MN, from 2013 to 2015.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Fusarium root rot</th>
<th>Halo blight</th>
<th>Days to flower</th>
<th>Plant survival</th>
<th>100-seed weight</th>
<th>Seed yield kg ha⁻¹</th>
<th>Growth habit†</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1-9</td>
<td>1-9</td>
<td>No.</td>
<td>%</td>
<td></td>
<td></td>
<td>1-2</td>
</tr>
<tr>
<td>VAX3-resistant check</td>
<td>2</td>
<td>2</td>
<td>48</td>
<td>59</td>
<td>27</td>
<td>2450</td>
<td>2</td>
</tr>
<tr>
<td>ADP462-PI527540B</td>
<td>2</td>
<td>4</td>
<td>45</td>
<td>57</td>
<td>27</td>
<td>1201</td>
<td>2</td>
</tr>
<tr>
<td>ADP48-W6_6534</td>
<td>3</td>
<td>3</td>
<td>48</td>
<td>58</td>
<td>26</td>
<td>1201</td>
<td>2</td>
</tr>
<tr>
<td>ADP624-Dolly</td>
<td>3</td>
<td>3</td>
<td>42</td>
<td>50</td>
<td>58</td>
<td>2298</td>
<td>1</td>
</tr>
<tr>
<td>ADP68-Soya</td>
<td>3</td>
<td>4</td>
<td>49</td>
<td>52</td>
<td>34</td>
<td>1220</td>
<td>2</td>
</tr>
<tr>
<td>GTS104-susceptible check</td>
<td>7</td>
<td>5</td>
<td>44</td>
<td>45</td>
<td>49</td>
<td>1241</td>
<td>1</td>
</tr>
<tr>
<td>LSD</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VAX3</td>
<td>2</td>
<td>2</td>
<td>48</td>
<td>59</td>
<td>27</td>
<td>2450</td>
<td>2</td>
</tr>
<tr>
<td>ADP84-Kablanketi_ndefu</td>
<td>4</td>
<td>2</td>
<td>52</td>
<td>51</td>
<td>32</td>
<td>1185</td>
<td>2</td>
</tr>
<tr>
<td>ADP454-INIAP429</td>
<td>4</td>
<td>2</td>
<td>58</td>
<td>53</td>
<td>38</td>
<td>1694</td>
<td>2</td>
</tr>
<tr>
<td>ADP55-Kabuku</td>
<td>4</td>
<td>2</td>
<td>48</td>
<td>52</td>
<td>33</td>
<td>1493</td>
<td>2</td>
</tr>
<tr>
<td>ADP122-Kranskop</td>
<td>4</td>
<td>2</td>
<td>52</td>
<td>48</td>
<td>39</td>
<td>1093</td>
<td>2</td>
</tr>
<tr>
<td>ADP242-G9013</td>
<td>4</td>
<td>8</td>
<td>38</td>
<td>77</td>
<td>49</td>
<td>1735</td>
<td>1</td>
</tr>
<tr>
<td>LSD</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ADP676-CELRK</td>
<td>6</td>
<td>7</td>
<td>37</td>
<td>57</td>
<td>50</td>
<td>862</td>
<td>1</td>
</tr>
<tr>
<td>ADP242-G9013</td>
<td>4</td>
<td>8</td>
<td>38</td>
<td>77</td>
<td>49</td>
<td>1735</td>
<td>1</td>
</tr>
<tr>
<td>ADP644-FoxFire</td>
<td>5</td>
<td>4</td>
<td>38</td>
<td>67</td>
<td>48</td>
<td>1650</td>
<td>1</td>
</tr>
<tr>
<td>ADP5-Kabuku</td>
<td>5</td>
<td>4</td>
<td>38</td>
<td>59</td>
<td>41</td>
<td>1392</td>
<td>1</td>
</tr>
<tr>
<td>ADP648-RedKloud</td>
<td>4</td>
<td>5</td>
<td>38</td>
<td>65</td>
<td>49</td>
<td>1686</td>
<td>1</td>
</tr>
<tr>
<td>ADP621-JaloEEP558</td>
<td>4</td>
<td>3</td>
<td>58</td>
<td>57</td>
<td>30</td>
<td>715</td>
<td>2</td>
</tr>
<tr>
<td>LSD</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ADP242-G9013</td>
<td>4</td>
<td>8</td>
<td>38</td>
<td>77</td>
<td>49</td>
<td>1735</td>
<td>1</td>
</tr>
<tr>
<td>ADP172</td>
<td>4</td>
<td>3</td>
<td>41</td>
<td>69</td>
<td>26</td>
<td>2038</td>
<td>2</td>
</tr>
<tr>
<td>ADP644-FoxFire</td>
<td>5</td>
<td>4</td>
<td>38</td>
<td>67</td>
<td>48</td>
<td>1650</td>
<td>1</td>
</tr>
<tr>
<td>ADP648-RedKloud</td>
<td>4</td>
<td>5</td>
<td>38</td>
<td>65</td>
<td>49</td>
<td>1686</td>
<td>1</td>
</tr>
<tr>
<td>ADP680-Clouseau</td>
<td>4</td>
<td>6</td>
<td>40</td>
<td>63</td>
<td>59</td>
<td>1675</td>
<td>1</td>
</tr>
<tr>
<td>ADP646-Myasi</td>
<td>5</td>
<td>5</td>
<td>42</td>
<td>27</td>
<td>32</td>
<td>521</td>
<td>1</td>
</tr>
<tr>
<td>LSD</td>
<td>18</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 5. Top five and one last genotypes for six traits from 92 combined analysis from ADP grown at Perham, MN, from 2013 to 2015 (continued).

