

IDENTIFICATION OF NEW SOURCES OF RESISTANCE TO ANTHRACNOSE IN
CLIMBING BEAN GERMPLASM FROM GUATEMALA

A Thesis
Submitted to the Graduate Faculty
of the
North Dakota State University
of Agriculture and Applied Science

By

Carlos Raúl Maldonado Mota

In Partial Fulfillment of the Requirements
for the Degree of
MASTER OF SCIENCE

Major Department
Plant Sciences

November 2017

Fargo, North Dakota

North Dakota State University
Graduate School

Title

IDENTIFICATION OF NEW SOURCES OF RESISTANCE TO
ANTHRACNOSE IN CLIMBING BEAN GERMPLASM FROM
GUATEMALA

By

Carlos Raúl Maldonado Mota

The Supervisory Committee certifies that this *disquisition* complies with
North Dakota State University's regulations and meets the accepted
standards for the degree of

MASTER OF SCIENCE

SUPERVISORY COMMITTEE:

Ph.D. Juan M. Osorno

Chair

Ph.D. Phillip McClean

Ph.D Julie Pasche

Ph.D James Beaver

Approved:

12/12/17

Date

Richard D. Horsley

Department Chair

ABSTRACT

Anthracnose, caused by *Colletotrichum lindemuthianum* (Sacc. and Magnus) Briosi and Cavara is a fungal disease that affects common bean worldwide. Seed yield losses sometimes reach 100% when the seed is infected and environmental conditions favor the disease. Climbing beans in Guatemala represent the main source of protein for the habitants of this region (9.4 kg/person/year). Unfortunately, anthracnose threatens climbing bean production in the region. Six races were found among samples collected in Guatemala Highlands using the standard common bean differential lines. Also, a germplasm collection from ICTA Guatemala was evaluated for resistance to *C. lindemuthianum* race 73, which is the predominant race in the U.S. Approximately 10% of 369 climbing bean accessions showed no symptoms (score of 1). GWAS results using 78754 SNP markers indicated that genomic regions for resistance to *C. lindemuthianum* exist in Pv04 and Pv07.

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude to my major advisor, Dr. Juan Osorno for the encouragement, assistance, and the knowledge that he shared during my time in graduate school. In the same way, I would like to thank my graduate committee members, Dr. Julie Pasche, Dr. Phil McClean and Dr. James Beaver for their guidance and knowledge shared for this project and their support during my time at NDSU. In addition, my gratitude to Dr. Marcial A. Pastor Corrales and Dr. Oscar P. Hurtado Gonzales for their guidance, patience, encouraging and for sharing their knowledge for this project during my visit at USDA-ARS, Beltsville, Maryland.

I would like to express my gratitude to the Dry Bean Breeding program team, Jody Vanderwal, Katelynn Walter, and Luz Montejo. Also to the Dry Bean Genomics lab group Maria Gabriela Tobar Piñon and Rian Lee, and Robin Lamppa from the NDSU pulse pathology lab, for the help provided. In addition, I will not forget the help of ICTA team in Guatemala, Julio Villatoro, Angela Miranda, Jessica Moscoso, Karen Agreda, Dr. Erick De Leon, Elmer Estrada and Eduardo Fuentes for their support during the collection of samples. I am grateful to the department of Plant Sciences for the assistance provided. Also especial thanks to Dr. Samira Mafi, Dr. Ali Soltani, and Dr. Stephan Schroder for their guidance and cooperation during my research.

I would like to thank the many friends that I made during my years at NDSU who made my time here so enjoyable, unique and an unforgettable experience.

In addition, I would like to express my gratitude to USAID-Legume Innovation Lab and ICTA in Guatemala for their financial support for this project, including my scholarship.

Finally, I would like to express my gratitude to my family for their wisdom, encouragement, love and guidance during these years.

DEDICATION

To the glory of the grand Architect of the universe

To my parents Romelia Argentina Mota Jerez and Raúl Alejandro Maldonado Alfaro

TABLE OF CONTENTS

ABSTRACT.....	iii
ACKNOWLEDGEMENTS.....	iv
DEDICATION.....	v
LIST OF TABLES.....	viii
LIST OF FIGURES.....	ix
LIST OF APPENDIX TABLES.....	x
LIST OF APPENDIX FIGURES.....	xi
INTRODUCTION.....	1
LITERATURE REVIEW.....	3
Common bean.....	3
Common bean domestication.....	3
Market classes of common bean.....	5
Economic relevance of bean production.....	5
The milpa system and climbing beans in Guatemala.....	6
Anthracnose (<i>Colletotrichum lindemuthianum</i> (Sacc. and Magnus) Briosi and Cavara).....	8
Genome wide association study (GWAS).....	16
MATERIAL AND METHODS.....	19
Plant material.....	19
Field sampling of <i>C. lindemuthianum</i> infected tissue in common bean in the highlands of Guatemala.....	19
Pathogen isolation.....	20
Host inoculation.....	21
Identification of resistant lines in the climbing bean collection from Guatemala.....	23
Genotypic data.....	24

Statistical procedures and GWAS	24
RESULTS	27
Evaluation for resistance to race 73 of <i>C. lindemuthianum</i> in climbing bean germplasm from Guatemala.....	27
Race characterization of <i>C. lindemuthianum</i> in the Guatemalan highlands	31
DISCUSSION	35
Evaluation for resistance to race 73 of <i>C. lindemuthianum</i> in climbing bean germplasm from Guatemala.....	35
Race characterization	38
REFERENCES	41
APPENDIX.....	51

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Differential lines, Binary code, resistance genes and gene pool origin of differential cultivars used to characterize races of <i>Colletotrichum lindemuthianum</i>	11
2. Resistance genes, resources, gene pool, linked markers and map location for anthracnose in common bean.....	15
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).	17
4. Evaluation scale for screening for anthracnose.	23
5. Top ten SNPs significantly associated, chromosome, position, significant P-values and R ² values per individual marker and grouped for the trait anthracnose on 369 climbing bean accessions from Guatemala, sorted by lowest P-value.	29
6. Recovered isolates used for race characterization	32
7. Reaction of common bean differential lines to 16 isolates of <i>Colletotrichum lindemuthianum</i> from Guatemala.	33

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. QQ-plots from 369 phenotypic data from climbing bean accession from Guatemala associated with 78754 SNP markers using anthracnose scores: a) PCA b) Mixed Model (MM) c) EMMA and d) Naïve.	28
2. Manhattan plot using Efficient mixed model analysis (EMMA) for <i>C. lindemuthianum</i> resistance to race 73. The green line is the cut-off value to call a peak significant. SNPs above the 0.01 percentile are highlighted in red, while those above 0.1 are highlighted in blue above the yellow line. Numbers below the Manhattan plot represent chromosomes.	30

LIST OF APPENDIX TABLES

<u>Table</u>	<u>Page</u>
A.1. Anthracnose sample identification code, location of sample, inoculation dates and monosporic culture information.....	52
A.2. Geographical position of Anthracnose samples collected at the western Guatemalan Highlands.....	58
A.3. Climbing bean accession from Guatemala reaction (score 1-9) to race 73 of <i>C. lindemuthianum</i> , in three repetitions and the Least Square Means	60
A.4. SNPs significantly associated, chromosome, position, minor allele frequency (maf) and significant P-values for the trait anthracnose on 369 climbing bean accessions from Guatemala for PCA model, sorted by lowest P-value, using GenABEL software.....	72
A.5. Reaction of different Andean sources of resistance to race 556 and 3981 of <i>C. lindemuthianum</i>	73
A.6. Reaction of the differential cultivar of anthracnose to isolates of <i>C.lindemuthianum</i>	74

LIST OF APPENDIX FIGURES

<u>Figure</u>	<u>Page</u>
A.1. Manhattan plots using different models for <i>C. lindemuthianum</i> resistance to race 73 and QQ-plots using GenABEL software, the MSD value is on the top left. From bottom the first green line is for 0.1 percentile and the second is for 0.01. The green line is the cut-off value to call a peak significant. SNPs above the 0.01 percentile are highlighted in red, while those above 0.1 are highlighted in blue.	71

INTRODUCTION

Common bean (*Phaseolus vulgaris* L.) is the most important food legume consumed in the world (Broughton et al., 2003; Miklas et al., 2006). Breeding programs use germplasm to improve disease resistance and other traits of economic importance. The diseases, that affect the normal function of plants, are the result of an interaction among the host, the environment, and the organism causing the disease.

Anthraxnose, caused by the hemibiotrophic fungus *Colletotrichum lindemuthianum* (Sacc. and Magnus) Briosi and Cavara, is a disease that affects common bean in temperate, subtropical, and tropical zones. The pathogen affects several parts of the plant and the production of common bean is reduced by the damage on the foliage, stems, pods and seeds. Seed yield losses sometimes reach up to 100% when the seed is infected and environmental conditions favor disease development (Schwartz et al., 2005). *C. lindemuthianum* thrives in cool and humid conditions with temperatures between 18 to 26°C and relative humidity of 80% or higher (Del Rio and Bradley, 2002).

In the Guatemalan highlands, climbing beans are relevant because they are an important component in the farmer's diets. Common bean has socioeconomic importance and is considered a basic grain with an annual per capita consumption of 9.4kg (Legume Innovation Lab, 2015).

Unfortunately, anthracnose reduces yield and quality of seed of climbing beans produced in this developing country, and it is aggravated by the fact that growers cannot afford fungicides. Also, it is hard to have good chemical coverage when spraying within the maize (*Zea mays* L.)-bean intercropping system (locally known as Milpa) commonly used to produce climbing beans because maize plants are much taller than dry bean (Burlakoti, 2008). Chemical use for controlling anthracnose is expensive and the generation and/or purchase of disease-free seed is often difficult in developing countries (Meziadi et al, 2016). The ICTA (Institute of Agricultural

Science and Technology) breeding program in Guatemala has a valuable climbing bean germplasm collection from the highland regions. This collection contains the following species: common bean (*P. vulgaris* L.), lima bean (*P. lunatus* L.), scarlet runner bean (*P. coccineus* L.) and year-bean (*P. dumosus* Macfady Syn. *P. polyanthus* Greenman) (Orellana et al., 2006).

Climbing bean accessions from Guatemala belong to Race Guatemala and have type (IV) growth habits (Beebe et al., 2000; Chacon et al, 2005; Blair et al, 2006; Tobar-Pinon et al, 2017). Genetic variability of climbing bean in this region is like to other Middle American races (Blair et al., 2006).

Some field data related to anthracnose resistance based on natural pressure exist for the germplasm collection. In the past, a few studies have identified races of *C. lindemuthianum* in Guatemala. However, there has not been a systematic effort to categorize the predominant races in the highlands of the country and identify the potential sources of anthracnose resistance within the collection of the climbing bean germplasm from Guatemala.

Therefore, new sources of resistance for climbing beans need to be identified to provide sources of resistance for bean breeding programs in Guatemala and other countries where anthracnose is a serious disease of beans. The objectives of this study were: 1) to identify the most predominant races of *C. lindemuthianum* in Guatemala; 2) use the climbing bean collection from Guatemala to identify germplasm with resistance to *C. lindemuthianum* races from Guatemala and North Dakota; and 3) to identify genomic regions associated with resistance to *C. lindemuthianum* using Genome Wide Association Study (GWAS) approach.

LITERATURE REVIEW

Common bean

Common beans are grain legumes that belong to family Fabaceae, which is the third-largest family of flowering plants. This family represents the second most important family of crop plants after the grass family, (Poaceae) (Smýkal et al., 2015) and is vitally important to agriculture and the environment. Legumes provide a substantial portion of all nutritional protein to the human diet (Kumar et al., 2014). Grain legumes account for 27% of world crop production and provide 33% of the dietary protein consumed by humans, while pasture and forage legumes provide a significant part of animal diet (Smýkal et al., 2015).

Legumes comprise several evolutionary lineages derived from a common ancestor 60 million years ago. Papilionoids are the largest clade, dating nearly to the origin of legumes and containing most cultivated species (Lavin et al., 2005). When cultivated grain legumes, or pulses, are considered, the Papilionoideae can be divided into the following four clades: (1) Phaseoloids (*Glycine* spp. Willd., *Phaseolus* spp. L., *Cajanus* spp. L. and *Vigna* spp. Savi), (2) Galegoids (*Pisum* spp. L., *Lens* spp. Millp. *Lathyrus* spp. L., *Vicia* spp. L., *Medicago* spp. L. and *Cicer* spp. L.), (3) Genistoids (*Lupinus* spp. L.) and (4) Dalbergoids (*Arachis* spp. L. and *Stylosanthes* spp. Sw.) (Lewis et al., 2005).

Common bean domestication

The domestication of legumes includes: changes in plant architecture, increased seed size, transition from outcrossing to selfing, reduced seed dispersal, and loss of seed dormancy, among other traits (Hammer, 1984). An increase in the seed size of domesticated genotypes compared to their wild relatives is suggested to be related to greater planting depth in agricultural systems, with larger seeds producing more vigorous seedlings (Abbo et al., 2011). At the same time, increased seed size was selected by early farmers, which unintentionally may have selected

for a higher content of starch, oil and protein to obtain a better product. Seed shattering was avoided during the selection process to reduce the occurrence of the natural seed pod shattering mechanism of wild legumes (Abbo et al., 2014; Smykal et al., 2015).

Common bean in the Americas has a long history of domestication, with two centers of domestication, the Andean mountains of South America, giving rise to the Andean gene pool, and the Central American highlands and lowlands, giving rise to the Mesoamerican (Middle American) gene pool (Blair et al., 2009). Moreover, these centers of domestication are subdivided into groups called races (Singh et al., 1991). The currently recognized races are, Nueva Granada, Peru and Chile (Andean gene pool), and Mesoamerica, Jalisco, Durango and Guatemala (Middle-American gene pool) (Beebe et al., 2000).

A fourth race in the Middle American genepool named race Guatemala was proposed in a study that evaluated the structure of the Middle American races using RAPD markers. This research was the first in propose that race Mesoamerica be divided into two sub races, with having different plant growth habits. Race Guatemala contains materials originated in Guatemala and Chiapas (Mexico) (Beebe et al., 2000). Race Guatemala has been differentiated from Mesoamerican sub-races in other studies. This race contains climbing beans, usually with black and shiny seeds (Chacon et al., 2005; Blair et al., 2009; 2006; Blair et al., 2013; Tobar-Piñon et al., 2017). The study of Blair et al., 2009 utilized 604 accessions from CIAT (International Center of Tropical Agriculture), and 36 SSR markers to determine molecular diversity, in this study race Guatemala was grouped within the Mesoamerican genepool with 61 genotypes. Moreover, the study of Chacon et al., 2005 was performed using 165 accessions from Latin America and USA, 23 from weedy beans and 134 of wild beans. The existence of race Guatemala was suggested based on 10 restriction fragment length polymorphism (RFLP)

markers used, to determine chloroplast DNA polymorphism. Tobar-Piñon et al., 2017, using 45,000 SNP markers, and 369 accessions of *P. vulgaris* climbing bean germplasm from Guatemala, accessions from race Mesoamerica, race Durango-Jalisco, and race Nueva Granada, concluded that race Guatemala grouped separately from the other races, but is part of the Middle American gene pool.

Market classes of common bean

Common bean market classes are grouped by different physical characteristics including seed coat color, color pattern, and size. Market classes commonly grown in the Americas are: pinto, navy, black, dark red kidney, light red kidney, North American small red, Central American small red, great northern, carioca, red mottled, yellow, and alubia (MSU, 2017). In the US, market classes widely grown include pinto, navy, black, kidney, and snap beans (USDA-NASS, 2017). In Guatemala, only a few market classes are grown: black beans, Central American small red (MAGA, 2014), and some white beans (Flores and Bernsten, 2008) In Central America, the most produced market classes are black and small red bean. These market classes are also relevant in Mexico, Cuba, Haiti, and Dominican Republic (Rosas et al., 2014). The predominant market class consumed in Guatemala is the black bean (MAGA, 2014).

Economic relevance of bean production

Common bean is the most important food legume consumed in the world and production and area covers 46% of total grain legumes worldwide. An average of 26.6 million ha of dry beans were harvested between 2008 to 2010, producing an average of 18.8 million of tons (Akibode and Maredia, 2011). Common bean, according to FAOSTAT (2016), is cultivated in 129 countries across five continents. Latin America is an important production region accounting for more than 45% of the worldwide production (IICA, 2014). In the US, production of common

bean by market classes are approximately: pinto (33%), navy (12%), black (15%), and red kidney (5%) (USDA-NASS, 2017). In 2016, the Census of Agriculture noted that 6,896 US farms produced common bean in 737,741 ha (excluding lima bean), and the average seed yield was 2064 kg- ha⁻¹. Total production including all market classes was 1,458,636 MT (USDA-NASS, 2017). Mexican and Canadian market import about 40% of US beans produced for exportation (USDA-ERS. 2017).

In 2012, 340,000 ha of common bean grown in Guatemala by a total of 292,961 local farmers and an average seed yield of 843 kg.ha⁻¹ (IICA, 2014). Most bean production in developing countries is small-scale agriculture (Miklas et al. 2006), with an average farm size of less than 2.2 ha (Fischer and Victor, 2014). Bush type beans (indeterminate Type II and III) are produced in the eastern lowlands of Guatemala (IICA, 2014) and while climbing beans are grown in the western highlands (Beebe et al, 2000). Climbing beans are usually grown in association with maize and others crops (known as milpa system), and in trellises as a monoculture (Moscoso, 2017).