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Fusarium root rot 1-9</th>
<th>Halo blight 1-9</th>
<th>Days to flower No.</th>
<th>Plant survival %</th>
<th>100-seed weight</th>
<th>Seed yield kg ha(^{-1})</th>
<th>Growth habit 1-2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seed weight</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ADP649-Kamiakin</td>
<td>5</td>
<td>3</td>
<td>43</td>
<td>61</td>
<td>59</td>
<td>2091</td>
<td>1</td>
</tr>
<tr>
<td>ADP680-Clouseau</td>
<td>4</td>
<td>6</td>
<td>40</td>
<td>63</td>
<td>59</td>
<td>1675</td>
<td>1</td>
</tr>
<tr>
<td>ADP616-OAC_Lyric</td>
<td>6</td>
<td>6</td>
<td>38</td>
<td>57</td>
<td>58</td>
<td>1025</td>
<td>1</td>
</tr>
<tr>
<td>ADP624-Dolly</td>
<td>3</td>
<td>3</td>
<td>42</td>
<td>50</td>
<td>58</td>
<td>2298</td>
<td>1</td>
</tr>
<tr>
<td>ADP225-G6415</td>
<td>5</td>
<td>3</td>
<td>42</td>
<td>56</td>
<td>57</td>
<td>1489</td>
<td>1</td>
</tr>
<tr>
<td>ADP93-Moro</td>
<td>4</td>
<td>3</td>
<td>50</td>
<td>48</td>
<td>25</td>
<td>627</td>
<td>2</td>
</tr>
<tr>
<td>LSD</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>6</td>
</tr>
</tbody>
</table>

| Seed yield       |                       |                 |                    |                  |                 |                             |                  |
| VAX3             | 2                     | 2               | 48                 | 59               | 27              | 2450                        | 2                |
| ADP624-Dolly     | 3                     | 3               | 42                 | 50               | 58              | 2298                        | 1                |
| ADP649-Kamiakin  | 5                     | 3               | 43                 | 61               | 59              | 2091                        | 1                |
| ADP172           | 4                     | 3               | 41                 | 69               | 26              | 2038                        | 2                |
| ADP614-Rosie     | 4                     | 3               | 43                 | 59               | 49              | 1924                        | 1                |
| ADP646-Myasi     | 5                     | 5               | 42                 | 27               | 32              | 521                         | 1                |
| LSD              |                       |                 |                    |                  |                 |                             | 657              |

†1=determinate; 2=indeterminate

(P≤0.01) in each individual year (Table 4). The average during 2013 for 310 genotypes was 4. During 2014, the average for 144 early genotypes was 6 and for 121 late genotypes was 5; during 2015, the average for 49 early genotypes was 4 and for 49 late genotypes was 3. In all trials the disease scores ranged from 1 to 9, standard deviation was 2.

The early upright genotypes tend to be more susceptible to halo blight probably due to smaller canopy area compared larger canopy to late-climbing genotypes. Late genotypes recovered from early infections through new canopy formation since most of them have indeterminate growth habit. Schwartz (1989) stated that, in general, older plants are more resistant to infection.

All trials were homogeneous for halo blight, the difference was less than 10-fold and therefore, combined ANOVA and Pearson’s simple linear correlation was performed. In the combined ANOVA, the genotypic effect was significant (P≤0.01) (Table 4). The FRR averaged 5, ranging from 1 to 9, and the standard deviation was 2. From the genotypes tested, VAX3, ADP84-Kablanketi_ndefu, DP454-INIAP429, ADP55-Kabuku, and ADP122-Kranskop were the top resistant and ADP242-G9013 was the
most susceptible (Table 5). All top resistant had indeterminate growth habit and the susceptible genotype indeterminate. Among the checks, VAX3 was resistant, Cabernet susceptible, Dynasty, GTS104, and Talon intermediate resistant.

Halo blight and FRR diseases were not correlated (r=0.20) (Table 7). Thus each disease seems like is governed by independent genes. However, the genotypes VAX3, ADP48-W6_6534, ADP624-Dolly, and ADP438-46_1 were resistant to both diseases. From the three genotypes, ADP624-Dolly had determinate growth habit (Table A13).

Disease severity of halo blight in 2013 started with 3, raised to 5 in 2014, and was 3 in 2015 (Table 6). Increased infection in 2014 was due to higher plant population (plant survival 65%) and canopy development compared to the other two years. Moreover, favorable weather conditions promoted halo blight attack (Markell and Pasche, 2014). Halo blight was negatively correlated with growth habit (r=-0.54***) (Table 7). Halo blight symptoms increased in determinate growth habit genotypes and decreased in indeterminate as has been suggested by Schwartz (1989).

**Days to flower**

The genotypic effect was significant (P≤0.01) in each individual trials (Table 4). In 2013, for 302 genotypes the average was 47 days, ranged from 36 to 76, and standard deviation was 7. In 2014, for 144 early genotypes, the average was 41 days, and for 121 late genotypes 49 days. In 2015, for 49 early genotypes the average was 43 days, and for 49 late genotypes was 48 days.

All trials were homogeneous for days to flower, the difference was less than 10-fold and therefore, combined ANOVA and Pearson’s simple linear correlation was performed. In the combined ANOVA across years, the genotypic effect was significant (P≤0.01) (Table 4), the average was 45, ranged from 36 to 64, and the standard deviation was 5. From the genotypes tested, ADP676-CELRK, ADP242-G9013, ADP644-Foxfire, ADP5-Kabuku, and ADP648-Redcloud were among the earliest with 38 days after planting and ADP621-JaloEEP558 was the latest with 55 days average after planting. All five earliest had determinate growth habit and all ADP621-JaloEEP558 indeterminate growth habit (Table 5). Among the checks, Cabernet flowered at 41 days, Dynasty at 42 days, Talon at 43 days, GTS104 at 44 days, and VAX3 at 48 days after planting (Table A13). Population average for days to flower across years ranged from 45 to 46 days after planting (Table 6) being the most stable trait.
Days to flower was positively correlated with growth habit ($r=0.56^{***}$) and negatively correlated with seed weight ($r=-0.60^{***}$) (Table 7). Early genotypes were mostly determinate growth habit with high 100-seed weight at Perham, MN. This correlation agrees with Kelly et al. (1998b) and Kornegay et al. (1992) findings.
Table 6. Means of six traits measured on the 92 common genotypes grown across three years at Perham, MN, from 2013 to 2015.