The milpa system and climbing beans in Guatemala

The Mesoamerican region covers the south of Mexico and extends to the central valley of Costa Rica. In Mesoamerica, species of maize, beans, and squash (*Cucurbita spp.*) were domesticated and simultaneously incorporated in an intercropping system known in the region as Milpa (Zizumbo-Villarreal et al., 2012). According to molecular and genetic evidence, during the late pre-ceramic period (5,550-4,300 BP), Mesoamerican people (mostly Aztecs and Mayans) succeeded in domesticating maize by selecting genotypes with improved plant architecture. This step of domestication allowed the bean plants to climb on the stalk of maize. (Jaenicke–Després et al., 2003; Jaenicke–Després and Smith, 2006).

Common bean is classified based on its growth habit. To characterize the four major growth habits in common bean, it is necessary to consider the type of terminal bud, stem stiffness, twining ability, distribution of pod load or the fruit pattern. Common bean growth habits are: determinate upright (I); indeterminate upright (II); indeterminate, weak stemmed, prostrate nonclimbing or semiclimbing (III); and indeterminate weak stemmed, with long guides or leaders and strong climbing ability (IV) (Singh et al, 1991). Climbing beans have type (IV) growth habit. Race Guatemala also contains Guatemalan climbing beans. Most climbing beans of race Guatemala are locally called “Bolonillos” due the particular spherical seed shape. (Beebe et al., 2000). Worldwide most of the breeding efforts have been focused on developing new resistant (biotic and/or abiotic) and productive bush type varieties. Efforts for improving climbing bean in Guatemala started in 2004 at ICTA, where the main traits of study were climbing aggressiveness, earliness, seed yield and quality, and disease resistance. Recently in the Guatemalan highlands two varieties of climbing bean have been released “ICTA Labor Ovalle” and “ICTA Utatlan”, both with a potential seed yield $>700 \text{ kg ha}^{-1}$ (Osorno et al, 2017).

In Guatemala, there is a *Phaseolus spp.* germplasm collection located at the ICTA-Chimaltenango Research Station with almost 600 climbing bean accessions including: common bean, scarlet runner bean, and year-bean. This germplasm represents beans of different locations from the highlands in Guatemala. Gentry (1966), Cojulun (1970), Freytag (1978), Rodriguez (1982), and Debouck (1986) collected the germplasm in this collection. Orellana et al. (2006) made a preliminary agro-morphological characterization of the 558 genotypes of *P. vulgaris* L. using varietal descriptors from Van Schoohoven and Pastor-Corrales (1987) for 34 variables (12 quantitative and 24 qualitative). Some examples are: flowering time, flower color, pod color, and grain color. They found groups with 71% similarity. In this case, duplicated lines were not

identified, but the species and growth habit were characterized. Additionally, disease resistance to bean rust *Uromyces appendiculatus* (Pers) Unger, anthracnose caused by *C. lindemuthianum* and diseases were measured. The germplasm collection in average showed to be resistant to *C. lindemuthianum* in this study. Unfortunately, the results were based field on natural pressure of the diseases with possible mixture of pathogen races and conducted without repetitions across time.

Ponciano-Samayoa et al. (2009) screened 558 lines of *P. vulgaris* from the climbing bean germplasm of Guatemala, with 6 microsatellite markers with the objective of identifying duplicated lines. Using cluster analysis, the collection was divided into 12 groups and 46% of the collection was classified as duplicates and consequently, the number of accessions could be reduced to 261 to maximize genetic diversity. However, the experiment also concluded that the research should include additional markers to have better resolution and find more differences among the lines.

Recently, Tobar-Piñon et al. (2017), did a new characterization of the genetic diversity contained within the collection using ~75,000 single nucleotide polymorphism (SNP) markers and an improved resolution. The authors concluded that Guatemalan climbing beans are a distinct race of beans within the Mesoamerican gene pool that represents a new source of genetic diversity. The degree of genetic diversity of this race is similar when compared to other races.

Anthracnose (*Colletotrichum lindemuthianum* (Sacc. and Magnus) Briosi and Cavara)

Bean anthracnose is caused by the fungus *Colletotrichum lindemuthianum* (Sacc. and Magnus) Briosi and Cavara. This disease can cause significant reductions levels in seed yield (up to 100%) and quality in susceptible plants (Zuiderveen, 2015). *C. lindemuthianum* is a seed-borne pathogen and when the environment is favorable for infection, the fungus can spread

quickly and can cause an epidemic (Markell et al, 2012). The quality of infected seed is reduced and the pathogen may be introduced to other areas or regions with infected seed. Anthracnose management is complex since the fungus can live up to 22 months in plant debris in northern latitudes (Chen et al, 2007). Anthracnose is one of the most serious diseases that affects common bean in the world due to its pathogenic variability and efficient seed to seedling transmission. Genetic resistance is recognized as the most effective disease management strategy for the control of bean anthracnose (Kelly and Vallejo, 2004) because it is economical and environmentally benign (Meziadi et al, 2016). Although the use of fungicides provides effective management of many crop diseases, their use, when available to small-scale farmer in developing countries, increases costs of production. Incorrect and/or inefficient application of fungicides can produce negative effects on beneficial organisms and the environment (Paparou et al, 2014).

Anthracnose symptoms may appear on any part of the plant. The spread of the disease depends on weather conditions and inoculum source and susceptibility of the host. Infected seed is the principal inoculum source and initial symptoms usually appear on cotyledonary leaves as small, dark brown to black lesions. The infection also can produce minute flesh to rust-colored specks. These specks enlarge lengthwise and partially around hypocotyls and young stems to form a sunken lesion. The damage found in the pod is flesh to rust-colored lesions which develop in sunken cankers and are bordered by slightly raised black rings encircled by a reddish brown edge (Castellanos et al., 2015). Favorable conditions for the development of *C. lindemuthianum* include temperatures ranging between 13 and 25°C, and high relative humidity. The disease can be devastating for common bean growers, causing total crop loss when disease onset occurs at early stages (Castellanos et al. 2015).

Coevolution of common bean and the pathogen *C. lindemuthianum* has been demonstrated based on the genetic variability among the host and the pathogen populations. Coevolution of this host pathosystem has been studied in both Andean and Middle American gene pool (Balardin et al., 1998). Mutation, population gene flow, and recombination are mechanism for genetic diversity in the pathogen. The reciprocal selection pressure within the host and pathogen, and environmental conditions are responsible for the variability and frequency of resistance and virulence genes (Araya, 2003). Results from pathogen population studies consisting of isolates of *C. lindemuthianum* collected from the Andean and Mesoamerican regions showed that Mesoamerican pathogenic populations are more diverse. Most of the Mesoamerican races found in this geographical region were not found in the Andean region. This suggest that pathogenic races coevolved with cultivars from the same region (Pastor-Corrales et al, 1993).

Pastor-Corrales (1991) proposed a set of differential lines to characterize anthracnose races. A binary value is assigned to each differential so that a unique number can be generated for each anthracnose race (Table 1). More than 100 races of *C. Lindemuthianum* have been reported worldwide using the 12 differential cultivars and the binary naming system (Ferreira et al., 2013; Gonzáles et al., 2015). In North America (Manitoba, Ontario, Michigan, and North Dakota), anthracnose races 7, 65, 73, and 89 were previously identified (del Rio and Bradley., 2002; Yang Dongfang et al., 2007). In North Dakota, races 7, 9, 72, 73, 89, 1153 and 1161 were identified in two separate studies (del Rio et al., 2002; Halvorson et al, 2016). All these races are of Mesoamerican origin, however race 73 is the most frequent (Halvorson et al., 2016). In Guatemala, previous studies have identify several races of anthracnose: 9, 73, 520, 521, 648,

1024, 1025, 1097, 1544, 1545, 1549, and 1645. The most common races of anthracnose reported in these studies were 520, 1024, and 1545 (Mahuku et al., 2004, Awale et al., 2008)

Table 1. Differential lines, Binary code, resistance genes and gene pool origin of differential cultivars used to characterize races of *Colletotrichum lindemuthianum*.

Differential lines	Binary Code	Resistance Gene	Gene Pool ^a
Michelite	1	<i>Co-11</i>	MA
Michigan Dark Red Kidney	2	<i>Co-1</i>	A
Perry Marrow	4	<i>Co-1</i> ³	A
Cornell 49-242	8	<i>Co-2</i>	MA
Widusa	16	<i>Co-1</i> ⁵	A
Kaboon	32	<i>Co-1</i> ²	A
Mexico 222	64	<i>Co-3</i>	MA
PI 207262	128	<i>Co-3</i> ³ , <i>Co-4</i> ³	MA
TO	256	<i>Co-4</i>	MA
TU	512	<i>Co-5</i>	MA
AB 136	1024	<i>Co-6</i> , <i>co-8</i>	MA
G2333	2048	<i>Co-4</i> ² , <i>Co-3</i> ⁵ , <i>Co-5</i> ²	MA

^aMA= Middle American A= Andean. Modified from: http://bic.css.msu.edu/_pdf/Anthracnose.pdf (accessed 29 October 2015).

The most recent study of characterization of isolates of *C. lindemuthianum* in Guatemala to identify resistance genes was conducted by Awale et al., in 2008. In this study, samples were collected from infected common bean tissue (stem and pods). A total of 12 isolates of the pathogen were characterized based on the 12 differential cultivars, and a race number was assigned based on the binary code (Table 1). Pathogen isolates were virulent to differential cultivars containing *Co-1*², *Co-2*, *Co-3*, *Co-4*, *Co-5* and *Co-6*, which are Mesoamerican genes. None of the races reported in Guatemala have shown any compatibility with the Andean resistant genes, suggesting that incorporating Andean genes of resistance could provide a broad range of

resistance in Guatemalan cultivars. Awale et al, 2008 noted that the combination of *Co-1*² and *Co-4*² genes for resistance could provide resistance to most races, excluding races 1572 and 1645. However, the authors also mentioned that a way to provide resistance for these races are the combination of *Co-1* and *Co-4*².

Anthracnose resistance genes generally follows a qualitative mode of inheritance. Resistant and susceptible reactions are well differentiated, because the plant pathogen interaction is specific and follows the gene for gene model (Flor 1955). Most of the genes reported show complete dominance and several ways of interaction can occur (complete dominance, partial dominance, additive effect or over dominance) due to the alleles involved (Ferreira et al., 2013).

A total of 21 specific genes for resistance to *C. lindemuthianum* in common bean have been identified. Aside from the differential cultivars, breeding programs are continuously searching for new sources of resistance to the pathogen and other sources of resistance genes have been found in both Middle American and Andean gene pools (Table 2).

Resistance genes commonly used for resistance to anthracnose are present in different bean genotypes. The resistance genes most commonly used for breeding programs are: *Co-1* locus and alleles, which are present in most of the Andean genotypes. This locus is relevant because it offers a broad spectrum of resistance for those races of *C. lindemuthianum* from Mesoamerican origin, since the pathogen interaction is very specific for genotypes of this gene pool (Kelly and Vallejo, 2004). A source of this type of resistance is the genotype AND 277, which belongs to the Andean gene pool, and has the *Co-1*⁴ gene for anthracnose and *Phg-1* gene for angular leaf spot resistance. This genotype has also shown resistance to 21 races of *C. lindemuthianum* including race 73 (Gonçalves-Vidigal et al, 2011). The effectiveness of *Co-1* locus also has been demonstrated against race 73 in the black bean cultivars (Jaguar, Phantom

and Raven), and Navy bean cultivars (Newport and Seafarer) (Kelly and Vallejo, 2004). Another important resistance gene is *Co-4*, although the most commonly used alleles in this locus are *Co-4*³ reported in PI 207262, which have been useful in Brazil; and *Co-4*², both located in linkage group Pv08. *Co-4*² is present in genotypes such as G2333, G2338 and SEL1308 (Kelly and Vallejo, 2004). Genotype G2333, has shown resistance under greenhouse conditions and field conditions to several races of *C.lindemuthianum* (Pastor-Corrales et al., 1994). G2333 has three anthracnose resistance genes pyramided including *Co-4*², which have been reported to be resistant to the highly virulent race 2047 (Kelly and Vallejo, 2004). In some countries of Africa, genotype G2333 was released as a commercial cultivar (Pastor-Corrales et al., 1994) and has been used for the introgression of resistance genes (Kanzimoto, 2016).

Other sources of resistance such as Ouro Negro (Honduras 35), from the Mesoamerican gene pool. It has shown resistance to 19 races of the pathogen including race 73 and it is known to contain the *Co-10* resistance gene. (Alzate-Marin et al, 2003). Cultivar Jalo Vermelho from the Andean gene pool is also a source of resistance, and contains the *Co-12* resistance gene. This cultivar shows resistance to races 23, 55, 89, and 453 (Gonçalves-Vidigal et al, 2008). Another resistant cultivar from an Andean source is Jalo Listras Pretas, which contains the resistant gene *Co-13*, and has shown resistance to races 9, 64, 65, and 73 (Gonçalves-Vidigal et al, 2008b). The Andean cultivar Pitanga, has the *Co-14* resistance gene and was evaluated for resistance using races 23, 64, 65, 73, and 2047 (Gonçalves-Vidigal et al, 2011). Recently, sources of resistance have been found in the Andean cultivar Paloma which has a designation of *Co-Pa* resistant gene and had shown resistance to races 2047 and 3481, which represent among the most virulents races of *C. lindemuthianum* (de Lima Castro et al, 2017). Another example of a new resistant cultivar from an Andean source is Amendoim Cavalo, this cultivar has resistance to different

racess, including race 73. The symbol proposed for this resistance gene is *Co-AC* (Nanami et al, 2017).

Table 2. Resistance genes, resources, gene pool, linked markers and map location for anthracnose in common bean.

Gene	Genetic Resource	Gene Pool	Linked Markers	Map Location
<i>Co-1</i>	MDRK	Andean	OF10 ₅₃₀	Pv01
<i>Co-1</i> ²	Kaboon	Andean	SE _{ACT} /M _{CCA}	
<i>Co-1</i> ³	Perry Marrow	Andean		
<i>Co-1</i> ⁴	AND 277	Andean	CV542014 ⁴⁵⁰ , TGA1.1 ⁵⁷⁰	
<i>Co-1</i> ⁵	Widusa	Andean	OA18 ₁₅₀₀	
<i>Co-2</i>	Cornell 49242	MA	OQ4 ₁₄₄₀ , OH20 ₄₅₀ , B355 ₁₀₀₀	Pv11
<i>Co-3</i>	Mexico 222	MA	SSR PV-ctt001	Pv04
<i>Co-3</i> ²	Mexico 227	MA		
<i>Co-3</i> ³	BAT 93, PI207262	MA		
<i>Co-4</i>	TO, G2333	MA	SAS13, SH18	Pv08
<i>Co-4</i> ²	SEL 1308	MA	SBB14, OC8	
<i>Co-4</i> ³	PI 207262 ^y	MA	OY20	
<i>Co-5</i>	TU, G2333	MA	OAB3 ₄₅₀	Pv07
<i>Co-5</i> ²	SEL 1360, G2333		SAB3, g1233 ₃₂₅₀	
<i>Co-6</i>	AB 136	MA	OAH1 ₇₈₀ , OAK20 ₈₉₀	Pv07
<i>Co-8</i>	AB 136	MA	OPAZ20	NA
<i>Co-9</i>	BAT 93	MA	SB12	Pv04
<i>Co-10</i>	Ouro Negro	MA	F10	Pv04
<i>Co-11</i>	Michellite	MA	NA	Pv03
<i>Co-12</i>	Jalo Vermelho	Andean	NA	NA
<i>Co-13</i>	Jalo Listas Pretas	Andean	OPV20 700	Pv03
<i>Co-14</i>	Pitanga	Andean	NA	Pv01
<i>Co-15</i>	Corinthiano	Andean	G2685	Pv04
<i>Co-16</i>	Crioulo 159	MA	NA	
<i>Co-17</i>	SEL 1308	MA	G19833	Pv03
<i>Co-18</i>	Jalo Pintado 2	Andean		NA
<i>Co-Pa</i>	Paloma	Andean		Pv01
<i>Co-AC</i>	Amendoim Cavalo	Andean		Pv01
<i>Co-Pe</i>	Perla	Andean		NA

NA None available; MDRK – Michigan Dark Red Kidney; MA – Middle American; ^y PI 207262 possesses 2-genes; G 2333 possesses 3-genes Modified from: http://bic.css.msu.edu/_pdf/Anthracnose.pdf

Genome wide association study (GWAS)

GWAS has been used to identify Quantitative Trait Loci (QTL) in humans and animals (Begum et al, 2015). In recent years, GWAS is a widely used tool for dissecting complex traits in plants, by comparing between the genotype and the phenotype (Mammadov et al., 2012). This type of study helps to identify QTL in panels of diverse germplasm through linkage disequilibrium (LD). LD is a non-random association between markers, genes or QTL (Gupta et al., 2005). LD is also caused by population structure and, for this reason it is important that association mapping studies to be performed within genotypes of the same gene pool or race (Blair et al., 2009). In addition, GWAS is revolutionary because candidate genes of larger and more diversified populations can be mapped (i.e. collections of germplasm) and compared with bi parental QTL analysis, where diversity is lower (contrasting parents for the trait of interest) (Stanton-Geddes et al., 2013; Huang and Han, 2014). One application example is the use of marker assisted selection (MAS) in breeding programs, by using markers tightly linked to the trait of interest (QTL), identified with the GWAS approach (Biscarini et al, 2015). Also, due to the GWAS improvement in recent years i.e. Genotyping by sequencing (GBS) (Schröder et al, 2016) and the use of more efficient software and new techniques to optimize the genome complexity to provide an appropriate level of marker density, is making of GWAS a widely used tool.