<table>
<thead>
<tr>
<th>Year</th>
<th>Fusarium root rot 1-9</th>
<th>Halo blight 1-9</th>
<th>Days to flower No.</th>
<th>Plant survival %</th>
<th>100-seed weight g</th>
<th>Seed yield kg ha⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>2013</td>
<td>4</td>
<td>3</td>
<td>46</td>
<td>29</td>
<td>46</td>
<td>1465</td>
</tr>
<tr>
<td>2014</td>
<td>5</td>
<td>5</td>
<td>45</td>
<td>65</td>
<td>44</td>
<td>1174</td>
</tr>
<tr>
<td>2015</td>
<td>6</td>
<td>3</td>
<td>46</td>
<td>60</td>
<td>35</td>
<td>1002</td>
</tr>
</tbody>
</table>

**Growth habit**

Growth habit was evaluated as discrete variable (determinate/indeterminate), and consequently it was not used for ANOVA. Instead, it was used for correlation purposes. Growth habit was negatively correlated with seed weight ($r=-0.50^{***}$) (Table 7). From 92 genotypes, 52 genotypes had determinate growth habit, 40 indeterminate (Table A13). Most Andean genotypes from Nueva Granada race usually have determinate growth habit and larger seed than Mesoamerican races (Kornegay et al., 1992). Among the checks, VAX3 was indeterminate, whereas Cabernet, Dynasty, GTS104, and Talon had determinate growth habit.

**Plant survival**

The genotypic effect was significant ($P≤0.01$) for all trials, except for the 2015 early trial (Table 4). In 2013, for 280 genotypes the average was 30%, ranged from 4 to 59%, and standard deviation was 11. In 2014, for 144 early genotypes, the average was 70%, ranged from 23 to 99%, and standard deviation was 17; for 121 late genotypes 55%, ranged from 22 to 96%, standard deviation was 14. In 2015, for 49 early genotypes the average was 61%, ranged from 17 to 90%, standard deviation was 13 and for late genotypes the average was 6%, ranged from 38 to 91%, standard deviation was 11.

All trials were homogeneous, the difference was less than 10-fold for plant survival, therefore combined ANOVA and Pearson’s simple linear correlation was performed. In the combined ANOVA, the genotypic effect was significant ($P≤0.01$) (Table 4). The average was 52%, ranged from 7 to 98%, and the standard deviation was 20. From the genotypes tested, ADP242-G9013, ADP172, ADP644-Foxfire, ADP648-Redkloud, and ADP680-Clouseau had the top plant survival with 70% average and ADP646-Myasi had the lowest plant survival with 27% average (Table 5). Among checks, VAX3 had 59%, Cabernet 52%, Dynasty 51%, Talon 48%, and GTS104 45% plant survival (Table A13).
From the yearly mean population, in 2013, plant survival average was the lowest with 30%, increased to 65% in 2014 and to 60% in 2015 (Table 6). Low plant survival was due to low seedling emergence after heavy rainfall in 2013, even though seed was treated. In 2014 and 2015, low plant survival was due to seed-borne fungi \textit{F. solani} and \textit{P. syringae} attack and poor adaptation of some introduced Andean genotypes. Plant survival was positively correlated with seed yield \((r=0.61^{***})\) (Table 7), Thus, higher plant survival produced higher seed as expected.

**Seed weight**

The genotypic effect was significant \((P \leq 0.01)\) (Table 4) in all trials. In 2013, the average for 280 genotypes was 44 g, ranged from 20 to 71, standard deviation was 11. In 2014, the average was 43 g, ranged from 20 to 64 g, standard deviation was 9 for early trial; and the average 39 g, ranged from 23 to 58 g, standard deviation was 7 for late trial. In 2015, the average 40 g, ranged from 22 to 58, standard deviation was 40 g for early trial; and average 32 g, ranged from 18 to 57 g, standard deviation was 8 for late trial.

All trials were homogeneous seed weight, the difference was less than 10-fold and therefore, combined ANOVA and Pearson’s simple linear correlation was performed. In the combined analysis the genotypic effect was significant \((P \leq 0.01)\) (Table 4). The average was 42 g, ranged from 20 g to 69 g, and the standard deviation was 10 g. From the genotypes, ADP649-Kamiakin, ADP680-Clouseau, ADP616-OAC_Lyrick, ADP624-Dolly, and ADP225-G6415 had the highest seed weight with 58 g average, and ADP93-Moro had the lowest seed weight with 25 g average (Table 5). Among checks, Dynasty 57 g, Cabernet, GTS104, and Talon 49 g each, and VAX3 29 g per seed weight (Table A13). From yearly population mean, in 2013, seed weight average was 44 g, in 2014 was 46 g, and in 2015 was 35 g (Table 6). In 2015 harvested plots were harvested with reduced moisture content in the seed.

**Seed yield**

The genotypic effect was significant \((P \leq 0.01)\) for all trials (Table 4). In 2013, the average was 1407 kg ha\(^{-1}\), ranged from 62 to 3960 kg, standard deviation was 818; in 2014, for early the average was 974 kg ha\(^{-1}\), ranged from 68 to 3300 kg, standard deviation was 543, and for late was 1093 kg ha\(^{-1}\), ranged from 79 to 2880 kg, standard deviation was 617. In 2015, for early the average was 1257 kg ha\(^{-1}\),
ranged from 140 to 2917 kg, standard deviation was 537, and for late trial the average was 813 kg ha⁻¹; ranged from 115 to 3029 kg, standard deviation was 522.

All trials were homogeneous for seed yield, the difference was less than 10-fold and therefore, combined ANOVA and Pearson's simple linear correlation was performed. In the combined analysis the genotypic effect was significant (P≤0.01) (Table 4). The average was 1214 kg ha⁻¹, ranged from 206 to 3096, and standard deviation was 540 kg ha⁻¹. From the genotypes tested, VAX3, ADP624-Dolly, ADP649-Kamiakin, ADP172, and ADP614-Rosie had the highest seed yield with 2160 kg ha⁻¹ average, and ADP646-Myasi had the lowest seed yield with 521 kg ha⁻¹ average (Table 5). Among checks, VAX32450 kg, Talon 1659 kg, Dynasty1607, Cabernet 1268, and GTS104 kg ha⁻¹ (Table A13).