Several studies in common bean have shown the effectiveness of GWAS to identify genomic region associated with traits of economic importance, including disease resistance. In 2016, K. Ghising identified a genomic region associated to resistance to Halo Blight [*Pseudomonas syringae* pv. *phaseolicola* (Burkholder)]. In the same year Vasquez-Guzman found genomic regions associated to Fusarium root rot (*Fusarium oxysporum* f. sp. *dianthi*), and

Perseguini et al., 2016 in angular leaf spot (*Phaeoisariopsis griseola* (Sacc.) Ferraris). An anthracnose resistance study in Andean beans was performed using GWAS to identify new sources of resistance using a panel of 230 *P. vulgaris* genotypes from different areas of the world. These genotypes were tested with eight races of *C. lindemuthianum*. The study detected significant QTLs for resistance in Pv01, Pv02 and Pv04, and minor QTL in Pv10 and Pv11 (Zuiderveen et al., 2016). Recently, a GWAS was performed, and identified NBS-LRR genes related to anthracnose and common bean bacterial blight (CBB) caused by *Xanthomonas axonopodis* pv. *phaseoli* (*Xap*) (Wu et al., 2017). One of the objectives of this study was to develop SSR markers around these pathogen resistant genes. The study found not only previous reported associated regions but also new regions of resistance for both Anthracnose and CBB. Nine resistant loci for anthracnose and seven for CBB were detected. (Wu et al., 2017).

For GWAS, multiple models are tested (Table 3). The Naive general linear model without correction of structure; principal component analysis (PCA), which is a general linear model with fixed effects to control population structure (Yu et al., 2006); family relatedness is controlled by the Efficient mixed model analysis (EMMA) algorithm; and the Mixed model (MM) that control both relatedness and population structure.

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).

Model	Linear regression equation	Information captured in the model
Naive	$y = X\alpha + \varepsilon^\dagger$	y is related to X, without correction for structure
PCA	$y = X\alpha + P\beta + \varepsilon$	y is related to X, with correction for structure
EMMA	$y = X\alpha + Ku + \varepsilon$	y is related to X, with correction for kinship
MM	$y = X\alpha + P\beta + Ku + \varepsilon$	y is related to X, with correction structure and kinship

† 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 ε is the error term.

Since the germplasm from Guatemala could represent a potential source of resistance to *C. lindemuthianum*, the causal agent of anthracnose, which is one of the most devastating diseases for common bean worldwide, and is necessary to know the current diversity of the pathogen in Guatemala to the develop resistant cultivars against the disease.

The objectives of this research were:

- 1) To identify the most predominant races of *C. lindemuthianum* (Sacc. and Magnus) Briosi and Cavara present in the Guatemalan highlands.
- 2) To evaluate the climbing bean collection from Guatemala for resistance to anthracnose races from both Guatemala and North Dakota.
- 3) To identify genomic regions associated with anthracnose resistance using a GWAS approach.

MATERIAL AND METHODS

Plant material

To determine *C. lindemuthianum* races from Guatemala, the standard set of 12 race differentials was used (Table 1), (Pastor Corrales, 1991). Also, in order to rescue the pathogen from the samples with infected tissue, common bean seedlings from the Andean gene pool (Slenderette and Mountaineer snap beans) and Middle-American gene pool (black beans Zorro, Cornell 49242 and Black Knight, small red bean Merlot and navy bean Michelite) were used. Additionally, other sources of resistance were evaluated in the study: Amendoim Cavalo, AND 277, Jalo Vermelho, Jalo Listras Pretas, Pitanga, Corinthiano, Paloma, Jalo Pintado 2, Perla and BGF20 (A. 5).

The climbing bean collection from ICTA in Guatemala was used to identify potential accession with resistance to anthracnose (Orellana et al., 2006). From a total 604 accessions containing three different species *P. vulgaris*, *P. dumosus*, and *P. coccineus*, 369 accessions of *P. vulgaris* were used in this study. Accessions with differences in color and shape within the same accession were discarded to avoid inconsistency in the results, accessions utilized were bulked increased.

Field sampling of *C. lindemuthianum* infected tissue in common bean in the highlands of Guatemala

During the 2016 growing season from July to November, field sampling was conducted in the following departments of the highlands from Guatemala: Quetzaltenango, San Marcos, Huehuetenango, Quiche, and Totonicapán. These departments are considered the main areas of production and diversity for Guatemalan climbing beans (Beebe, 2007). Infected tissue with symptoms of the pathogen in leaves, stems, and pods of climbing beans and/or bush beans were collected in small farms or in the wild areas. A total of 132 samples, were collected at

Chimaltenango (28), Huehuetenango (18), Quetzaltenango (57), Quiche (4), San Marcos (4), and Totonicapán (21) (Table A. 1). Each sample was wrapped in a paper towel and placed into a paper bag or envelope with the corresponding label. The label contained the date, name of farmer, type of bean, country, location, GPS coordinates, and name of collector (Table A. 2). Samples were dried using paper towels according to the protocol described by Castellanos et al., (2015).

Pathogen isolation

Anthraxnose samples from Guatemala were sent to USDA-ARS Beltsville-MD (Dr. Pastor-Corrales) with previous approval of the Animal and Plant Health Inspection Service (APHIS). A Plant Protection and Quarantine (PPQ) form 599 was requested to authorize the shipment of the pathogen. The isolates were evaluated at USDA-ARS Beltsville because the laboratory is authorized to work with common bean biological materials (*C. lindemuthianum*, *Phaeoisoriopsis griseola*, *Pseudomonas syringae pv phaseolicola*, *Uromyces appendiculatus var appendiculatus*, *Xanthomonas axonopodis pv. phaseoli*, *Xanthomonas axonopodis pv. phaseolicolifuscans*) that can be considered a risk of accidental release or misuse.

A total of 88% of samples from leaves or pods either had weak anthracnose symptoms or showed contamination with other fungi. The samples were processed as follows: The tissue infected with the disease was crushed in a beaker and 10 ml of a solution of 1 ml Tween 20 and one liter of sterilized water was added; the solution was mixed for 2 min using a small and sterilized spatula. After this step, plants from different genotypes representing both gene pools (Slenderette, Merlot, Zorro, Cornell 49242, Michelite, Mountaineer White Half Runner, and Black Knight) were inoculated using a cotton swab by rubbing the primary leaves of the plant with the inoculum solution. Plants were incubated in a humidity chamber with 80% humidity at

24°C for 2 days and then placed in a greenhouse bench. A week after the inoculation, susceptible plants showed the typical anthracnose symptoms in leaves and stems. Infected leaves from these plants were collected (Castellanos et al., 2015).

Common bean tissue samples collected were surface sterilized by soaking the samples for one minute in a 10% bleach solution, using household bleach (5.25% NaOCl) to eliminate other undesirable microorganisms. The samples were rinsed three times in sterile distilled water (Castellanos et al., 2015). Tissue showing symptoms of *C. lindemuthianum* was crushed, and placed on potato dextrose agar (PDA, Merck ®); the PDA was prepared using 39g L⁻¹ distilled water and 10% streptomycin; or in APDA (Acidified PDA) media (25.6g of PDA, and 14 drops of lactic acid 50%/ liter distilled water) (M. Romberg, Pers. Comm., 2017). The plates were incubated for 4 to 5 days in the dark at 22°C. Hyphal tip or single spore isolation methods were used to establish a pure culture of the pathogen (Castellanos et al., 2015).

Host inoculation

After obtaining the mycelia and/or inoculum of *C. lindemuthianum*, the isolations were placed into APDA media. Sterilized bean leaves were placed onto the growth media. These leaves were collected from 15-day-old plants of any genotype of common bean, but without any previous fungicides application, in order to enhance the sporulation of the pathogen (Castellanos et al., 2015). Agar plugs that contained the *C. lindemuthianum* were placed into petri dishes. Sporulation was observed after 14 days of incubation at 22°C in the dark. Twelve differential lines for race identification (Table 1) were planted, in trays (25 cm x 50 cm) containing Promix®, until they presented their first fully-expanded trifoliate leaf (growth stage V1). Inoculum was obtained by the following protocol: sterilized distilled water was added into the APDA petri dish containing the pathogen sporulation onto the sterilized bean leaves, media was

scraped on the surface with a spatula. The suspension was filtered through a sterilized gauze to separate unwanted particles (sterilized leaf and/or APDA residues) from the conidia; then, the suspension was collected in a sterilized beaker (Castellanos et al., 2015). A hemocytometer was used to count conidia according to a previous described protocol (Bastidas, 2017) and the concentration was adjusted to 1.2×10^6 conidia mL^{-1} , and a portion of the suspension was poured into a 250-mL Erlenmeyer flask. The flask was connected to a DeVilbiss nebulizer (or airbrush) and to a compressor. Then plants were inoculated spraying a suspension of *C. lindemuthianum* onto the leaves and stems of seedling plants until the inoculum ran-off. The experiment was conducted as a completely randomized design where four plants (in the case of the Guatemalan climbing bean germplasm) per in three replicates cultivar were inoculated. For the differential cultivars, five plants per cultivar were used. The plants were maintained under high humidity (>80%) in a humidity chamber for a minimum of 48 hours, the range is 48 to 72 hours. Then the plants were moved to a greenhouse bench and grown at 24-30°C, and symptoms of anthracnose were observed on susceptible plants 8-10 days after inoculation. Ten days after of inoculation, disease severity was rated using the standard visual scale (1-9) for disease severity (Table 4) (Van Schoohoven A., and M.A. Pastor-Corrales. 1987). After rating the disease severity, a race designation number was assigned for each race of the pathogen determined by adding the binary numbers of each differential that showed susceptibility score between 4 and 9, (Table 1).

Additionally, different sources of resistance to anthracnose from the Andean gene pool were evaluated (Amendoim Cavalo, AND 277, Jalo Vermelho, Jalo Listras Pretas, Pitanga, Corinthiano, Paloma, Jalo Pintado 2, Perla and BGF20), using *C.lindemuthianum* races 556 and 3981 found in this study. These races were selected for this evaluation since they also affected differential lines containing genes from the Andean pool, and because this evaluation shows an

example of how useful races found in this study could be used to find resistance in other common bean lines. Spores of *C. lindemuthianum* race 556 and 3981 were increased and host inoculation and score evaluation was performed using the same protocol explained above (table A. 5)

Table 4. Evaluation scale for screening for anthracnose.

Score	Phenotype	Symptoms
1	Resistant	No visible
2	Resistant	Only a few lesions in primary leaf and/or veins.
3	Resistant	Very small lesions in primary leaf and/or veins.
4-5	Susceptible	Presence of several small lesions on the primary leaf veins and stems.
6-7	Susceptible	Numerous lesions on the leaf, stems, and evident necrotic lesions
8	Susceptible	Severe necrosis on leaves and/or stems.
9	Susceptible	Severe necrosis and plant death

Modified from: Van Schoohoven A., and M.A. Pastor-Corrales. 1987

Identification of resistant lines in the climbing bean collection from Guatemala.

C. lindemuthianum race 73 has been reported in North America, South America, and Guatemala. For this reason, it does not represent a danger of introducing a new exotic race of anthracnose into the region. Race 73 was used to evaluate the collection of climbing beans at the NDSU greenhouse complex, with the objective of find resistance to this race and to use the resistance not only in breeding programs from Guatemala but elsewhere. Since the most frequent race reported in North Dakota is race 73, resistance found could be used in the bean breeding program at NDSU. A completely randomized design with three repetitions per cultivar of the experiment were used for this evaluation. Five seedlings for each accession from Guatemala were planted in a tray (25 cm x 50 cm) containing Promix ®, the plants grown at 22°C with

light. Check used for susceptibility was Michelite, and the check for resistance were G2333 (Pastor Corrales, 1991) and Montcalm (Michigan Crop, 2017). When plants presented their first fully expanded primary leaf (growth stage V1), the inoculum of race 73 was provided by the pulse pathology lab at NDSU with the required concentration of 1.2×10^6 conidia mL⁻¹. Then the same protocol described above for inoculation of the pathogen and scoring for disease severity was used.

Genotypic data

SNPs were provided by the Dry Bean Genomics Lab at NDSU. A set of 102,000 SNPs were obtained using genotype by sequencing (GBS) (He et al. 2014), using the improved method developed and described by Schröder et al (2015). Sequences were aligned to the reference genome of common bean G19833 (Schmutz et al. 2014), and SNPs were called using GATK (McKenna et al. 2010). The total of accessions used for genotyping were 369. Markers were filtered for more than 50% missing data and then imputed using fastPHASE 1.3 (Scheet and Stephens, 2006). After filtering for more than 50% heterozygosity and 5% minor allele frequency, 78,754 SNPs remained (Tobar-Piñon et al, 2017).

Statistical procedures and GWAS

A statistical analysis was performed using SAS version 9.4 software, where the Least Square (LS) Means were calculated using the phenotypic data of the three replicates. The output data from the LS Means was used, continuous results used were the values that showed resistance (1-3 values) and susceptibility (4-9 values). Both the phenotypic and genotypic data were used in this study for GWAS, by using an R package called Genome Association and Prediction Integrated Tool (GAPIT) software (Zhang et al., 2010). R is an open source software used in statistical analysis, it provides extensive statistical analysis and graphical facilities

(<http://www.r-project.org/>). GAPIT uses mixed linear models (MLM) which incorporate fixed and random effects. The software uses several combinations of genotypic, phenotypic data, and external data obtained from kinship and PCA. For this study, genotypic data and matrices used were provided by Dry Bean Genomics Lab at NDSU. The hapmap used in this study, was also used for the study of Genetic Diversity of the Guatemalan Climbing Bean Collection performed by Tobar-Piñon, 2017. Multiple models were tested using R, structure fixed effect control model, relatedness random effect control model and also a mixed model to control both relatedness and population structure. Relatedness was calculated using EMMA and structure was calculated using principal components. The model with the lowest mean square deviation (MSD) was selected. The procedure for MSD is the following: first for each model all marker p-values were ranked from the smaller to the larger value, and then the calculations were done by using the formula, $MSD = \{\sum_{i=1}^n [p_i - (i/n)^2]\}/n$, where the rank number is designated as i , the probability of the i th ranked p -value is p_i and n means the number of markers (Mamidi et al. 2011). Significant SNP markers were defined using a permutation test and a cut-off p-value of 0.1% in the normal distribution (Mamidi et al., 2014). A Manhattan plot was constructed and used to visualize the results.

A logistic regression analysis to reconfirm significant associations using GenABEL software was performed. Logistic regression analysis is only based in two discrete values (dichotomous), binary values were used as follow: values with no symptoms (1 in the scale showed above) were scored as 0 and the other values (>1 that showed any symptom) were scored as 1. GenABEL software was used for this procedure, which is a fast tool for GWAS procedures and permits developing logistic regression analysis for qualitative traits. As other programs, GenABEL tests for association of single nucleotide polymorphisms (SNP) and phenotypes, and

finally the software allows to visualize the results using graphical procedures (Zhang et al., 2010).

The position of significant associations were compared with the common bean genome v2.1 (DOE-JGI and USDA-NIFA. 2017) to identify potential candidate genes. After comparing the significant SNPs with the genome annotation, candidate genes within 100 Kb (Moghadam et al., 2016) from the markers were selected, allowing insight into potential regions of interest. In addition, Jbrowse and Phytosome were searched for information related to proteins involved in plant biological processes for the candidate genes selected (Goodstein et al. 2012).

Additionally, an effort to locate the physical position of the GWAS significant peak relative to the physical position of *Co-5* and *Co-6* genes, based on the sequence of markers linked to these genes was performed. Markers previously reported (Table 2) linked to *Co-5* and *Co-6* genes were searched in PhaseolusGenes bean breeder's molecular marker toolbox (<http://phaseolusgenes.bioinformatics.ucdavis.edu/>) and then marker's sequence (forward and reverse) was searched in Phytosome (Goodstein et al. 2012; DOE-JGI and USDA-NIFA. 2017). The results allow to have an approximate physical position of genes, and then this position was compared with the position of the significant SNPs found in this study.

RESULTS

Major objective of dry bean breeding programs around the world are to improve seed yield potential and the deployment of resistance genes to reduce yield loss due to diseases. During May, June and July of 2016, 369 climbing bean accessions were evaluated to identify resistant lines to different races of *C. lindemuthianum*, which is one of the most devastating pathogens affecting common bean worldwide.

Furthermore, a race characterization of *C. lindemuthianum* in the Guatemalan highlands was conducted. The results of this study show the great degree of virulence diversity of the pathogen in Guatemala, and are a useful tool for developing resistant cultivars against the disease.

Evaluation for resistance to race 73 of *C. lindemuthianum* in climbing bean germplasm from Guatemala

Climbing bean accessions from Guatemala were evaluated for resistance using race 73 of *C. lindemuthianum* from North Dakota. Resistant checks for race 73, G2333 and Montcalm had an average score of 1 (no symptoms) and the susceptible check Michelite had the highest average value of 8 (susceptible). The LSM results (Table A. 3) indicate that 10% of 369 climbing bean accessions showed no symptoms and were classified as resistant. The mean was 3 (resistant), standard deviation was 1.48. The disease scores ranged from 1 and 8, and 56% of the population was rated between 2 and 3 (Table 4).

GAPIT results using the quantitative scale were not different when compared to results obtained by using the binary scale in GenABEL (Table A. 4, Figure A. 1) software. Only the GAPIT results are described since continuous data also provided appropriate results. The genomic regions associated with anthracnose resistance were identified using a GWAS approach with GAPIT using four statistical models, PCA, EMMA, MM and Naïve (Mamidi et al., 2011).

Race 73 Anthracnose phenotypic data from 369 climbing bean accessions from Guatemala and the genotypic data with 78754 SNPs were used in the analysis. Four regression models were used to obtain QQ-plots generated by plotting observed $-\log_{10} P$ -value against expected $-\log_{10} P$ -value (Lipka et al., 2012) (Figure 1). The model with the best mean square deviation (MSD) was selected according to Mamidi et al. (2011). The QQ-plots showed that MM and EMMA models are the closest to the regression line (Figure 1b, 1c), PC and Naïve models are separated of the regression line (Figure 1a, 1d). For all the QQ-plots, the model that fitted the best regression line for trait was EMMA and showed the lowest MSD value (Figure 1c).

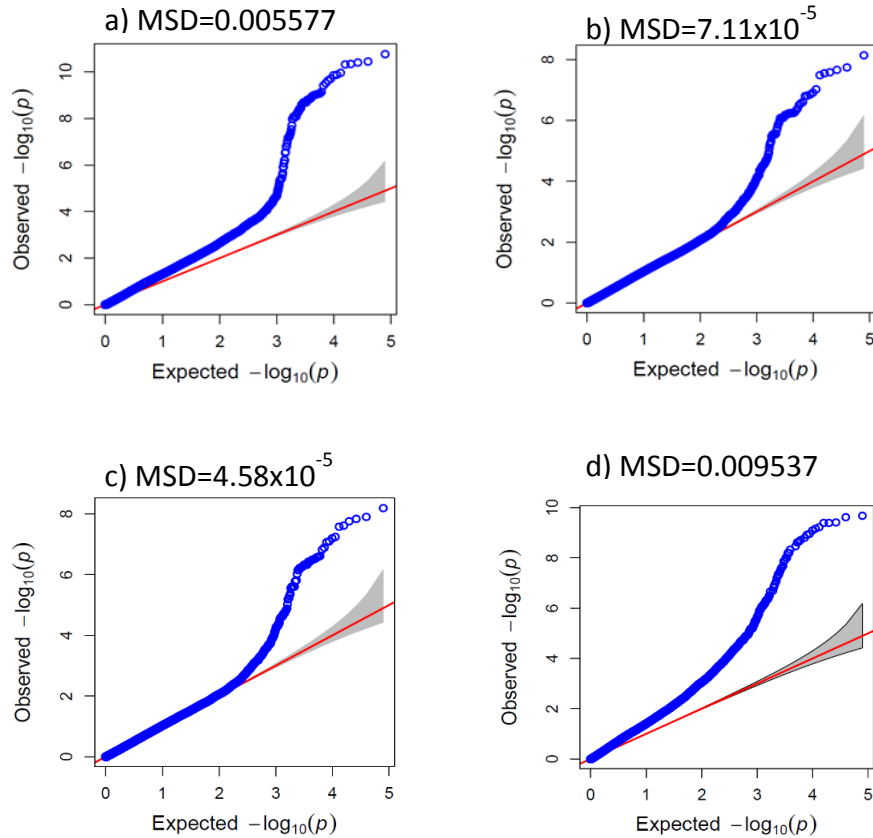


Figure 1. QQ-plots from 369 phenotypic data from climbing bean accession from Guatemala associated with 78754 SNP markers using anthracnose scores: a) PCA b) Mixed Model (MM) c) EMMA and d) Naïve.

The results indicate that significant associations with resistance in the Guatemalan climbing bean panel to *C. lindemuthianum* race 73 exist on Pv07 ($P \leq 0.001$) (Table 5). In

addition, another region is detected in Pv04 but at the 0.1 percentile (Figure 2). The Manhattan plots were graphed from the EMMA model, using $-\log_{10}$ of transformed P -values on the Y-axis against the X-axis which consisted in the physical position of the SNPs on the chromosome.

Table 5. Top ten SNPs significantly associated, chromosome, position, significant P -values and R^2 values per individual marker and grouped for the trait anthracnose on 369 climbing bean accessions from Guatemala, sorted by lowest P -value.

SNP	Chromosome	Position	P.value	Individual R^2	Grouped R^2
S07_8683756	7	8683756	6.28E-09	0.13	
S07_8726264	7	8726264	1.24E-08	0.12	
S07_8692719	7	8692719	1.42E-08	NA	
S07_8767491	7	8767491	1.69E-08	NA	0.16
S07_8683594	7	8683594	2.38E-08	NA	
S07_8672434	7	8672434	2.54E-08	NA	
S07_9162644	7	9162644	5.64E-08	0.09	
S07_8874842	7	8874842	6.26E-08	0.11	
S07_8874881	7	8874881	7.80E-08	NA	
S07_8874790	7	8874790	8.42E-08	NA	
S04_527782	4	527782	2.37E-07	0.08	
S04_1022377	4	1022377	6.28E-06	0.06	
S04_1254784	4	1254784	1.57E-05	0.05	0.11
S04_1327258	4	1327258	1.87E-05	0.05	
S04_1276626	4	1276626	2.88E-05	0.05	
S04_376239	4	376239	3.75E-05	NA	
S04_376230	4	376230	4.65E-05	NA	
S04_376249	4	376249	7.10E-05	NA	
S04_376227	4	376227	7.22E-05	NA	
S04_1327283	4	1327283	7.49E-05	NA	

NA: Not available

Significant associations were found in the Manhattan plot on Pv07 (86.8 Mb) (Figure 2). Resistance genes and alleles *Co-5* (Young et al, 1998; Vallejo and Kelly, 2009), *Co-5²* (Sousa et al, 2014), and *Co-6* (Schwartz et al, 1982; Campa et al, 2007) were previously reported and were located in Pv07.

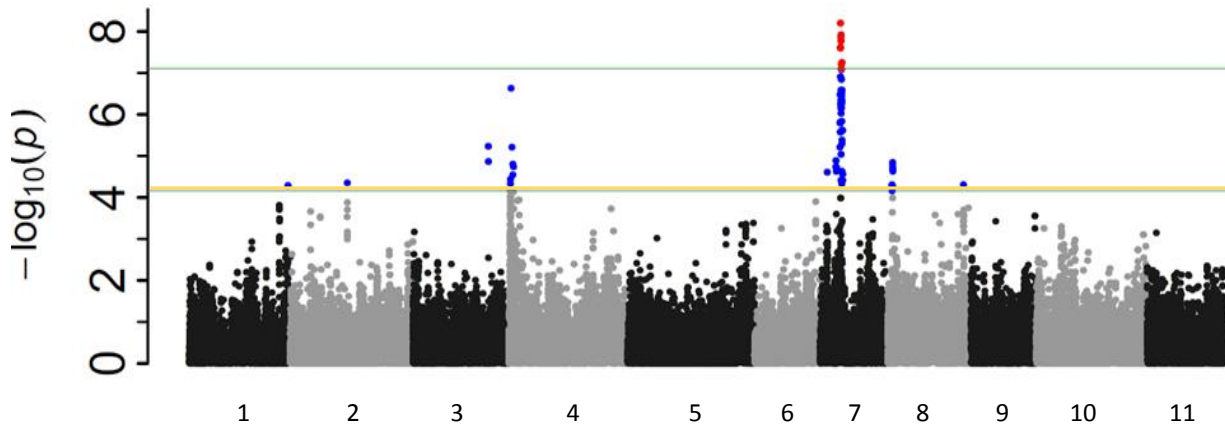


Figure 2. Manhattan plot using Efficient mixed model analysis (EMMA) for *C. lindemuthianum* resistance to race 73. The green line is the cut-off value to call a peak significant. SNPs above the 0.01 percentile are highlighted in red, while those above 0.1 are highlighted in blue above the yellow line. Numbers below the Manhattan plot represent chromosomes.

Using the position of the significant SNPs (Table5), and comparing the common bean genome in Jbrowse on Phytozome v 12 (Goodstein et al. 2012; DOE-JGI and USDA-NIFA. 2017), potential candidate genes in the region were selected. Candidate genes found were Phvul.007G086400 for SNP S07_8726264, Phvul.007G087200 for S07_8874842 and Phvul.007G085900 for SNP S07_8692719.

Phvul.007G086400 is a Laccase/Diphenol oxidase family protein ATLAC15, LAC15, TT10 (<https://phytozome.jgi.doe.gov/pz/portal.html#>), which is a gene involved in the lignification process of cell walls (Mayer, A.M. and Staples, R.C., 2002; Wang et al, 2015), a possible method of defense against *C. lindemuthianum*. In addition, this marker is located only 7.3 Kb from a leucine-rich repeat (LRR) and nucleotide binding APAF-1 (apoptotic protease-activating factor-1), R proteins and CED-4 (*Caenorhabditis elegans* death-4 protein) NB-ARC domain located in Phvul.007G086300 (<https://phytozome.jgi.doe.gov/pz/portal.html#>).

Phvul.007G087200 is a disease resistance family protein/LRR family protein (<https://phytozome.jgi.doe.gov/pz/portal.html#>) and Phvul.007G085900 is a serine protease inhibitor, Kazal-type family protein, (<https://phytozome.jgi.doe.gov/pz/portal.html#>) which is a

gene involved in the Serine-protease inhibitor, known to be involved in defense process against pathogens (Tian et al, 2004) and is only ~26Kb away from Phvul.007G086300.

In Pv04 major resistant genes have been reported, *Co-3*, *Co-3³*, and *Co-3⁵* (Young and Kelly, 1996; Kelly and Vallejo, 2004; Campa et al., 2017). For Pv04 (5.2Mb), in the SNP position 527,782, the candidate gene chosen based on the proximity of significant SNPs is gene Phvul.004G007750. This gene is ~40Kb apart from an LRR and NB-ARC cluster (<https://phytozome.jgi.doe.gov/pz/portal.html#>).

Marker's sequences found in PhaseolusGenes bean breeder's molecular marker toolbox (<http://phaseolusgenes.bioinformatics.ucdavis.edu/>) used to locate the physical position were g1233 for *Co-5²* (7.8 Mb) and SCAR AZ20 for *Co-6* (9.4Mb) genes. The significant association in this study on Pv07 is located approximately in 8.7 Mb, so the relative position of the significant peak is 0.9 Mb upstream from *Co-5²* and is 0.7Mb upstream from *Co-6*.

Race characterization of *C. lindemuthianum* in the Guatemalan highlands

From 132 samples with symptoms of anthracnose collected in the highlands of Guatemala during 2016, 88% could not be recovered, due the extent of the tissue infected with the pathogen. Only 16 samples produced viable mycelium to be characterized (Table 6), according the methodology explained previously. A total of 6 races of *C. lindemuthianum* were identified (Table 7).

Table 6. Recovered isolates used for race characterization

Isolate ID	Origin of isolate	State	Host plant in field	*GH isolation from
CLQ-1-2	ICTA	Quetzaltenango	L-6 (ICTA)	Zorro
CLQ-7-1	ICTA	Quetzaltenango	L-316 (ICTA)	MHWR
CLQ-8-1	ICTA	Quetzaltenango	L-92 (ICTA)	Zorro
CLQ-11-1	ICTA	Quetzaltenango	L-51 (ICTA)	Zorro
CLQ-30-4	Cajolá	Quetzaltenango	Hunapu (ICTA)	Black Knight
CLC-4-1	Acatenango	Chimaltenango	Climbing Bean (farmer)	Zorro
CLC-5-1	San Andres Itzapa	Chimaltenango	Climbing Bean (farmer)	Merlot
CLC-6-2	San Andres Itzapa	Chimaltenango	Climbing Bean (farmer)	Merlot
CLC-13-1	Chimaltenango	Chimaltenango	Climbing Bean (farmer)	Cornell 49242
CLC-18-2	Patzicía	Chimaltenango	Climbing Bean (farmer)	Cornell 49242
CLC-19-1	Patzcía	Chimaltenango	Bush Bean (farmer)	Slenderette
CLC-20-3	Patzicía	Chimaltenango	Bush Bean (farmer)	Zorro
CLC-26-2	Chimaltenango	Chimaltenango	Climbing Bean (farmer)	Slenderette
CLC-28-1	Chimaltenango	Chimaltenango	Climbing Bean (farmer)	Slenderette
CLH-3-1	Aguacatan	Huehuetenango	Guate 1026 (ICTA)	Zorro
CLH-5-3	Aguacatan	Huehuetenango	Guate 1026(ICTA)	Zorro

*GH=Greenhouse

ICTA= Experimental station of ICTA (Institute of Agricultural Science and Technology)

Table 7. Reaction of common bean differential lines to 16 isolates of *Colletotrichum lindemuthianum* from Guatemala.

Differentials Cultivars	Gene Pool	Anthracnose Resistant Gene	Linkage Group of <i>Phaseolus vulgaris</i>	Binary code**	Reaction of common bean differentials to isolates of <i>C. lindemuthianum</i>															
					CLC-13-1	CLQ-1-2	CLQ-7-1	CLQ-8-1	CLQ-11-1	CLH-3-1	CLH-5-3	CLC-18-2	CLC-26-2	CLC-20-3	CLC-28-1	CLQ-30-4	CLC-19-1	CLC-5-1	CLC-6-2	CLC-4-1
Michelite	MA	<i>Co-11</i>	Pv03	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9	5
MDRK*	A	<i>Co-1</i>	Pv01	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Perry Marrow	A	<i>Co-1³</i>	Pv01	4	7	1	1	1	1	1	1	1	1	1	1	1	1	1	1	6
Cornell 49242	MA	<i>Co-2</i>	Pv11	8	9	9	9	9	9	9	9	9	9	9	9	1	9	9	9	9
Widusa	A	<i>Co-1⁵</i>	Pv01	16	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Kaboon	A	<i>Co-1²</i>	Pv01	32	9	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Mexico 222	MA	<i>Co-3</i>	Pv04	64	1	7	7	7	7	7	7	7	7	7	7	1	7	7	7	3
PI 20762	MA	<i>Co-3³, Co-4³</i>	Pv04, 08	128	1	1	1	1	1	1	1	1	1	1	1	7	1	8	8	9
TO	MA	<i>Co-4</i>	Pv08	256	1	1	1	1	1	1	1	1	1	1	9	1	9	9	9	
TU	MA	<i>Co-5</i>	Pv07	512	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
AB 136	MA	<i>Co-6, co-8</i>	Pv07, NA	1024	1	1	1	1	1	1	1	1	1	1	1	1	8	8	8	7
G2333	MA	<i>Co-4², Co-3⁵, Co-5²</i>	Pv04,08, 07	2048	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	5
				Race	556	585	585	585	585	585	585	585	585	585	585	585	1609	1993	1993	3981

*Differential Andean cultivar MDRK=Michigan Dark Red Kidney

**Binary value: The designation of the race results from the addition of the binary value of each susceptible differential

Rating (1-3) resistant reaction; rating (4-9) susceptible reaction

NA: Not available

MA: Mesoamerican gene pool; A: Andean gene pool

A total of six races were identified: 556, 585, 897, 1609, 1993, and 3981. Race 556 was virulent on differential lines Perry Marrow and Kaboon, which contains *Co-1*², *Co-1*³, *Co-2* and *Co-5* resistance genes, from the Andean gene pool.

Race 585 was virulent to the *Co-2*, *Co-3*, *Co-5*, and *Co-11* resistance genes. Race 897 was virulent on differential cultivars containing the *Co-3*³, *Co-4*, *Co-4*³, *Co-5* and *Co-11* genes and alleles. Race 1609 was virulent to *Co-6* and *Co-8* and the same *Co* genes overcome by race 585. Resistant genes *Co-3*⁵, *Co-4*², and *Co-5*², found in G2333 were effective against race 1993, this race overcome genes *Co-2*, *Co-3*, *Co-3*³, *Co-4*, *Co-4*³, *Co-5*, *Co-6*, *co-8* and *Co-11*. Race 3981 was the most virulent among all six races, overcoming almost all the Mesoamerican resistant genes. The difference between this race and the previous one was that race 3981 was also virulent to Perry Marrow, which contains *Co-1*³, and G2333, which contains *Co-3*⁵, *Co-4*², and *Co-5*². Additionally, race 3981 was virulent to newer sources of resistance recently reported: Amendoin Cavalo, Paloma and Perla (Table A. 5) (de Lima Castro et al, 2017; Nanami et al, 2017). However, race 3981 was not virulent to Mexico 222, containing *Co-3* (Table 7).

With 10 samples identified with the same race based on the reaction of the differential lines, the most common race among all isolates was race 585. This race was found at Quetzaltenango at the ICTA research station, Chimaltenango in Patzicia and Chimaltenango counties, and Huehuetenango in Aguacatan village. However, most of the diversity of *C. lindemuthianum* was found in Chimaltenango state. Five of six races were present just in this department.

DISCUSSION

Evaluation for resistance to race 73 of *C. lindemuthianum* in climbing bean germplasm from Guatemala

Race 73 is one of the most common races of *C. lindemuthianum* worldwide. Moreover, several exotic sources of resistance have been found in the nature, i.e. G2333, which was collected in the state of Chiapas in the south of Mexico, and was locally known as Colorado de Teopisca (Pastor-Corrales et al., 1994). Amendoim Cavalo, an Andean bean collected in State of Santa Catarina in Brazil (Nanami et al, 2017), has been used for introgression of resistance in common bean cultivars and used as a commercial cultivar. Moreover, the population of climbing beans from Guatemala had shown resistance to natural pressure of the disease (Orellana et al., 2006). Our research suggests that climbing bean germplasm collected in highlands from Guatemala is a good potential source of resistance against race 73. Ten percent of the population is symptomless (score of 1) and 56% of the population is resistant (scored of 2-3).