Seed yield of 1214 kg ha⁻¹ averaged across three years was (Table 4) low compared to 2185 kg ha⁻¹ Minnesota seed yield average (Lofthus and Byrne, 2015). It was due to FRR and halo blight infection, poor adaptation and late maturity of some introduced genotypes included in the Andean panel.

Seed yield was positively correlated with plant survival as expected (r=0.61***) (Table 7). Likewise, FRR and halo blight affected negatively slight affected seed yield (r=-0.24*). On the other hand, late-indeterminate-small-seeded genotypes usually have higher seed yield than early-determinate-large-seeded genotypes (Kelly et al., 1998b; Schneider et al., 2001), although the short cropping season, 105 days, at Perham, MN, did not allow to express all seed yield potential to late-indeterminate-small-seeded genotypes.
Table 7. Pearson correlation coefficients among seven traits measured on 92 genotypes grown at Perham, MN, from 2013 to 2015.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Halo blight 1-9</th>
<th>Days to flower No.</th>
<th>Growth habit</th>
<th>Plant survival %</th>
<th>100-seed weight g</th>
<th>Seed yield kg ha⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fusarium root rot</td>
<td>0.20</td>
<td>-0.22*</td>
<td>-0.28**</td>
<td>-0.27**</td>
<td>0.38***</td>
<td>-0.24*</td>
</tr>
<tr>
<td>Halo blight</td>
<td>-0.43***</td>
<td>0.54***</td>
<td>0.00</td>
<td>0.30***</td>
<td>-0.24*</td>
<td></td>
</tr>
<tr>
<td>Days to flower</td>
<td>0.56***</td>
<td>-0.40***</td>
<td>-0.50***</td>
<td>-0.60***</td>
<td>-0.37***</td>
<td></td>
</tr>
<tr>
<td>Growth habit</td>
<td>-0.08</td>
<td>0.11</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant survival</td>
<td>0.11</td>
<td></td>
<td></td>
<td></td>
<td>0.61***</td>
<td></td>
</tr>
<tr>
<td>100-seed weight</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.32***</td>
</tr>
</tbody>
</table>

*Significant at the 0.05 probability level; ** Significant at the 0.01 probability level; *** Significant at the 0.001 probability level

**Genome-wide association study**

**Population structure**

Using two years data an ANOVA was computed (Table A7). With the exception of plant survival, significant (P≤0.05) genotypic differences for FRR, halo blight, days to flower, seed weight, and seed yield were found. For GWAS, Lsmeans from all traits, including determinacy growth habit, is in Table A14.

For 246 genotypes, 3525 SNP markers were used to evaluate population structure via principal component analysis using a correlation matrix on GAPIT package. SNP markers were plotted in two-dimension graphs using principal component approach. For 246 Andean panel, the first principal component (PC1) comprised ADP in two sub populations, which correspond to the two gene pools: Andean and Mesoamerican. The second PC2 separated Andean panel in a sub set groups, probably corresponding to admixtures among the two gene pools (Figure 1). Similar two subpopulations and subset groups described Cichy et al. (2015) for 374 accessions from ADP and 3385 SNP markers using the software STRUCTURE. Likewise Kamfwa et al. (2015), also using STRUCTURE, described two subpopulations within 237 accessions from ADP and 4850 SNP markers, one big subpopulation from Andean gene pool and one small subpopulation from Mesoamerica gene pool.
Fitting the best trait-marker regression model

Using FRR phenotypic data from the 246 Andean panel and their corresponding 3525 SNPs in order to select the best statistical approach, four linear regression models using QQ-plots (quantile-quantile plots) were analyzed. QQ-plots were generated by plotting observed $-\log_{10} P$-values against expected $-\log_{10} P$-values GAPIT package (Lipka et al., 2012).

From the four QQ-plots, the Naïve model is far from the regression line with the higher amount of $P$-values far from the regression line (Figure 2a); whereas PCA, EMMA and MM are closer to the regression line (Figure 2b, 2c, 2d). However, EMMA model fits better the regression line for FRR (Figure 2d), halo blight, days to flower, growth habit, and plant survival (Figures not shown). Moreover, EMMA model produced more redundant markers. The $P$-value distribution for the full model follows the expected distribution under the null hypothesis of independence between the SNPs and the trait.
Figure 2. QQ-plots from 246 phenotypic data from Andean panel associated with 3525 SNP markers using FRR score: a) Naïve, b) Principal component analysis (PCA), c) Mixed model (MM=PCA+EMMA), d) Efficient mixed model analysis (EMMA).

Trait-marker associations

Significant associations were found for FRR, halo blight, days to flower, growth habit, and plant survival ($P \leq 0.001$) (Table 8). There were no significant associations for seed weight and seed yield. Manhattan plots were drawn from EMMA model to represent the chromosomal position of outstanding
markers. Plots were built using -log10 of transformed $P$-values on the Y axes against the physical positions of the SNPs on chromosome location on the X axes.

Table 8. Top three SNPs, chromosome, position and significant $P$-values ($P \leq 0.001 = -\log_{10} (P) \geq 3.0$) for seven traits measured on 246 genotypes in the Andean diversity panel grown at Perham, MN, in 2013 and 2014.