However, GWAS results for resistance of the climbing bean germplasm from Guatemala showed that the most significant chromosomal region involved in the resistance to *C. lindemuthianum* is located in Pv07. Genes *Co-5*, *Co-5²* and *Co-6* (Table 7) on Pv07 have been previously reported to confer resistance to race 73 of *C. lindemuthianum* (Fouilloux, 1976; Trabanco et al., 2015; Campa et al, 2005; Gonçalves-Vidiga et al., 2003; Young and Kelly, 1996; Vallejo and Kelly, 2009; Alzate-Marin et al., 2009). This gene cluster has shown resistance to reported races of the pathogen including races 3, 6,7,31, 38, 39, 102 and 449 (Campa et al., 2009). Molecular markers have been developed and linked to some of these genes. Moreover, markers already identified, could be used to screen the resistant accessions found in the climbing bean collection from Guatemala in order to compare genomic regions related with resistance to anthracnose of this research with any *Co* resistance genes previously reported. Some examples of

markers previously reported are, the SCAR marker SAB3₄₀₀ (Vallejo and Kelly, 2001) which is linked to the *Co-5* locus at a distance of 12.98 cM, on Pv07 (Campa et al., 2005). g1233₃₂₅₀, an STS marker, is in coupling phase at a distance of 1.2cM developed for the *Co-5*² gene, which has been reported in Pv07 (Sousa et al., 2014). For the *Co-6* gene, a random amplified polymorphic DNA (RAPD) marker, OPAZ20₉₄₀, linked in coupling phase at 7.1 cM, has also been reported (Alzate-Marin et al., 2000).

Other significant markers for resistance to race 73 of *C. lindemuthianum* were found in Pv04. The *Co-3* cluster of resistance genes and the recent genes *Co-15* and *Co-16* are located in Pv04 (Zuiderveen et al., 2016). Many molecular markers are linked to these genes, some examples are: gene *Co-3* present in Mexico 222 has an SSR marker, PV-ctt001, at 11 cM (Rodriguez-Suarez et al., 2008; Boersma et al., 2013). However, *Co-3*³ has been associated with resistance to several races including race 73 and SCAR marker SAH18₁₁₀₀, is 3.7 cM apart of *Co-3*³ (Mendez-Vigo et al., 2005; Boersma et al., 2013); a sequence-tagged site (STS) marker, g2685, is linked in coupling phase at 5.6 cM from the *Co-15* locus (Sousa et al., 2015); similarly, STS, g2467_{900/800}, is in coupling phase at 4.8 cM from *Co-16* (Coimbra-Gonçalves et al., 2016).

Furthermore, in this study an effort to locate the map physical position of GWAS significant peak relative to the physical position of *Co-5*² and *Co-6* genes, based on the sequence of markers g1233, g2531 and SCAR AZ20 linked to these genes was performed. However, significant GWAS association (8.7Mb) was located between genes *Co-5*² (7.8 Mb) and *Co-6* (9.4Mb). Since there is no clear association between the significant peak and these genes previously reported, further study needs to be done to finely map the gene of interest and confirm if the region found is either *Co-5* and/or *Co-6* genes, or a new gene is conferring resistance in the climbing bean germplasm to *C. lindemuthianum* race 73.

Previous research has indicated that the resistance and susceptibility in the host, or virulence and avirulence of *C. lindemuthianum* are controlled by major genes (Beebe and Pastor-Corrales, 1991). In this study, four candidate genes were chosen for the regions in Pv07 and Pv04, based on their proximity to the significant SNP markers. A Laccase/Diphenol oxidase family protein, involved in the lignification process of cell walls (Mayer, A.M. and Staples, R.C., 2002; Wang et al, 2015). This protein activates the response of defense and increases the resistance against hemibiotrophic fungi, enhancing the cell wall resistance against the mechanical pressure of the specialized organ (appresoria) used to infect the host (Bellincampi et al, 2014). This type of resistance has been reported in alfalfa (*Medicago sativa L.*) as a defense response against *Colletotrichum trifolii*, the causal agent of alfalfa anthracnose (Gallego-Giraldo et al., 2011). Additionally, our candidate gene is 7.3 Kb from a plant disease resistance (R) gene, LRR and NB-ARC reported by Meziadi et al, 2015. The second candidate gene is located at 9 Kb from the marker S07_8874842, it is a cluster of disease resistance family protein/LRR family protein containing R genes. R genes of this type have been identified in many plant species, and have been reported its effectiveness against pathogens (Meziadi et al., 2016). When NB-ARC proteins recognize pathogen effectors, a signal activates immunity systems in resistant genotypes (Elmore et al., 2011)

The third candidate gene on Pv07, a serine protease inhibitor, Kazal-type family protein is involved in defense process against pathogens. This defense process has been reported in the oomycete *Phytophthora infestans* which cause late blight in potato and tomato (Tian et al, 2004).

On Pv04, the significant SNP is ~40Kb apart from the candidate gene; the candidate gene based on the proximity of the marker belongs to a cluster of disease resistance family protein/LRR family protein containing R genes.

The use of recombinant inbred lines (RIL) populations or a F2 population is suggested in order to develop markers useful for MAS. SNPs considered as significant markers should to be developed, and tested as potential diagnostic markers for the significant regions on Pv07 and Pv04. A fine mapping of genomic regions showing resistance is also suggested, by using flanking markers linked to the gene of interest. Also, it is recommended to screen this germplasm against different races of *C.lindemuthianum*, to identify additional resistant lines and genomic regions associated with anthracnose resistance. The results obtained in this work are of great importance, since resistant accessions could be used to introgress resistance into lines of interest. In addition, since race Guatemala is a new source of diversity (Tobar-Piñon et al., 2017), new genes conferring resistance to other races of the pathogen could be discovered.

Race characterization

In this study, 6 races were characterized based on the response of the differential set, the most frequent among the isolates was race 585. All the isolates were virulent to the Mesoamerican differential cultivar TU. Michelite, Cornell 49242 and Mexico 222 also were affected by almost all races. The races identified displayed more Mesoamerican virulence genes than Andean virulence genes. Races 556 and 3981 showed compatibility with Andean genes in locus *Co-1* (Table 7). Previous studies have reported races 585 in Guatemala (Awale et al, 2007), 1609 in Costa Rica (Mahuku et al, 2004), and 1993 in Costa Rica and Honduras (Mahuku et al, 2004) (Balardin et al, 1997). However, races 556, 897 and 3981 have not been reported in Guatemala before. This could be probably because in previous studies the sampled area was different, the host or weather conditions were not appropriate for the disease to show enough symptoms at the sampling time, or because some races changed across time. These results respond to the geographic coevolution pattern where Middle American gene pool hosts are

mostly affected by *C. lindemuthianum* races that correspond to these genes, while Andean gene pool origin hosts are mainly affected by the pathogen that had coevolved in that specific region. It has been demonstrated that virulence of *C. lindemuthianum* is specific for each gene pool (Pastor-Corrales, 1996).

A challenge in the bean-anthracnose patho-system are the existence of different races of the pathogen, which represent a threat for resistance breeding. Diversity of the pathogen is higher in Central America than in South and North America (Pastor-Corrales, 1996; Sicard et al., 1997; Balardin et al., 1997). This may result in the eventual breakdown of resistance in cultivars of the highlands of Guatemala.

The identified races of the pathogen should be used to evaluate resistance in the climbing bean accessions from Guatemala or other accessions from dry bean breeding programs around the world, since the most effective and environmentally control approach for this disease is genetic resistance (Mohammed, 2013). Because, resistance genes for all known races of anthracnose exist and therefore gene pyramiding would help to obtain more durable resistance in dry bean cultivars against the pathogen (Mahuku et al, 2002). Previous studies have evaluated the virulence patterns of the pathogen in Guatemala, and have suggested the pyramiding of *Co-1²* and *Co-4²* genes from both gene pools (Awale et al, 2007). However, races 556 and 3981, found at one location in the highland represent a threat by overcoming the resistance of *Co-1²* and *Co-4²*. Race 3981, was also virulent to additional sources of resistance from the Andean gene pool that contain *Co-13*, *Co-15*, and the recent reported *Co-Pa*, *Co-AC* and *Co-Pe* genes. This virulent race could be used to search for new sources of resistance and test sources of resistance previously reported.

Results suggest that cultivars and/or sources of resistance genes of Andean origin *Co-1* and *Co-1⁵*, are needed to develop common bean cultivars with broad and durable resistance to *C. lindemuthianum* in the highlands of Guatemala or other regions. In addition, a confirmation of the virulence of each race reported is necessary and additional sampling is needed to evaluate possible changes and/ or new races, due the pathogen diversity in this region.

This study contributes, knowledge regarding which resistance sources is needed to develop new climbing bean cultivars that will be resistant to *C. lindemuthianum* races found in Guatemala. Furthermore, the identification of races not previously reported are of great relevance to the common bean research community, since they could be used to detect new resistant genes in common bean lines of potential value to breeding programs.

REFERENCES

- Abbo, S., Y.T. Mesghenna, and H. Van Oss. 2011. Interspecific hybridization in wild Cicer sp. *Plant Breed.* 130:150–155.
- Abbo, S., S. Lev-Yadun, and A. Gopher. 2014. Plant domestication in the Near East. p. 1-9. *In* Encyclopedia of the History of Science, Technology, and Medicine in Non-Western Cultures. Springer Netherlands.
- Akibode, A., and M. Maredia. 2011. Global and regional trends in production, trade and consumption of food legume crops. Available at [Spia.http://impact.cgiar.org/sites/default/files/images/Legumetrends2.pdf](http://impact.cgiar.org/sites/default/files/images/Legumetrends2.pdf). (Accessed November 17, 2017)
- Aulchenko, Y.S., S. Ripke, A. Isaacs, and C.M. van Duijn. 2007. GenABEL: an R library for genome-wide association analysis. *Bioinformatics* 23: 1294–1296.
- Alzate-Marin, A.L., H. Menarim, J.M. Chagas, E.G.D. Barros, and M.A. Moreira. 2000. Identification of a RAPD marker linked to the *Co-6* anthracnose resistant gene in common bean cultivar AB 136. *Genet. Mol. Biol.* 23:633-637.
- Alzate-Marin, A. L., M. R. Costa, K. M. Arruda, E. G. de Barros, and M. A. Moreira. 2003. Characterization of the anthracnose resistance gene present in Ouro Negro (Honduras 35) common bean cultivar. *Euphytica* 133:165-169.
- Awale, H., E. Falconi, J.C. Villatoro, and J. D. Kelly. 2007. Control and characterization of *Colletotrichum lindemuthianum* isolates from Ecuador and Guatemala. *Annu. Rept. Bean Improv. Coop.* 50:85-86.
- Balardin, R.S., A.M. Jarosz, and J.D. Kelly. 1997. Virulence and molecular diversity in *Colletotrichum lindemuthianum* from South, Central, and North America. *Phytopathol.* 87:1184-1191.
- Bannerot, H. 1965. Résultats de l'infection d'une collection de haricots par six races physiologiques d'anthracnose. *Ann Amélior Plantes* , 15:201-222 Available at <http://www.sidalc.net/cgi-bin/wxis.exe/?IsisScript=catalco.xis&method=post&formato=2&cantidad=1&expresion=mfn=054033> (Accessed August 27, 2017)
- Bastidas, O. 2017. Cell Counting with Neubauer Chamber Basic Hemocytometer Usage Technical note, p. 6. Available at <http://celeromics.com/en/resources/docs/Articles/Cell-counting-Neubauer-chamber.pdf> (Accessed August 28, 2017)
- Beebe, S.E. and M.A. Pastor-Corrales. 1991. Breeding for disease resistance. *Common beans: research for crop improvement.* p. 561-617.
- Beebe, S., P. W. Skroch, J. Tohme, M. C. Duque, F. Pedraza, and J. Nienhuis. 2000. Structure of genetic diversity among common bean landraces of Middle American origin based on correspondence analysis of RAPD. *Crop Sci.* 40:264-273.
- Begum, H., J.E. Spindel, A. Lalusin, T. Borromeo, G. Gregorio, J. Hernandez, P. Virk, B. Collard, and S.R. McCouch. 2015. Genome-wide association mapping for yield and other agronomic traits in an elite breeding population of tropical rice (*Oryza sativa*). *PloS one.* p. 19.
- Bellincampi, D., F. Cervone, and V. Lionetti. 2014. Plant cell wall dynamics and wall-related susceptibility in plant–pathogen interactions. *Front. Plant Sci.* p. 8.
- Biscarini, F., P. Cozzi, L. Casella, P. Riccardi, A. Vattari, G. Orasen, R. Perrini, G. Tacconi, A. Tondelli, C. Biselli, and L. Cattivelli. 2016. Genome-wide association study for traits related to plant and grain morphology, and root architecture in temperate rice accessions. *PloS one.* p. 28.

- Blair, M.W., M.C. Giraldo, H.F. Buendía, E. Tovar, M.C. Duque, and S.E. Beebe. 2006. Microsatellite marker diversity in common bean (*Phaseolus vulgaris* L.). *Theor Appl Genetics* 113:100-109.
- Blair, M.W., L.M. Díaz, H.F. Buendía, and M.C. Duque. 2009. Genetic diversity, seed size associations and population structure of a core collection of common beans (*Phaseolus vulgaris* L.). *Theor. Appl. Genet.* 119: 955–972.
- Blair, M.W., A.J. Cortés, R.V. Penmetsa, A. Farmer, N. Carrasquilla-García and D.R. Cook. 2013. A high-throughput SNP marker system for parental polymorphism screening and diversity analysis in common bean (*Phaseolus vulgaris* L.). *Theor. Appl. Genetics* 126:535–548.
- Boersma, J.G., R.L. Conner, P.M. Balasubramanian, K. Yu, and A. Hou. 2013. Marker-assisted dissection of anthracnose resistance in the dry bean cultivar Morden003. *Canadian J. of Plant Science* 93:1115-1123.
- Broughton, W.J., G. Hernández, M. Blair, S. Beebe, P. Gepts, and J. Vanderleyden. 2003. Beans (*Phaseolus spp.*) – model food legumes. *Plant Soil* 252:55–128.
- Burlakoti, R. R. 2008. *Gibberella Zeae*: Population structure, mycotoxin profiles, Real-time PCR quantification, and host resistance. North Dakota State University. 83p.
- Campa, A., C. Rodríguez-Suárez, A. Pañeda, R. Giraldez, J.J. Ferreira and V. Serida. 2005. The bean anthracnose resistance gene *Co-5* is located in linkage group B7. *Annu. Rept. Bean Improv. Coop.* 48:68-69.
- Campa, A., E.P. Vega, R. Giraldez, J.J. Ferreira and V. Serida. 2007. Inheritance of race-specific resistance to anthracnose in the differential cultivar AB136. *Annu. Rept. Bean Improv. Coop.* 50:87-88.
- Campa, A., R. Giraldez, and J.J. Ferreira. 2011. Genetic analysis of the resistance to eight anthracnose races in the common bean differential cultivar Kaboon. *Phytopathology* 101: 757-764.
- Campa, A., N. Trabanco, and J.J. Ferreira. 2017. Identification of clusters that condition resistance to Anthracnose in the common bean differential cultivars AB136 and MDRK. *Phytopathology* 107:1515-1521.
- Castellanos, G., C. Jara., and G. Mosquera. 2015. Bean pathogens: practical guide for lab and greenhouse work. Centro Internacional de Agricultura Tropical (CIAT). Cali, Colombia. p. 244.
- Chacón, M.I., B. Pickersgill, and D.G. Debouck. 2005. Domestication patterns in common bean (*Phaseolus vulgaris* L.) and the origin of the Mesoamerican and Andean cultivated races. *Theor. Appl. Genetics* 110:432-444.
- Chen, Y.-Y., R.L. Conner, C.L. Gillard, G.J. Boland, C. Babcock, K.F. Chang, S.F. Hwang, and P.M. Balasubramanian. 2007. A specific and sensitive method for the detection of *Colletotrichum lindemuthianum* in dry bean tissue. *Plant Dis.* 91:1271-1276.
- Chicas, A., and G. Macino. 2001. Characteristics of post- transcriptional gene silencing. *EMBO reports.* 2:992-996.
- Coimbra-Gonçalves, G.K., M.C. Gonçalves-Vidigal, R.T. Coelho, G. Valentini, P.S. Vidigal Filho, G.F. Lacanallo, L.L. Sousa, and H.T.Elias. 2016. Characterization and mapping of Anthracnose resistance gene in Mesoamerican common bean cultivar Crioulo 159. *Crop Science*, 56:2904-2915.
- del Rio, L and C. Bradley. 2002. Anthracnose of dry beans. NDSU Extension Service: PP-1233.

- del Río, L.E., R.S. Lamppa, and P.L. Gross. 2003. Characterization of the reaction of North Dakota dry bean cultivars to three races of *Colletotrichum lindemuthianum*. *Plant Dis.* 87:263-265.
- de Lima Castro, S.A., M.C. Gonçalves-Vidigal, T.A.S. Gilio, G.F. Lacanallo, G. Valentini, V. da Silva Ramos Martins, Q. Song, M.Z. Galván, O.P. Hurtado-Gonzales, and M.A. Pastor-Corrales. 2017. Genetics and mapping of a new anthracnose resistance locus in Andean common bean Paloma. *BMC Genomics.* p. 12.
- DOE-JGI and USDA-NIFA. 2017. *Phaseolus vulgaris* v2.1. Available at <http://phytozome.jgi.doe.gov/> (Accessed April 24, 2017)
- Elmore, J.M., Z.J.D. Lin, and G. Coaker. 2011. Plant NB-LRR signaling: upstreams and downstreams. *Current opinion in plant biology.* 14:365-371.
- FAOSTAT. 2016. Beans, dry. Available at <http://faostat3.fao.org/faostat-gateway/go/to/home/E> (Accessed May 25, 2016)
- Ferreira, J.J., A. Campa, and J.D. Kelly. 2013. Organization of genes conferring resistance to Anthracnose in common bean. p. 151–181. *In* Translational Genomics for Crop Breeding. John Wiley & Sons Ltd.
- Fouilloux, G., 1976. Bean anthracnose: new genes of resistance. *Ann.Rep. Bean Improv. Coop.* 19:36-37.
- Fouilloux, G. 1979. New races of bean anthracnose and consequences on our breeding programs. *In* H. Marañón, and J. A. Meyer (eds), *International Symposium on Diseases of Tropical Food Crops 3*, proceedings. p. 221-235. Université Catholique de Louvain, Louvain la Neuve, Belgium.
- Fischer, E.F., and B. Victor. 2014. High-end coffee and smallholding growers in Guatemala. *Lat. Am. Res. Rev.* 49:155–177.
- Flores, L. and R.H. Bernsten., 2008. Pilyo beans in Guatemala. *Annu. Rept. Bean Improv. Coop.* 51:154-155.
- Funck, D., K. Clauß, W.B. Frommer and H.A. Hellmann. 2012. The Arabidopsis CstF64-like RSR1/ESP1 protein participates in glucose signaling and flowering time control. *Front. Plant Sci.* 13p.
- Gallego-Giraldo, L., Y. Jikumaru, Y. Kamiya, Y. Tang, and R.A. Dixon. 2011. Selective lignin downregulation leads to constitutive defense response expression in alfalfa (*Medicago sativa* L.). *New Phytol.* 190:627-639.
- Gepts, P., F.J.L. Aragão, E. de Barros, M.W. Blair, R. Brondani, W. Broughton, I. Galasso, G. Hernández, J. Kami, P. Lariguet, P. McClean, M. Melotto, P. Miklas, P. Pauls, A. Pedrosa-Harand, T. Porch, F. Sánchez, F. Sparvoli, and K. Yu. 2008. Genomics of *Phaseolus* beans, a major source of dietary protein and micronutrients in the tropics. p. 113-143. *In* *Genomics of Tropical Crop Plants. Plant Genetics and Genomics: Crops and Models.* Springer New York.
- Geffroy, V., S. Delphine, J. C. F. de Oliveira, M. Se´vignac, S. Cohen, P. Gepts, C. Neema, T. Langin, and M. Dron. 1999. Identification of an ancestral resistance gene cluster involved in the coevolution process between *Phaseolus vulgaris* and its fungal pathogen *Colletotrichum lindemuthianum*. *Mol. Plant Microb. Interact.* 12:774-784.
- Ghising, K. 2016. Screening of The USDA Core collection of common bean for reaction to Halo Blight and identification of genomic regions associated with resistance. Ph.D. Thesis, North Dakota State University, Fargo, North Dakota. p. 103.

- González A.M., F.J. Yuste-Lisbona, A.P. Rodiño, A.M. De Ron, C. Capel, M. García-Alcázar, R. Lozano and M. Santalla. 2015. Uncovering the genetic architecture of *Colletotrichum lindemuthianum* resistance through QTL mapping and epistatic interaction analysis in common bean. *Frontiers in Plant Sci.* 13p.
- Gonçalves-Vidigal, M.C., V. Vallejo and J.D. Kelly. 2003. Characterization of the anthracnose resistance in the differential cultivar Widusa. *Annu. Rept. Bean Improv. Coop.* 151:411-419.
- Gonçalves-Vidigal, M.C., A.S. Cruz, A. Garcia, J. Kami, P.S. Vidigal Filho, L.L. Sousa, P. McClean, P. Gepts, and M.A. Pastor-Corrales. 2011. Linkage mapping of the *Phg-1* and *Co-14* genes for resistance to angular leaf spot and anthracnose in the common bean cultivar AND 277. *Theor. Appl. Genet.* 122:893–903.
- Gonçalves- Vidigal, M.C., G.F. Lacanallo, and P.S. Vidigal Filho. 2008. A new gene conferring resistance to anthracnose in Andean common bean (*Phaseolus vulgaris* L.) cultivar ‘Jalo Vermelho’. *Plant Breed.* 127:592-596
- Goodstein, D.M., S. Shu, R. Howson, R. Neupane, R.D. Hayes, J. Fazo, T. Mitros, W. Dirks, U. Hellsten, N. Putnam and D.S. Rokhsar. 2012. Phytozome: a comparative platform for green plant genomics. *Nucleic acids research*, 40:1178-1186
- Halvorson, J.M., R.S. Lamppa, S.G. Markell, and J.S. Pasche. 2016. Characterization of *Colletotrichum lindemuthianum* races infecting dry edible bean in North Dakota. *Can. J. Plant Pathol.* 38:64-69.
- Hammer, K. 1984. Das Domestikationssyndrom. Die Kulturpflanze: Berichte Und Mitteilungen Aus Dem Institut Fur Kulturpflanzenforschung Der Deutschen Akademie Der Wissenschaften Zu Berlin in Gatersleben Krs. Aschersleben (Domestication syndrome. The crop. Reports and messages from the institute for crop plant research the national academy of sciences to Berlin in Gatersleben Krs Aschersleben). 32:11–34
- He, J., X. Zhao, A. Laroche, Z.X. Lu, H. Liu, and Z. Li. 2014. Genotyping-by-sequencing (GBS), an ultimate marker-assisted selection (MAS) tool to accelerate plant breeding. *Front. Plant Sci.* p. 8.
- Huang, X., and B. Han. 2014. Natural variations and genome-wide association studies in crop plants. *Annu. Rev. Plant Biol.* 65:531-551.
- IICA Instituto Interamericano de Cooperación para la Agricultura. 2014. Las cadenas de valor de maíz blanco y frijol en Centroamérica: actores, problemas y acciones para su competitividad (Value chains of white maize and beans in Central America: actors , issues and actions for competitiveness) I IICA, Red SICTA, Cooperación Suiza en América Central. San José, C.R. p. 127.
- Jänicke-Després, V.R., and B.D. Smith. 2006. Ancient DNA and the integration of archaeological and genetic approaches to the study of maize domestication. p. 83-95. *In Histories of maize.* Elsevier.
- Jaenicke-Després, E. S. Buckler, B. D. Smith, M. T. P. Gilbert, A. Cooper, J. Doebley, and S. Pääbo. 2003. Early allelic selection in maize as revealed by ancient DNA. *Science* 302:1206-1208.
- Kazimoto, G.K. 2016. Identification of *Colletotrichum lindemuthianum* and introgression of its resistance gene (s) to common bean (*Phaseolus vulgaris* L.) adapted in Tanzania Available at <http://suaire.suanet.ac.tz:8080/xmlui/handle/123456789/1523>. (Accessed November 16, 2017)

- Käss, E., and M. Wink. Molecular phylogeny and phylogeography of *Lupinus* (*Leguminosae*) inferred from nucleotide sequences of the *trbcL* gene and ITS 1 + 2 regions of rDNA. *Plant Syst. Evol.* 208:139-167.
- Kelly, J.D., P. Gepts, P.N. Miklas and D.P. Coyne. 2003. Tagging and mapping of genes and QTL and molecular marker-assisted selection for traits of economic importance in bean and cowpea. *Field Crops Research*, 82:135-154.
- Kelly, J.D., and V.A. Vallejo. 2004. A Comprehensive review of the major genes conditioning resistance to anthracnose in common bean. *HortScience* 39:1196-1207.
- Kumar, J., E. Srivastava, M. Singh, and A. Pratap. 2014. Genomics in studying the legume genome evolution. p. 287-300. *In* *Legumes in the Omic Era*. Springer New York
- Kelly, J., G. Zuiderveen., and B. Padder, 2015. Common bean disease workshop-2015 anthracnose update. MSU. Available at http://arsfifbean.uprm.edu/bean/wpcontent/uploads/2015/09/BDW-Day4-Anthrachnose_James-Kelly.pdf (Accessed October 29, 2015)
- Lamesch, P., T.Z. Berardini, D. Li, D. Swarbreck, C. Wilks, R. Sasidharan, R. Muller, K. Dreher, D.L. Alexander, M. Garcia-Hernandez, and A.S. Karthikeyan. 2012. The Arabidopsis Information Resource (TAIR): improved gene annotation and new tools. *Nucleic acids research*, 40:1202-1210.
- Lavin, M., P.S. Herendeen, and M.F. Wojciechowski. 2005. Evolutionary rates analysis of *Leguminosae* implicates a rapid diversification of lineages during the tertiary. *Syst. Biol.* 54:575-594.
- Legume Innovation Lab. 2015. FY 2014 Report Feed the Future Innovation Lab for Collaborative Research on Grain Legumes (Legume Innovation Lab). Available at http://pdf.usaid.gov/pdf_docs/PA00KR44.pdf (Accessed November 16, 2017)
- Lewis, G., B. Mackinder, and M. Lock. 2005. *Legumes of the world*. Kew: Royal Botanic Gardens, Kew. p. 577.
- Lipka, A.E., F. Tian., Q. Wang., J. Peiffer., M. Li., P.J. Bradbury., M.A. Gore., E.S. Buckler and Z. Zhang. 2012. GAPIT: genome association and prediction integrated tool. *Bioinformatics*. 28:2397-2399.
- MAGA Ministerio de Agricultura y Ganaderia Guatemala. 2014. Analisis de precios de frijol rojo y frijol negro. Available at http://web.maga.gob.gt/diplan/download/informacion_del_sector/publicaciones_diversas/An%C3%A1lisis%20de%20precios%20de%20frijol%20rojo%20y%20frijol%20negro%20-%20Mayo%202014.pdf (Accessed August 28, 2017)
- Mahuku, G.S., and J.J. Riascos. 2004. Virulence and molecular diversity within *Colletotrichum lindemuthianum* isolates from Andean and Mesoamerican bean varieties and regions. *Eur. J. Plant Path.* 110:253-263.
- Mammadov, J., R. Aggarwal, R. Buyyarapu, and S. Kumatla. 2012. SNP markers and their impact on plant breeding. *Int. J. Plant Genomics*. p. 11.
- Mamidi, S., S. Chikara, R. J. Goos, D. L. Hyten, D. Annam, S. M. Moghaddam, R. K. Lee, P. B. Cregan, and P. E. McClean. 2011. Genome-wide association analysis identifies candidate genes associated with iron deficiency chlorosis in soybean. *Plant Genome* 4:154-164.
- Mamidi, S., R.K. Lee, J.R. Goos, and P.E. McClean. 2014. Genome-wide association studies identifies seven major regions responsible for iron deficiency chlorosis in soybean (*Glycine max*). *PLoS One*. p. 13.

- Markell, S., M. Wunsh, and L. del Rio. 2012. Anthracnose of dry beans. NDSU Extension Service. Fargo, N.D. p. 2.
- Mastenbroek, C. 1960. A breeding program for resistance to anthracnose in dry shell haricot beans, based on a new gene. *Euphytica*. 9:177-184.
- Mayer, A.M, and R.C. Staples. 2002. Laccase: new functions for an old enzyme. *Phytochemistry*. 60:551-565.
- McKenna, A., M. Hanna, E. Banks, A. Sivachenko, K. Cibulskis, A. Kernytsky, K. Garimella, D. Altshuler, S. Gabriel, M. Daly, and M. A. DePristo. 2010. The Genome Analysis Toolkit: a MapReduce framework for analyzing next-generation DNA sequencing data. *Genome Res*. 20:1297-1303.
- Méndez-Vigo, B., C. Rodríguez-Suárez, A. Pañeda, J.J. Ferreira, and R. Giraldez. 2005. Molecular markers and allelic relationships of anthracnose resistance gene cluster B4 in common bean. *Euphytica*, 141:237-245.
- Meziadi, C., M.M.S. Richard, A. Derquennes, V. Thareau, S. Blanchet, A. Gratias, S. Pflieger, and V. Geffroy. 2015. Development of molecular markers linked to disease resistance genes in common bean based on whole genome sequence. *Plant Sci*. 242:351-357.
- Michigan Crop Improvement association. 2017. Montcalm Dark Red Kidney. Available at <http://www.michcrop.com/documents/MontcalmDarkRedKidney.pdf> (Accessed August 30, 2017)
- Michigan State University (MSU). 2017. Common bean in the Americas. Available at <https://msu.edu/~bernsten/beanatlas/II.Common%20Beans%20in%20the%20Americas/II.i.%20Common%20Beans%20in%20the%20Americas.htm> (Accessed August 30, 2017)
- Miklas, P.N., J.D. Kelly, S.E. Beebe, and M.W. Blair. 2006. Common bean breeding for resistance against biotic and abiotic stresses: From classical to MAS breeding. *Euphytica*. 147:105-131.
- Minor T., and J.K. Bond. 2017. Vegetables and pulses outlook. USDA-ERS United States Department of Agriculture, Economic Research Service. Available at <https://www.ers.usda.gov/webdocs/publications/83350/vgs-358.pdf?v=42853> (Accessed 10 November 2017).
- Moghaddam, S.M., S. Mamidi, J.M. Osorno, R. Lee, M. Brick, J. Kelly, P. Miklas, C. Urrea, Q. Song, P. Cregan, J. Grimwood, J. Schmutz, and P.E. McClean. 2016. Genome-Wide Association study identifies candidate loci underlying agronomic traits in a Middle American diversity panel of common bean. *Plant Genome*. 9:1-21.
- Mohammed, A. 2013. An overview of distribution, biology and the management of common bean anthracnose. *J. Plant Pathol. Microbiol*. 4:1-6.
- Moscoso J. 2017. Agro-economic evaluation of three varieties of climbing bean (*Phaseolus vulgaris* L.), Grown in Three Spatial Arrangements. *In* The Feed the Future Legume Innovation Lab Grain Legume Research Conference. Ouagadougou, Burkina Faso.
- North Dakota State Seed Department (NDSSD). 2008. Bean anthracnose; Available at http://www.nd.gov/seed/diag_nosticlab/beananthracnose.aspx (Accessed August 30, 2017)
- Orellana, A., J. Villatoro, and M. Mérida. 2006. Caracterización morfo agronómica y evaluación preliminar de la colección de germoplasma de frijol voluble (*Phaseolus vulgaris* L.) en Chimaltenango. (Morpho agronomic characterization and preliminary evaluation of climbing bean (*Phaseolus vulgaris* L.) in Chimaltenango.) Informe final. Guatemala, Guatemala. Instituto de Ciencia y Tecnología Agrícolas (ICTA). p. 17.

- Osorno J.M., P.E. McClean, J.C. Villatoro, A.N. Miranda, J. Moscoso, A. Karen, and L.F. Aldana. 2017. Two new climbing bean varieties adapted to the milpa system in the highlands of Guatemala. Oral session presented at: Feed the Future Innovation Lab for Collaborative Reserch on Grain Legumes. Ougadougou, Burkina Faso.
- Pastor-Corrales, M.A. 1991. Estandarización de variedades diferenciales y de designación de razas de *Colletotrichum lindemuthianum*. (Standardizing differential varieties and races designation of *Colletotrichum lindemuthianum*) Phytopathol. 81:694.
- Pastor-Corrales, M. A., M.M. Otoyá, and M.M. Maya. 1993. Diversidad de la virulencia de *Colletotrichum lindemuthianum* en Mesoamérica y la Región Andina. (Diversity in virulence of *Colletotrichum lindemuthianum* in Mesoamerica and Andean region). Fitopatología. 17:31-38.
- Pastor-Corrales, M.A., O.A. Erazo., E.I. Estrada., and S.P. Singh. 1994. Inheritance of anthracnose resistance in common bean accession G 2333. Plant Dis. 78:959-961.
- Pastor-Corrales, M. A. 1996. Traditional and molecular confirmation of the coevolution of beans and pathogens in Latin America. Annu. Rep. Bean Improv. Coop. 39:46-47.
- Paparu, P., M. Katafiire, M. Mcharo, and M. Ugen. 2014. Evaluation of fungicide application rates, spray schedules and alternative management options for rust and angular leaf spot of snap beans in Uganda. Int. J. Pest Manage. 60:82-89.
- Perseguiñi, J.M., P.R. Oblessuc, J.R. Rosa, K.A. Gomes, A.F. Chiorato, S.A. Carbonell, A.A. Garcia, R.P. Vianello, and L.L. Benchimol-Reis. 2016. Genome-Wide association studies of Anthracnose and Angular Leaf Spot resistance in common bean (*Phaseolus vulgaris* L.). PLoS One. p. 11.
- Ponciano-Samayoa, K., J. Villatoro, and L. Molina. 2009. Preliminary characterization with microsatellites from climbing bean collection from Guatemala. (Caracterización preliminar con microsatélites de la colección Guatemalteca de frijol común trepador). Agronomía Mesoamericana. 20:245-254.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <http://www.R-project.org/> (Accessed November 16, 2017)
- Rosas, J., A. Castro, and E. Flores. 2000. Breeding of the black and red Mesoamerican beans for Central America and the Caribbean (Mejoramiento genético del frijol rojo y negro mesoamericano para Centroamérica y El Caribe). Agronomía Mesoamericana. 11:37-43.
- Rodríguez-Suárez, C., J.J. Ferreira, A. Campa, A. Pañeda, and R. Giraldez. 2008. Molecular mapping and intra-cluster recombination between anthracnose race-specific resistance genes in the common bean differential cultivars Mexico 222 and Widusa. Theor. Appl. Genet. 116:807-814.
- Scheet, P., and M. Stephens. 2006. A fast and flexible statistical model for large-scale population genotype data: Applications to inferring missing genotypes and haplotypic phase. Am. J. Hum. Genet. 78:628-644.