<table>
<thead>
<tr>
<th>Traits</th>
<th>SNP</th>
<th>Chromosome</th>
<th>Position Mb</th>
<th>-log10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fusarium root rot (1-9)</td>
<td>m1545</td>
<td>4</td>
<td>3.3</td>
<td>3.6</td>
</tr>
<tr>
<td></td>
<td>m2129</td>
<td>5</td>
<td>13.4</td>
<td>3.0</td>
</tr>
<tr>
<td></td>
<td>m2172</td>
<td>5</td>
<td>17.9</td>
<td>3.0</td>
</tr>
<tr>
<td>Halo blight (1-9)</td>
<td>m2368</td>
<td>5</td>
<td>38.8</td>
<td>3.4</td>
</tr>
<tr>
<td></td>
<td>m2372</td>
<td>5</td>
<td>38.9</td>
<td>3.2</td>
</tr>
<tr>
<td></td>
<td>m2373</td>
<td>5</td>
<td>38.9</td>
<td>3.2</td>
</tr>
<tr>
<td>Days to flower (No.)</td>
<td>m373</td>
<td>1</td>
<td>48.3</td>
<td>6.2</td>
</tr>
<tr>
<td></td>
<td>m333</td>
<td>1</td>
<td>43.6</td>
<td>3.6</td>
</tr>
<tr>
<td></td>
<td>m19</td>
<td>1</td>
<td>3.0</td>
<td>2.8</td>
</tr>
<tr>
<td>Growth habit (determinate/indeterminate)</td>
<td>m333</td>
<td>1</td>
<td>43.6</td>
<td>3.8</td>
</tr>
<tr>
<td></td>
<td>m1566</td>
<td>4</td>
<td>3.8</td>
<td>3.6</td>
</tr>
<tr>
<td></td>
<td>m339</td>
<td>1</td>
<td>45.2</td>
<td>3.6</td>
</tr>
<tr>
<td>Plant survival (%)</td>
<td>m373</td>
<td>1</td>
<td>48.3</td>
<td>3.8</td>
</tr>
<tr>
<td></td>
<td>m1701</td>
<td>4</td>
<td>19.2</td>
<td>3.0</td>
</tr>
<tr>
<td></td>
<td>m1347</td>
<td>3</td>
<td>42.8</td>
<td>2.7</td>
</tr>
<tr>
<td>Seed weight (g)</td>
<td>m1939</td>
<td>5</td>
<td>1.0</td>
<td>2.7</td>
</tr>
<tr>
<td></td>
<td>m333</td>
<td>1</td>
<td>43.6</td>
<td>2.7</td>
</tr>
<tr>
<td></td>
<td>m4601</td>
<td>10</td>
<td>40.6</td>
<td>2.4</td>
</tr>
<tr>
<td>Seed yield (kg ha$^{-1}$)</td>
<td>m1328</td>
<td>3</td>
<td>39.8</td>
<td>2.9</td>
</tr>
<tr>
<td></td>
<td>m824</td>
<td>2</td>
<td>31.7</td>
<td>2.8</td>
</tr>
<tr>
<td></td>
<td>m4544</td>
<td>10</td>
<td>38.4</td>
<td>2.7</td>
</tr>
</tbody>
</table>

**Fusarium root rot**

A clear peak on Pv04/3.3 Mb was associated with FRR (Table 8, Figure 3) in this study. Schneider et al. (2001) found markers associated with FRR on Pv02, Pv03; Roman-Aviles and Kelly (2005) on Pv02 and Pv05; Navarro et al. (2008) on Pv06 by using RAPDs; Kamfwa et al. (2013), using SSR markers, on Pv03; Hagerty et al. (2015), using SNP markers, on Pv03 and Pv07 and Bello et al. (2014) found significant marker associated with FRR on chromosome Pv09.

One SNP marker, within the genomic region, found on Pv04 was significantly associated with FRR in this study. However, caution should be taken before making definite conclusions. GWAS depends
on regression model, software used, population size, population structure, and cut-off $P$-value. Consequently, data should be validated before making recommendation. Besides, FRR has complex inheritance, and the pathogen interact with other soil-borne pathogens making more difficult to identify

![Figure 3. Manhattan plots drawn using EMMA model for Fusarium root rot. Different colors represent different chromosomes.](image)

**Halo blight**

Halo blight Race 6 has been identified attacking common bean in MN/ND region in 2015 (K. Ghising, personal communication, 2016). One clear peak on Pv05/3.8 to 3.9 Mb was associated with halo blight resistance (Table 8, Figure 4). Ariyarathne et al. (1999), working with recombinant inbred lines derived from cross Neb-RR-1/A55 reported significant effect for halo blight resistance associated with one chromosomal region of Pv5 conferring resistance to two strains used. In other study, Robast et al. (2010) found one SSR marker on Pv04 closely linked to a major QTL involved in halo blight resistance. This marker was found in the 188 Fr-derived lines from a cross between Magister x Clovis and is being used in a marker assisted selection (MAS) programs. Unfortunately these authors did not report race specific resistance.

Evaluation with differential lines confirmed the monogenic inheritance of halo blight. The genes conditioning resistance to 1 to 9 Psp races are Pse-1, Pse-2, Pse-3, Pse-4, Pse5 (Singh and Schwartz, 2010). Genes Pse1, Pse2, Pse4, and Pse5 are located on Pv10 conditioning resistance to Races 1, 3, 4, 5, 7, 8, 9, whereas gene Pse3 on chromosome Pv02 conferring resistance to Races 2, 3, 4, 5, 7, 8 and 9
A new gene, Pse-6, was reported by Miklas et al. (2014), working with 76 F9-derived lines from a cross Neb-RR-1/A55. The gene is located on Pv04 conditioning resistance to Races 1, 5, 7 and 9.

Figure 4. Manhattan plots drawn using EMMA model for halo blight. Different colors represent different chromosomes.

In other study, Duncan et al. (2014) found resistance to Race 6 on cultivar US14HBR6 but molecular characterization of the resistant gene and chromosome localization is not reported. However, Trabanco et al. (2014), working with 110 F7-derived lines from the cross Xana\Cornell 49242 found one RAPD marker on Pv4 and one on Pv6, conferring tolerance to Race 6.

Major R genes are implicated in resistance to Psp, however, specific bean genotypes exhibit a quantitative mode of inheritance of resistance to Psp (Trabanco et al., 2014). Accordingly, Miklas and Fourie (2015) stated that none of the R genes condition resistance to the most prevalent Race 6 but some lines like CAL 143, PI150414, and GN #1 sel 27, have quantitative resistance to this race. The QTL for resistance to Race 6 in CAL 143 resides within a large R gene cluster toward the proximal end of Pv04. US14 pinto has resistance to Race 6 conferred by two independent recessive resistance genes.

The genomic regions found in this study on Pv05 and significant marker on Pv04 should be validated to assure that they are related to resistant factors located on these chromosomes conferring resistance to Race 6 before using as MAS in the breeding programs.
**Days to flower**

Two significant genomic regions were identified associated with days to flower on Pv01/43.7 Mb and Pv10148.3 Mb (Table 8, Figure 5). Kamfwa et al. (2015), working with 237 genotypes from Andean panel, found one SNP marker associated with days to flower on Pv01 using GWAS. Likewise, Moghaddam (2015), found one SNP marker (m32210) on Pv01 and one (m2535) on Pv03 associated with days to flower in 280 genotypes from the Mesoamerica diversity panel through GWAS. Consequently, this study confirmed the existence of genes on Pv01 determining the period from planting to flowering in the Andean panel. Genomic region on Pv1 also was associated with growth habit in this study.

![Figure 5. Manhattan plots drawn using EMMA model for days to flower. Different colors represent different chromosomes.](image)

**Growth habit**

A region composed by significant markers on Pv01/45.2 Mb and Pv01/43.7 Mb was linked to determinacy growth habit (Table 8, Figure 6). A major signal on Pv01 was detected by Moghaddam (2015) working with 280 genotypes from Mesoamerica panel. Similarly, Cichy et al. (2015), working with 374 genotypes from Andean panel, found a significant region associated with determinacy on Pv01. Kwak et al. (2008) identified Fin locus for determinacy co-segregating with TFL1 locus for terminal flower on Pv01. The genomic region on Pv01 associated with determinacy growth habit overlapped with genomic
region for days to flower. Kwak et al. (2008) stated that determinacy causes early flowering, thus selecting for one trait also the other trait is being selected, since they close linked.

![Manhattan plots drawn using EMMA model for growth habit. Different colors represent different chromosomes.](image)

**Plant survival**

One marker on Pv01/48.3 Mb was the unique significant SNP marker associated with percentage of plant survival (Table 8, Figure 7). However, a genomic region on Pv04/19.2 Mb (Figure 3.5) was associated to plant survival. Since plant survival and FRR are close to each other, genes associated with both traits could be involved. Otherwise, plant survival has not been studied yet, thus it should be validated in further studies since it is an important trait correlated with seed yield.

**Seed weight**

Seed weight was not significantly associated with any SNP marker in this study (Table 8, Figure 8), probable due to low amount of small-seeded genotypes from Mesoamerican origin within the 246 Andean panel. However, Moghaddam (2015) confirmed three SNP markers on Pv07 by employing GWAS in 280 genotypes from Mesoamerica gene pool. Other major peaks residing on Pv010, Pv06, and Pv03 were found by the same author in the same Mesoamerica panel. High seed weight correlated with large seed size is important in societies than consume beans in physiological stage. This character is
important in Nueva Granada race that invariably should be taken in account in bean breeding programs working for this type of seed market preferences.

Seed yield

Seed yield was not significantly associated with any SNP marker in this study (Table 8, Figure 9). However, Kamfwa et al. (2015) found SNP markers associated with seed yield on Pv03 and Pv09 through GWAS by employing 237 genotypes from the ADP. In other study, using Mesoamerican panel,
Moghaddam (2015) found significant genomic region on Pv03 and Pv06 associated with seed weight and seed yield. Linares-Ramirez (2013) working with 335 F$_{5.9}$ derived lines from a cross between Buster/Ser22 found a mayor QTL on Pv03. Since, a consistent genomic region affected seed weight and seed yield on Pv03, although not detected in this research, this region should be validated to use in bean breeding programs.

Figure 9. Manhattan plots drawn using EMMA model for seed yield. Different colors represent different chromosomes.
SUMMARY AND CONCLUSIONS

It is important to be cautious when interpreting GWAS data, peaks can change depending on population structure, environment, sample size, and evaluation criteria. GWAS analyses can produce both false positive and false negatives. False negatives might not only be due to the nature of regression analysis but also the significant cutoff value to control for experiment-wide error rate that is chosen. Repeatability, validation, unified phenotyping criteria, sample size, molecular techniques employed are key points before making conclusions about makers involved in or close to the genes associated with the trait of interest.

Fusarium root rot, halo blight, days to flower, determinacy growth habit, plant survival, seed weight are significant traits related to seed yield. Phenotyping under natural field conditions helped identifying resistant and susceptible genotypes to the prevalent diseases and characterize for valuable agronomic traits. Discovering the genetic architecture of these traits was done thought GWAS using a set of genotypes from Andean pool. GWAS takes advantage of the historic recombination that exist in the population to find trait-markers associations. The availability of whole genome sequence data in Andean panel helped to accomplish the genomic study. Marker-assisted selection has been proposed as a means of identifying markers linked to important traits that follow a quantitative inheritance. However, this utility will depend on how reliable trait-marker associations are for predicting the phenotype based on the genotype. Ideally, a genomic region or SNP marker should invariably express the trait without being greatly affected by the environment. Up-to-date only major genes/markers have been used successfully in MAS breeding programs.

Fusarium root rot, caused by Fsp, along with halo blight, caused by Psp, were found to be the most significant biotic constraints in beans at Perham, MN, for three years. The genotypes VAX3 (check), ADP48-W6_6534, ADP624-Dolly, and ADP438-46_1 were resistant to both diseases. These genotypes can be used as parents in the bean breeding programs.

ADP676-CEL RK, ADP242-G9013, ADP644-Foxfire, ADP648-Redkloud, ADP5-Kabuku, and ADP616-OAC_Lyric were the earliest days to flower genotypes with 38 days average, whereas ADP621-JaloEEP558 and ADP454-INIAP429 were the latest with 58 days. The earliest flowering group had determinate growth habit, the latest flowering group were indeterminate growth habit.
On plant survival ADP242-G9013, ADP172, ADP644-Foxfire, and ADP648-Redkloud presented the highest plant survival, whereas ADP514-Mantegaamarela, ADP269-G13092, ADP105-Sewani_97 and ADP646-Myasi presented the lowest percentage of plant survival.