- Schmutz, J., P.E. McClean, S. Mamidi, G.A. Wu, S.B. Cannon, J. Grimwood, J. Jenkins, S. Shu, Q. Song, C. Chavarro, M. Torres-Torres, V. Geffroy, S.M. Moghaddam, D. Gao, B. Abernathy, K. Barry, M. Blair, M.A. Brick, M. Chovatia, P. Gepts, D.M. Goodstein, M. Gonzales, U. Hellsten, D.L. Hyten, G. Jia, J.D. Kelly, D. Kudrna, R. Lee, M.M.S. Richard, P.N. Miklas, J.M. Osorno, J. Rodrigues, V. Thareau, C.A. Urrea, M. Wang, Y. Yu, M. Zhang, R.A. Wing, P.B. Cregan, D.S. Rokhsar, and S.A. Jackson. 2014. A reference genome for common bean and genome-wide analysis of dual domestications. *Nat. Genet.* 46:707-13.
- Schröder, S., S. Mamidi, R. Lee, M.R. McKain, P.E. McClean, and J.M. Osorno. 2016. Optimization of genotyping by sequencing (GBS) data in common bean (*Phaseolus vulgaris* L.). *Mol. Breed.* 36:1-9.
- Schwartz, H. F., J.R. Steadman, R. Hall, and R.L. Foster. 2005. Anthracnose. *Compendium of bean diseases, Second Edition.* The Am. Phytopathol. Society, USA. p. 109.
- Shen, Q., M. Bao, and X. Zhou. 2012. A plant kinase plays roles in defense response against geminivirus by phosphorylation of a viral pathogenesis protein. *Plant Signal. Behav.* 7:888-892.
- Sicard, D., Y. Michalakakis, M. Dron, and C. Neema. 1997. Genetic diversity and pathogenic variation of *Colletotrichum lindemuthianum* in the three centers of diversity of its host, *Phaseolus vulgaris*. *Phytopathol.* 87:807-813
- Singh, S.P., P. Gepts, and D.G. Debouck. 1991. Races of common bean (*Phaseolus vulgaris*, Fabaceae). *Econ. Bot.* 45:379-396.
- Smýkal, P., C.J. Coyne, M.J. Ambrose, N. Maxted, H. Schaefer, M.W. Blair, J. Berger, S.L. Greene, M.N. Nelson, N. Besharat, T. Vymyslický, C. Toker, R.K. Saxena, M. Roorkiwal, M.K. Pandey, J. Hu, Y.H. Li, L.X. Wang, Y. Guo, L.J. Qiu, R.J. Redden, and R.K. Varshney. 2015. Legume crops phylogeny and genetic diversity for science and breeding. *CRC Crit. Rev. Plant Sci.* 34:43-104.
- Sousa, L.L., A.S. Cruz, P.S. Vidigal Filho, V.A. Vallejo, J.D. Kelly, and M.C. Gonçalves-Vidigal. 2014. Genetic mapping of the resistance allele *Co-5²* to *Colletotrichum lindemuthianum* in the common bean MSU 7-1 line. *Aust. J. Crop Sci.* 8:317-323.
- Sousa, L.L., A.O. Gonçalves, M.C. Gonçalves-Vidigal, G.F. Lacanallo, A.C. Fernandez, H. Awale, and J.D. Kelly. 2015. Genetic characterization and mapping of anthracnose resistance of common bean landrace cultivar Corinthiano. *Crop Sci.* 55:1900-1910.
- Stanton-Geddes, J., T. Paape, B. Epstein, R. Briskine, J. Yoder, J. Mudge, A.K. Bharti, A.D. Farmer, P. Zhou, R. Denny, G.D. May, S. Erlandson, M. Yakub, M. Sugawara, M.J. Sadowsky, N.D. Young, and P. Tiffin. 2013. Candidate genes and genetic architecture of symbiotic and agronomic traits revealed by whole-genome, sequence-based association genetics in *Medicago truncatula*. *PLoS One.* p. 9.
- Tian, M., E. Huitema, L. da Cunha, T. Torto-Alalibo, and S. Kamoun. 2004. A Kazal-like extracellular serine protease inhibitor from *Phytophthora infestans* targets the tomato pathogenesis-related protease P69B. *J. Biol. Chem.* 279:26370-26377.
- Tobar-Piñon, M.G., S. Moghaddam, R. Lee, J.C. Villatoro, J. M. Osorno, and P. E. McClean. 2017. Genetic diversity of the guatemalan climbing bean collection. Oral session presented at: Central American Cooperative Program for the Improvement of Crops and Animals (PCCMCA) conference. San Salvador, El Salvador.

- Trabanco, N., A. Campa, and J.J. Ferreira. 2015. Identification of a new chromosomal region involved in the genetic control of resistance to anthracnose in common bean. *The Plant Genome*. p. 11.
- U.S. Department of Agriculture. 2016. USDA/NASS QuickStats Ad-hoc Query Tool. Available at <https://quickstats.nass.usda.gov/#A7BAD1E7-E7C4-3657-B1BA-3182B1B4F0E2> (Accessed 9 Apr. 2017).
- Vallejo, V., and J.D. Kelly. 2009. New insights into the anthracnose resistance of common bean landrace G 2333. *Open Horticulture* 2:29-33.
- Van Schoonhoven A., and M.A. Pastor-Corrales. 1987. Standard system for the evaluation of bean germplasm. Centro Internacional de Agricultura Tropical, Cali, Colombia. 53pp. *In* Global and Regional Trends in Production, Trade and Consumption of Food Legume Crops
- Vasquez-Guzman, J.E. 2016. Identifying dry bean genotypes and genomic regions associated with root rot. Ph.D. Thesis, North Dakota State University, Fargo, North Dakota. p. 87
- Wang, J., J. Feng, W. Jia, S. Chang, S. Li and Y. Li. 2015. Lignin engineering through laccase modification: a promising field for energy plant improvement. *Biotechnol. Biofuels*. p. 11.
- Wojciechowski, M.F., M. Lavin, and M.J. Sanderson. 2004. A phylogeny of legumes (*Leguminosae*) based on analysis of the plastid matK gene resolves many well-supported subclades within the family. *Am. J. Bot.* 91:1846-1862.
- Wojciechowski, M.F. 2003. Reconstructing the phylogeny of legumes (*Leguminosae*): an early 21st century perspective. *Advances in legume systematics*. 10:5–35.
- Wu, J., J. Zhu, L. Wang, and S. Wang. 2017. Genome-wide association study identifies NBS-LRR-Encoding genes related with anthracnose and Common Bacterial Blight in the common bean. *Front. Plant Sci.* p. 15.
- Xing, T., and A. Laroche. 2011. Revealing plant defense signaling, *Plant Signaling & Behavior*. 6:1469-1474.
- Yang D.R.L.C., P. Balasubramanian, K. Yu, S.J. Park, W.C. Penner, and L.M. Yager. 2007. Phenotypic and genotypic identification of Anthracnose resistance in kidney bean cultivars grown in western Canada. *Can. J. Plant Sci.* 87:405-412.
- Young, R.A., and J.D. Kelly. 1996. Characterization of the genetic resistance to *Colletotrichum lindemuthianum* in common bean differential cultivars. *Plant Disease*. 80:650-654.
- Young, R.A., M. Melotto, R.O. Nodari, and J.D. Kelly. 1998. Marker-assisted dissection of the oligogenic anthracnose resistance in the common bean cultivar, “G2333.” *Theor. Appl. Genet.* 96: 87-94.
- Yu, J., and E.S. Buckler. 2006. Genetic association mapping and genome organization of maize. *Curr. Opin. Biotechnol.* 17:155–160.
- Zhang, Z., E. Ersoz, C.-Q. Lai, R.J. Todhunter, H.K. Tiwari, M.A. Gore, P.J. Bradbury, J. Yu, D.K. Arnett, J.M. Ordovas, and E.S. Buckler. 2010. Mixed linear model approach adapted for genome-wide association studies. *Nat. Genet.* 42:355–360.
- Zizumbo-Villarreal, D., and P. Colunga-GarcíaMarín. 2010. Origin of agriculture and plant domestication in West Mesoamerica. *Genet. Resour. Crop Evol.* 57: 813–825.
- Zizumbo-Villarreal, D., A. Flores-Silva, and P. Colunga-García Marín. 2012. The archaic diet in Mesoamerica: Incentive for milpa development and species domestication. *Econ. Bot.* 66: 328–343.

- Zuiderveen, G. H. 2015. The genetics of anthracnose resistance in common bean (Doctoral dissertation), Michigan State University. p. 75.
- Zuiderveen, G.H., B.A. Padder, K. Kamfwa, Q. Song, and J.D. Kelly. 2016. Genome-wide association study of anthracnose resistance in andean beans (*Phaseolus vulgaris*). PloS one. p. 17.

APPENDIX

Table A.1. Anthracnose sample identification code, location of sample, inoculation dates and monosporic culture information.

Field ID	Line (L) and/or name and/or specie	State	County/Locality	Inoculation date/Status	Screen through	Date of isolated	Monosporic culture
CLC-1	Climbing	CHIMALTENANGO	Chimaltenango	6/09/17	Plant	Failed	
CLC-2	Landrace	CHIMALTENANGO	Chimaltenango	Damaged			
CLC-3	Climbing	CHIMALTENANGO	Chimaltenango	Damaged			
CLC-4	Climbing	CHIMALTENANGO	Acatenango	5/19/17	Plant	6/01/17	Yes
CLC-5	Climbing	CHIMALTENANGO	Sn Andrés Itzapa	5/22/17	Plant	60/1/17	Yes
CLC-6	Climbing	CHIMALTENANGO	Sn Andrés Itzapa	5/22/17	Plant	6/01/17	Yes
CLC-7	Climbing	CHIMALTENANGO	Chimaltenango	Damaged			
CLC-8	Landrace Climbing	CHIMALTENANGO	Chimaltenango	14/01/2017	Plant	25/01/2017	Failed
CLC-9	Landrace Climbing	CHIMALTENANGO	Chimaltenango	14/01/2017	Plant	Failed	
CLC-10	Climbing	CHIMALTENANGO	Chimaltenango	14/01/2017	Plant	25/01/2017	Failed
CLC-11	Climbing	CHIMALTENANGO	Chimaltenango	14/01/2017	Plant	Failed	
CLC-12	Landrace Climbing	CHIMALTENANGO	Chimaltenango	18/01/2017	Plant	Failed	
CLC-13	Landrace Climbing	CHIMALTENANGO	Chimaltenango	19/01/2017	Plate	6/01/17	Yes
CLC-14	Climbing	CHIMALTENANGO	Chimaltenango	18/01/2017	Plant	Failed	
CLC-15	Climbing	CHIMALTENANGO	Chimaltenango	18/01/2017	Plant	Failed	
CLC-16	Climbing	CHIMALTENANGO	Chimaltenango	19/01/2017	Plate	6/01/17	
CLC-17	Landrace Climbing	CHIMALTENANGO	Chimaltenango	18/01/2017	Plant	Failed	
CLC-18	Landrace Climbing	CHIMALTENANGO	Patzicia	18/01/2017	Plate	6/01/17	Yes
CLC-19	Bushtype Landrace	CHIMALTENANGO	Patzicia	19/01/2017	Plate	6/01/17	Yes
CLC-20	Bushtype Landrace	CHIMALTENANGO	Patzicia	18/01/2017	Plant	26/01/2017	Yes
CLC-21	Climbing	CHIMALTENANGO	Chimaltenango	12/01/2017	Plant	Failed	
CLC-22	Landrace Climbing	CHIMALTENANGO	Chimaltenango	12/01/2017	Plant	Failed	
CLC-23	Climbing	CHIMALTENANGO	Chimaltenango	12/01/2017	Plant	Failed	
CLC-24	Climbing	CHIMALTENANGO	Chimaltenango	14/01/2017	Plant	Failed	
CLC-25	Climbing	CHIMALTENANGO	Chimaltenango	14/01/2017	Plant	Failed	

Table A.1. Anthracnose sample identification code, location of sample, inoculation dates and monosporic culture information (continued)

Field ID	Line (L) and/or name and/or specie	State	County/Locality	Inoculation date/Status	Screen through	Date of isolated	Monosporic Culture
CLC-26	Landrace Climbing	CHIMALTENANGO	Chimaltenango	14/01/2017	Plant	25/01/2007	Yes
CLC-27	Climbing	CHIMALTENANGO	Chimaltenango	14/01/2017	Failed		
CLC-28	Landrace Climbing	CHIMALTENANGO	Chimaltenango	6/09/17	Plate	6/19/17	Yes
CLH-1	Landrace	HUEHUETENANGO	Chiantla	Damaged			
CLH-2	hunapu	HUEHUETENANGO	Chiantla	6/19/17	Plant/plate	Failed	
CLH-3	Guate 1026	HUEHUETENANGO	aguacatan	12/01/2017	Plant	25/01/2017	Yes
CLH-4	hunapu	HUEHUETENANGO	Chiantla	12/01/2017	Plant	Failed	
CLH-5	Guate 1026	HUEHUETENANGO	aguacatan	17/01/2017	Plate	6/19/17	Yes
CLH-6	Guate 1026	HUEHUETENANGO	aguacatan	17/01/2017	Plate	Failed	
CLH-7	Texel	HUEHUETENANGO	Quilinco, Chiantla	13/01/2017	Plate	Failed	
CLH-8	Texel	HUEHUETENANGO	Quilinco, Chiantla	17/01/2017	Plate	Failed	
CLH-9	Landrace	HUEHUETENANGO	Chiantla	Damaged			
CLH-10	Landrace	HUEHUETENANGO	Quilinco, Chiantla	Damaged			
CLH-11	coccineus	HUEHUETENANGO	Chiantla	Damaged			
CLH-12	coccineus	HUEHUETENANGO	Chiantla	Damaged			
CLH-13	Landrace	HUEHUETENANGO	Chiantla	Damaged			
CLH-14	Landrace	HUEHUETENANGO	Chiantla	Damaged			
CLH-15	Landrace	HUEHUETENANGO	Chiantla	Damaged			
CLH-16	Labor Ovalle	HUEHUETENANGO	Chiantla	Damaged			
CLH-17	hunapu	HUEHUETENANGO	Chiantla	Damaged			
CLH-18	coccineus	HUEHUETENANGO	Chiantla	5/30/17	Plant/plate	Failed	
CLQ-1	L-6	QUETZALTENANGO	ICTA LOV	21/12/17	Plant	5/29/17	Yes
CLQ-2	L-274	QUETZALTENANGO	ICTA LOV	18/01/2017	Plant	Failed	
CLQ-3	L-223	QUETZALTENANGO	ICTA LOV	18/01/2017	Plant	Failed	
CLQ-4	L-191	QUETZALTENANGO	ICTA LOV	19/01/2017	Plant	Failed	
CLQ-5	L-116	QUETZALTENANGO	ICTA LOV	19/01/2017	Plant	Failed	

Table A.1. Anthracnose sample identification code, location of sample, inoculation dates and monosporic culture information (continued)

Field ID	Line (L) and/or name and/or specie	State	County/Locality	Inoculation date/Status	Screen through	Date of isolated	Monosporic culture
CLQ-6	L-224	QUETZALTENANGO	ICTA LOV	Damaged			
CLQ-7	L-316	QUETZALTENANGO	ICTA LOV	21/12/2016	Plant	21/12/2016	Yes
CLQ-8	L-92	QUETZALTENANGO	ICTA LOV	19/01/2017	Plate	26/01/2017	Yes
CLQ-9	L-222	QUETZALTENANGO	ICTA LOV	19/01/2017	Plant	26/01/2017	Failed
CLQ-10	L-190	QUETZALTENANGO	ICTA LOV	12/01/2017	Plant	Failed	
CLQ-11	L-51	QUETZALTENANGO	ICTA LOV	12/01/2017	Plant	25/01/2017	Yes
CLQ-12	L-184	QUETZALTENANGO	ICTA LOV	14/01/2017	Plant	25/01/2017	Failed
CLQ-13	L-182	QUETZALTENANGO	ICTA LOV	14/01/2017	Plant	25/01/2017	Failed
CLQ-14	L-10	QUETZALTENANGO	ICTA LOV	12/01/2017	Plant	25/01/2017	Failed
CLQ-15	L-277	QUETZALTENANGO	ICTA LOV	12/01/2017	Plant	25/01/2017	Failed
CLQ-16	L-272	QUETZALTENANGO	ICTA LOV	12/01/2017	Plant	25/01/2017	Failed
CLQ-17	Martin	QUETZALTENANGO	Concepción	1/25/17	Plant	Failed	
CLQ-18	Guate 1026	QUETZALTENANGO	Concepción	Damaged			
CLQ-19	Texel	QUETZALTENANGO	Concepción	Damaged			
CLQ-20	Texel	QUETZALTENANGO	Concepción	Damaged			
CLQ-21	Valle Nuevo	QUETZALTENANGO	Concepción	Damaged			
CLQ-22	Labor Ovalle	QUETZALTENANGO	Varsovia	6/12/17	Plant	Failed	
CLQ-23	Labor Ovalle	QUETZALTENANGO	Varsovia	6/12/17	Plant	Failed	
CLQ-24	Landrace	QUETZALTENANGO	Varsovia	6/12/17	Plant	Failed	
CLQ-25	Landrace	QUETZALTENANGO	Concepción	5/17/17	Plant	Failed	
CLQ-26	Landrace	QUETZALTENANGO	Cajola	13/01/2017	Plate	Failed	
CLQ-27	Landrace	QUETZALTENANGO	Cajola	17/01/2017	Plate	Failed	
CLQ-28	Landrace	QUETZALTENANGO	Cajola	Damaged			
CLQ-29	Landrace	QUETZALTENANGO	Cajola	Damaged			
CLQ-30	Hunapú	QUETZALTENANGO	Cajola	5/17/17	Plant	6/1/17	Yes
CLQ-31	Landrace	QUETZALTENANGO	Cajola	Damaged			