For seed weight, ADP680-Clouseau, ADP649-Kamiakin, ADP616-OAC_Lyric, and ADP624-Dolly presented the highest weight with 59 g average, whereas ADP172, ADP465-PI321094D, ADP48-W6_6534, and ADP93-Moro presented the lowest seed weight with 26 g average. Since this second group had small seed, most probably it belongs to Mesoamerican gene pool.

For seed yield, ADP624-Dolly, ADP649-Kamiakin, ADP172, ADP614-Rosie, ADP647-Redkanner, ADP75-Mabuku, ADP242-G9013, ADP454INIAP-429, ADP648-Redkloud, and ADP636-Montcalm had the highest seed yield with 1885 kg ha\(^{-1}\), whereas ADP514-Mantegaamarela, ADP652-Lisa, ADP269-G13092, and ADP646-Myasi were the lowest seed yield genotypes with 560 kg ha\(^{-1}\). From the top ten high-seed-yield genotypes, six are U.S inbred cultivars. ADP624-Dolly is cranberry seed type; ADP649-Kamiakin, ADP614-Rosie, ADP647-RedKanner, and ADP636-Montcalm are red kidney type.

The outstanding genotypes were ADP624-Dolly with resistance to FRR, high seed weight, and high seed yield; ADP649-Kamiakin with high seed weight and high seed yield; ADP648-Redkloud with early flowering, high plant survival and high seed yield; ADP172 with high plant survival and high seed yield; and ADP242-G9013 with early flowering, high plant survival and high seed yield, although susceptible to halo blight. Fusarium root rot and halo blight affected seed yield, whereas plant survival benefited.

GWAS provided significant markers and genomic regions associated with five out of seven traits in 246 Andean panel. After regression analysis, two genomic regions on Pv04 were linked to FRR and plant survival, one genomic region on Pv05 to halo blight, and two genomic regions on Pv01 linked to days to flower and growth habit. Genomic regions that were identified to be significantly associated with more than one trait should be validated before using in MAS. Most probably there are independent genes affecting each trait localized within the same DNA segment. Thus phenotyping cultivars and landraces, correlating to available annotated Andean panel though GWAS and estimating significant markers associated with traits of interest could help to select better parents to develop progenies in more efficient
way and in short time period. However, caution should be taken when the inheritance is polygenic such as in FRR.

Consequently, resistant genotypes can promptly be used as parents in bean breeding programs. However, markers conferring resistance to FRR and/or halo blight, the two prevalent disease in kidney beans in Minnesota, needs to be validated before using as molecular markers.
REFERENCES


Kamfwa, K., K.A. Cichy, and J.D. Kelly. 2015. Genome-wide association study of agronomic traits in common bean. The Plant Genome 8:1-12.


Moghaddam, S.M. 2015. Unraveling the genetic architecture of agronomic traits and developing a genome wide indel panel in common bean (*Phaseolus vulgaris*). Ph.D. diss., North Dakota State University.


construction, anchoring whole-genome sequence, and other genetic and genomic applications in common bean. G3: Genes, Genomes, Genetics 5:2285-2290.


**APPENDIX**

Table A1. Mean squares, F-tests, and percent coefficients of variation (CV%) from the analyses of variance of six agronomic traits measured on 310, 302, and 280 genotypes grown at Perham, MN, in 2013.

<table>
<thead>
<tr>
<th>SOV</th>
<th>df</th>
<th>Fusarium root rot df 1-9</th>
<th>Halo blight df 1-9</th>
<th>Days to flower No.</th>
<th>Plant survival %</th>
<th>100-seed weight g</th>
<th>Seed yield kg ha(^{-1})</th>
</tr>
</thead>
<tbody>
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<td>Rep</td>
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<td>0.4</td>
<td>19.9**</td>
<td>1</td>
<td>25.6</td>
<td>1</td>
<td>2762**</td>
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<td>18</td>
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<td>18</td>
<td>262**</td>
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<td>279</td>
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<td></td>
<td></td>
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Table A2. Mean squares, F-tests, and percent coefficients of variation (CV%) from the analyses of variance of six agronomic traits measured on 144 early genotypes grown at Perham, MN, in 2014.

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<th>Halo blight df 1-9</th>
<th>Days to flower No.</th>
<th>Plant survival %</th>
<th>100-seed weight g</th>
<th>Seed yield kg ha(^{-1})</th>
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</thead>
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<td>1.4</td>
<td>1.6</td>
<td>2.1</td>
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<td>16*</td>
<td>211347**</td>
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</tbody>
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Table A3. Mean squares, F-tests, and percent coefficients of variation (CV%) from the analyses of variance of six agronomic traits measured on 121 late genotypes grown at Perham, MN, in 2014.

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<th>Halo blight df 1-9</th>
<th>Days to flower No.</th>
<th>Plant survival %</th>
<th>100-seed weight g</th>
<th>Seed yield kg ha(^{-1})</th>
</tr>
</thead>
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</tr>
<tr>
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<td>1.1</td>
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<td>22**</td>
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<td></td>
<td></td>
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</tbody>
</table>
Table A4. Mean squares, F-tests, and percent coefficients of variation (CV%) from the analyses of variance of six agronomic traits measured on 49 early genotypes grown at Perham, MN, in 2015.

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<th>df</th>
<th>Fusarium root rot</th>
<th>Halo blight</th>
<th>Days to flower No.</th>
<th>Plant survival %</th>
<th>100-seed weight g</th>
<th>Seed yield kg ha⁻¹</th>
</tr>
</thead>
<tbody>
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<td>851512**</td>
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<td>1.1</td>
<td>4.1</td>
<td>156</td>
<td>6</td>
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<td>9.5**</td>
<td>12.0**</td>
<td>180</td>
<td>104**</td>
<td>318000**</td>
</tr>
<tr>
<td>Error</td>
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<td>0.9</td>
<td>2.7</td>
<td>142</td>
<td>4</td>
<td>96220</td>
</tr>
<tr>
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<td>26.0</td>
<td>3.8</td>
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<td>25</td>
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Table A5. Mean squares, F-tests, and percent coefficients of variation (CV%) from the analyses of variance of six agronomic traits measured on 49 late genotypes grown at Perham, MN, in 2015.

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<tr>
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<th>Fusarium root rot</th>
<th>Halo blight</th>
<th>Days to flower No.</th>
<th>Plant survival %</th>
<th>100-seed weight g</th>
<th>Seed yield kg ha⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rep</td>
<td>1</td>
<td>0.7</td>
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<td>330020**</td>
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<td>Blk(rep)</td>
<td>12</td>
<td>4.2*</td>
<td>1.6**</td>
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Table A6. Mean squares, F-tests, and percent coefficients of variation (CV%) from the combined analyses of variance of six agronomic traits measured on 92 common genotypes grown at Perham, MN, from 2013 to 2015.

<table>
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<tr>
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<th>Halo blight</th>
<th>Days to flower No.</th>
<th>Plant survival %</th>
<th>100-seed weight g</th>
<th>Seed yield kg ha⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>2</td>
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<td>34308**</td>
<td>2996**</td>
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</tr>
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<td>28.8</td>
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<td>9</td>
<td>34</td>
</tr>
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Table A7. Mean squares, F-tests, and percent coefficients of variation (CV%) from the combined analyses of variance of six agronomic traits measured on 246 common genotypes grown at Perham, MN, in 2013 and 2014.

<table>
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<th>Fusarium root rot</th>
<th>Halo blight</th>
<th>Days to flower No.</th>
<th>Plant survival %</th>
<th>100-seed weight g</th>
<th>Seed yield kg ha⁻¹</th>
</tr>
</thead>
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<td>Year</td>
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<td>447.1**</td>
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<tr>
<td>Genotypes</td>
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<td>154.9**</td>
<td>369007**</td>
</tr>
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Table A8. LSmeans for six traits measured on 310 common bean genotypes in the Andean diversity panel grown at Perham, MN, in 2013.

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<th>Plant survival %</th>
<th>100-ssed weight g</th>
<th>Seed yield kg ha⁻¹</th>
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</thead>
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<td>632</td>
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<td>3</td>
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<td>53</td>
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<td>3</td>
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<td>8</td>
<td>47</td>
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Table A9. LSmeans for six traits measured on 144 early flowering common bean genotypes in the Andean diversity panel grown at Perham, MN, in 2014 (continued).

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Table A11. LSmeans for six traits measured on 49 early flowering common bean genotypes in the Andean diversity panel grown at Perham, MN, in 2014.

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Table A11. LSmeans for six traits measured on 49 early flowering common bean genotypes in the Andean diversity panel grown at Perham, MN, in 2014 (continued).

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Table A12. LSmeans for six traits measured on 49 late flowering common bean genotypes in the Andean diversity panel grown at Perham, MN, in 2014.

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Table A12. LSmeans for six traits measured on 49 late flowering common bean genotypes in the Andean diversity panel grown at Perham, MN, in 2014 (continued).

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Table A13. LSmeans for seven agronomic traits measured on 92 common bean genotypes in the Andean diversity panel grown at Perham, MN, from 2013 to 2015.

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Table A13. LSmeans for seven agronomic traits measured on 92 common bean genotypes in the Andean diversity panel grown at Perham, MN, from 2013 to 2015 (continued).

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Table A13. LSmeans for seven agronomic traits measured on 92 common bean genotypes in the Andean diversity panel grown at Perham, MN, from 2013 to 2015 (continued).

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Table A14. LSmeans for seven traits measured on 246 common bean genotypes in the Andean diversity panel grown at Perham, MN, in 2013 and 2014 (continued).

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Table A14. LSmeans for seven traits measured on 246 common bean genotypes in the Andean diversity panel grown at Perham, MN, in 2013 and 2014 (continued).

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<th>100-seed weight</th>
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Table A15. Soil mechanical and chemical analysis done by Soil Testing Laboratory, NDSU. Perham, MN, in 2013.

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Mechanical Analysis by Hydrometer Method.

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<th>OM (%)</th>
<th>S (lb/acre)</th>
<th>Zn (ppm)</th>
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pH in water; NO₃-N (lb/acre) extracted with water; OM (%) by ignition; P=Phosphorus; P(ppm) by Olson procedure; K(ppm) by 1N ammonium acetate; soluble salts (EC-mmhos/cm) in 1:1 soil: water; Zn, Fe, Mn, and Cu by DTPA; SO₄-S (lb/acre) extracted with 500 ppm P as monobasic calcium phosphate; Cl (lb/acre) extracted with .01M Ca(NO₃)₂; Ca.


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Mechanical Analysis by Hydrometer Method.

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pH in water; NO₃-N (lb/acre) extracted with water; OM (%) by ignition; P=Phosphorus; P(ppm) by Olson procedure; K(ppm) by 1N ammonium acetate; soluble salts (EC-mmhos/cm) in 1:1 soil: water; Zn, Fe, Mn, and Cu by DTPA; SO₄-S (lb/acre) extracted with 500 ppm P as monobasic calcium phosphate; Cl (lb/acre) extracted with .01M Ca(NO₃)₂; Ca.

Table A17. Soil chemical analysis done by Agvise Laboratory. Perham, MN, in 2015.

<table>
<thead>
<tr>
<th>Laboratory No.</th>
<th>Sample I.D.</th>
<th>Depth (inches)</th>
<th>NO₃-N (lb/acre)</th>
<th>P (ppm)</th>
<th>K (ppm)</th>
<th>pH</th>
<th>EC (mmhos/cm)</th>
<th>O (%)</th>
<th>S (lb/acre)</th>
<th>Zn (ppm)</th>
<th>Fe (ppm)</th>
<th>Mn (ppm)</th>
<th>Cu (ppm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>175960 534</td>
<td>6</td>
<td>25</td>
<td>50</td>
<td>299</td>
<td>6.2</td>
<td>0.22</td>
<td>1.9</td>
<td>20</td>
<td>6.41</td>
<td>20.7</td>
<td>8.5</td>
<td>3.04</td>
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</tbody>
</table>