Table A.1. Anthracnose sample identification code, location of sample, inoculation dates and monosporic culture information (continued)

Field ID	Line (L) and/or name and/or specie	State	County/Locality	Inoculation date/Status	Screen through	Date of isolated	Monosporic culture
CLQ-32	Landrace	QUETZALTENANGO	Cajola	Damaged			
CLQ-33	Landrace	QUETZALTENANGO	Varsovia	6/7/17	Plant	Failed	
CLQ-34	Coccineus	QUETZALTENANGO	Varsovia	Damaged			
CLQ-35	Coccineus	QUETZALTENANGO	Varsovia	Damaged			
CLQ-36	Coccineus	QUETZALTENANGO	Varsovia	5/23/17	Plant/plate	Failed	
CLQ-37	Landrace	QUETZALTENANGO	Monrovia	Damaged			
CLQ-38	Landrace	QUETZALTENANGO	Monrovia	Damaged			
CLQ-39	Uatlán	QUETZALTENANGO	Monrovia	Damaged			
CLQ-40	Valle Nuevo	QUETZALTENANGO	Monrovia	Damaged			
CLQ-41	Texel	QUETZALTENANGO	Concepción	Damaged			
CLQ-42	Texel	QUETZALTENANGO	Concepción	Damaged			
CLQ-43	Uatlán	QUETZALTENANGO	Concepción	Damaged			
CLQ-44	Labor Ovalle	QUETZALTENANGO	Concepción	Damaged			
CLQ-45	Hunapú	QUETZALTENANGO	Concepción	Damaged			
CLQ-46	Landrace	QUETZALTENANGO	Concepción	Damaged			
CLQ-47	Landrace	QUETZALTENANGO	Concepción	Damaged			
CLQ-48	Landrace	QUETZALTENANGO	Concepción	Damaged			
CLQ-49	Landrace	QUETZALTENANGO	Concepción	Damaged			
CLQ-50	Landrace	QUETZALTENANGO	Concepción	Damaged			
			Barrio San Marcos,				
CLQ-51	Labor Ovalle	QUETZALTENANGO	Concepción	Damaged			
			Barrio San Marcos,				
CLQ-52	Uatlán	QUETZALTENANGO	Concepción	Damaged			

Table A.1. Anthracnose sample identification code, location of sample, inoculation dates and monosporic culture information (continued)

Field ID	Line (L) and/or name and/or specie	State	County/Locality	Inoculation date/Status	Screen through	Date of isolated	Monosporic culture
CLQ-53	Labor Ovalle	QUETZALTENANGO	Barrio San Marcos, Concepción	Damaged			
CLQ-54	Labor Ovalle	QUETZALTENANGO	Barrio San Marcos, Concepción	Damaged			
CLQ-55	Landrace	QUETZALTENANGO	Barrio San Marcos, Concepción	5/30/17	Plant	Failed	
CLQ-56	Landrace	QUETZALTENANGO	Barrio San Marcos, Concepción	6/9/17	Plant	Failed	
CLQ-57	Labor Ovalle	QUETZALTENANGO	Concepción	Damaged			
CLQU-1	Landrace	QUICHÉ	Cunén	6/12/17	Plant/plate	Failed	
CLQU-2	Landrace	QUICHÉ	Cunén	5/24/17	Plant/plate	Failed	
CLQU-3	Landrace	QUICHÉ	Cunén	6/5/17	Plant/plate	Failed	
CLQU-4	Landrace	QUICHÉ	Cunén	6/9/17	Plant/plate	Failed	
CLSM-1	Hunapu	SAN MARCOS	comitancillo	5/17/17	Plant/plate	Failed	
CLSM-2	Hunapu	SAN MARCOS	comitancillo	Damaged			
CLSM-3	Hunapu	SAN MARCOS	comitancillo	6/12/17	Plant/plate	Failed	
CLSM-4	Landrace	SAN MARCOS	Sn. Miguel Ixtahuacán	5/19/17	Plant/plate	Failed	
CLT-1	Quiche	TOTONICAPAN	Sta. Maria chiquimula	19/01/2017	Plant/plate	Failed	
CLT-2	Quiche	TOTONICAPAN	Momostenango	Damaged			
CLT-3	Quiche	TOTONICAPAN	Momostenango	17/01/2017	plate x		

Table A.1. Anthracnose sample identification code, location of sample, inoculation dates and monosporic culture information (continued)

Field ID	Line (L) and/or name and/or specie	State	County/Locality	Inoculation date/Status	Screen through	Date of isolated	Monosporic culture
CLT-4	Quiche	TOTONICAPAN	Sta. Maria chiquimula	17/01/2017	Plant/plate	Failed	
CLT-5	Altense	TOTONICAPAN	Momostenango	Damaged			
CLT-6	Landrace	TOTONICAPAN	Momostenango	5/24/17	Plant/plate	Failed	
CLT-7	Landrace	TOTONICAPAN	Momostenango	Damaged			
CLT-8	utatlan	TOTONICAPAN	Momostenango	Damaged			
CLT-9	utatlan	TOTONICAPAN	Momostenango	Damaged			
CLT-10	Labor Ovalle	TOTONICAPAN	Momostenango	Damaged			
CLT-11	Labor Ovalle	TOTONICAPAN	Momostenango	Damaged			
CLT-12	Labor Ovalle	TOTONICAPAN	Momostenango	Damaged			
CLT-13	Landrace	TOTONICAPAN	Momostenango	Damaged			
CLT-14	Landrace	TOTONICAPAN	Momostenango	Damaged			
CLT-15	Quiche	TOTONICAPAN	Momostenango	Damaged			
CLT-16	Landrace	TOTONICAPAN	Sta. Maria chiquimula	17/01/2017	Plant/plate	Failed	
CLT-17	Guate 1026	TOTONICAPAN	Sta. Maria chiquimula	13/01/2017	Plant/plate	Failed	
CLT-18	Labor Ovalle	TOTONICAPAN	Sta. Maria chiquimula	5/31/17	Plant/plate	Failed	
CLT-19	Labor Ovalle	TOTONICAPAN	Sta. Maria chiquimula	Damaged			
CLT-20	Labor Ovalle	TOTONICAPAN	Sta. Maria chiquimula	5/17/17	Plant	Failed	
CLT-21	Guate 1026	TOTONICAPAN	Sta. Maria chiquimula	6/5/17	Plant/plate	Failed	

Table A.2. Geographical position of Anthracnose samples collected at the western Guatemalan Highlands.

Locality	Producer	Host plant	N	O	MASL
Santa María Chiquimula, Totonicapan.	Placido Tzooy	ICTA Quiché	15.02	-91.34	2,112
Santa María Chiquimula, Totonicapan.	Placido Tzooy	ICTA Guate 1026	15.02	-91.34	2,112
Chequemeyá, Sicalbé, Momostenango, Totonicapan.	José Batén	ICTA Quiché	15.129117	-91.337145	1,891
Panimachaj, Cunén, Quiche.		Landrace	15° 19' 41"	91° 02' 29.06"	2,185
Chiantla, Huehuetenango.	Isabel Lopéz	Landrace	15° 23' 20.0"	91° 27' 11.6"	2,516
ICTA Labor Ovalle, Quetzaltenango.	Jessica Moscoso	Landrace	14° 52' 12"	91° 30' 50"	2,380
	Leticia				
Taltimiche, Comitancillo, San Marcos.	Crisostomo	Hunapú	15° 05' 38.2"	91° 46' 48.1"	2,360
Varsovia, Quetzaltenango.	Alba Méndez	Landrace	14° 53' 33.4"	91° 37' 51.9"	2,530
Varsovia, Quetzaltenango.	Alba Méndez	Labor Ovalle	14° 53' 33.4"	91° 37' 51.9"	2,530
Varsovia, Quetzaltenango.	Alba Méndez	Coccineus	14° 53' 33.4"	91° 37' 51.9"	2,530
Zona 2 Cajola, Quetzaltenango.	Micaela	Landrace	14° 55' 32.8"	91° 36' 45.7"	2,398
Cajola, Quetzaltenango.	Abigail Barrios	Landrace	14° 56' 08.3"	91° 36' 43.7"	NA
5 Cajola, Quetzaltenango.	Aurelio Lopéz	Landrace	14° 55' 47.7"	91° 35' 54.4"	2,560
Cajola, Quetzaltenango.	Aurelio Lopéz	Hunapú	14° 55' 47.7"	91° 55' 47.7"	2,561
Sicalbé, Momostenango, Totonicapan.	Tomás Argueta	Labor Ovalle	15° 09' 02"	91° 21' 03.7"	1,815
Palca, Miomostenango, Totonicapan.	José	Utatlán	15° 07' 44.6"	91° 20' 15.0"	1,900
Choacorrál 1, Santa María Chiquimula, Totonicapan.	Juan Lux Castro	Labor Ovalle	15.030217	-91.283191	2,063
Choacorrál 1, Santa María Chiquimula, Totonicapan.	Marcos Lux	Landrace Blanco	15.030217	-91.283191	2,063
Monrrovia, Quetzaltenango.	Gladys	Landrace	14° 54' 44.2"	91° 37' 58.8"	2,535
		Landrace Valle			
Monrrovia, Quetzaltenango.	Gladys	nuevo	14° 54' 44.2"	91° 37' 58.8"	2,535
Monrrovia, Quetzaltenango.	Gladys	Utatlán	14° 54' 44.2"	91° 37' 58.8"	2,535

NA: Not available

Table A.2. Geographical position of Anthracnose samples collected at the western Guatemalan Highlands (continued)

Locality	Producer	Host plant	N	O	MASL
Barrio San Marcos, Concepción Chiquirichapa, Quetgo.	Santos A. Esteban	Landrace	14° 51' 30.2"	91° 37' 18.6"	NA
Barrio San Marcos, Concepción Chiquirichapa, Quetgo.	Santos A. Esteban	Landrace	14° 51' 30.2"	91° 37' 18.6"	NA
Quetzaltenango.	Carlos Sánchez	Texel	14° 51' 51.1"	91° 36' 51.6"	2,440
Quetzaltenango.	Carlos Sánchez	Texel	14° 51' 51.1"	91° 36' 51.6"	2,440
Quetzaltenango.	Carlos Sánchez	Hunapú Landrace Valle	14° 51' 51.1"	91° 36' 51.6"	2,442
Quetzaltenango.	Carlos Sánchez	nuevo	14° 51' 51.1"	91° 36' 51.6"	2,443
Quetzaltenango.	Carlos Sánchez	Guate 1026	14° 51' 51.1"	91° 36' 51.6"	2,444
Quetzaltenango.	Carlos Sánchez	Martín	14° 51' 51.1"	91° 36' 51.6"	2,445

NA: Not available

Table A.3. Climbing bean accession from Guatemala reaction (score 1-9) to race 73 of *C. lindemuthianum*, in three repetitions and the Least Square Means

Genotype ID	Average R1	Average R2	Average R3	LSM estimate
AT18419cmcm	3.0	1.0	1.0	1.7
AT18430cmcm	4.0	3.8	2.3	3.3
AT18432cmcm	2.3	1.3	1.3	1.6
AT18435cmcma	1.5	2.0	1.5	1.7
AT18439cmcm	1.8	3.3	3.3	2.8
AT188422cmcm	4.0	3.3	2.0	3.1
c12311cmcm	3.0	2.0	3.3	2.8
c12312cmcm	3.0	4.0	2.5	3.2
c1231cmcmcm	1.3	2.5	1.8	1.8
c12332cmcm	2.8	1.8	1.5	2.0
c1235cmcmcm	3.0	1.5	2.8	2.4
c1831cmcmcm	5.0	3.8	3.8	4.2
c273cm2cm12cm6cm	4.0	4.5	3.5	4.0
c274cm6cm9cma5cm	7.7	5.5	5.3	6.1
c274cm6cm9cmb5cm	7.8	5.0	5.0	5.9
c495cm6cma12cm6cm	5.0	3.0	4.8	4.3
c495cm6cmb3cm2cm	3.0	1.0	2.3	2.1
c616cm6cm15cm6cm	1.3	1.0	1.0	1.1
C61cm8cm9cmcm5	6.0	3.0	4.0	4.3
c6910cm6cm9cm7cm	4.3	1.5	1.3	2.4
c6911cm6cm6cm6cm	5.3	4.0	3.8	4.3
c695cm6cm9cm5cm	2.5	2.3	3.0	2.6
c696cm4cm3cm3cm	6.8	2.5	4.0	4.4
c697cm4cm9cm3cm	6.3	3.8	4.0	4.7
c698cm4cm12cm6cm	2.5	1.0	2.0	1.8
c8110cm4cm2cm2cm	4.8	2.3	1.7	2.9
c8116cm6cm7cmb2cm	2.5	1.0	2.0	1.8
c8116cm6cm7cmb2cm.2	3.5	2.8	3.0	3.1
c811cm6cm6cm3cm	5.0	4.0	2.8	3.9
c813cma4cm6cm6cm	6.3	6.5	9.0	7.3
c815cm6cm9cm6cm	1.0	1.7	2.5	1.7
c819cm6cm9cm5cm	3.0	3.0	3.5	3.2
c8315cm6cma3cm3cm	4.5	2.0	3.0	3.2
c8315cm6cmb5cm4cm	5.5	1.5	3.5	3.5
c934cmb8cm3cm6cm	3.5	2.0	3.7	3.1
chajmaquiaj40	6.0	6.3	5.3	5.9

Table A.3. Climbing bean accession from Guatemala reaction (score 1-9) to race 73 of *C. lindemuthianum*, in three repetitions and the Least Square Means (continued)

Genotype ID	Average R1	Average R2	Average R3	LSM estimate
frijolboloj	6.0	4.0	4.8	4.9
frijolbonilla	3.8	3.5	5.3	4.2
FrijolEnredo1	1.0	1.5	1.0	1.2
G2333	1.0	1.0	1.0	1.0
G6076	1.0	1.0	1.0	1.0
guate1000	1.0	1.0	1.0	1.0
guate1001	3.8	3.5	2.0	3.1
guate1002	1.0	1.0	1.8	1.3
guate1004	3.8	1.7	1.5	2.3
guate1005	3.0	2.8	2.8	2.8
guate1006	2.8	1.3	3.5	2.5
guate1007	6.0	3.0	5.0	4.7
guate10071	6.5	3.8	4.3	4.8
guate1009	1.5	1.0	1.0	1.2
guate1010	5.8	4.3	4.8	4.9
guate1012	3.3	3.5	4.0	3.6
guate1014	3.3	3.0	2.3	2.8
guate1016	4.0	3.0	3.5	3.5
guate1019	3.5	3.3	3.5	3.4
guate1024	1.0	1.0	1.0	1.0
guate1025	1.0	1.0	1.0	1.0
guate1026	1.0	1.0	1.0	1.0
guate10261	1.5	1.8	1.0	1.4
guate1027	4.0	2.0	3.0	3.0
guate1029	4.8	3.5	4.7	4.3
guate1032	1.3	1.0	1.3	1.2
guate1036	6.0	4.8	2.0	4.3
guate1038	3.5	2.3	4.5	3.4
guate1040	3.5	4.0	3.3	3.6
guate1041	2.0	1.7	2.3	2.0
guate1042	3.8	4.0	5.0	4.3
guate1044	2.3	1.5	2.3	2.0
guate1045	2.3	1.0	1.0	1.4
guate1049	5.0	5.0	4.8	4.9
guate1051	3.3	2.0	2.8	2.7
guate1053	4.5	3.5	2.0	3.3

Table A.3. Climbing bean accession from Guatemala reaction (score 1-9) to race 73 of *C. lindemuthianum*, in three repetitions and the Least Square Means (continued)

Genotype ID	Average R1	Average R2	Average R3	LSM estimate
guate1055	4.8	3.3	3.0	3.7
guate1059	1.0	1.0	1.0	1.0
guate1063	1.0	1.0	1.0	1.0
guate1064	2.5	2.5	1.8	2.3
guate1066	5.0	2.5	1.5	3.0
guate1067	1.3	1.0	1.0	1.1
guate1068	1.0	1.0	1.0	1.0
guate1069	3.8	6.0	2.5	4.1
guate1071	1.5	1.0	1.0	1.2
guate1073	4.5	3.8	3.8	4.0
guate1074	4.8	3.0	3.5	3.8
guate10764PM	2.0	1.5	1.5	1.7
guate1077	2.3	2.3	2.0	2.2
guate1078	4.0	2.3	3.8	3.3
guate1079	1.5	1.0	1.0	1.2
guate1080	2.3	3.0	2.8	2.7
guate1081	2.7	3.5	3.5	3.2
guate1082	1.8	1.0	2.3	1.7
guate1084	5.0	4.0	4.3	4.4
guate1088	2.5	1.3	2.5	2.1
guate1089	1.0	1.0	1.0	1.0
guate10903PM	1.0	1.5	2.0	1.5
guate1091	4.5	2.0	2.0	2.8
guate1098	4.8	3.7	4.0	4.1
guate1100	5.3	5.5	4.8	5.2
guate1104	1.0	1.8	1.5	1.4
guate1105	4.0	2.8	4.0	3.6
guate1106	1.3	1.0	1.0	1.1
guate1107	3.8	2.8	5.0	3.8
guate1109	1.3	1.0	1.0	1.1
guate1112	1.0	1.0	1.0	1.0
guate1115	1.0	1.0	1.0	1.0
guate1117	4.0	6.0	2.0	4.0
guate1118	1.8	2.0	4.0	2.6
guate1121	4.3	2.0	3.5	3.3
guate11242	3.8	4.5	3.0	3.8

Table A.3. Climbing bean accession from Guatemala reaction (score 1-9) to race 73 of *C. lindemuthianum*, in three repetitions and the Least Square Means (continued)

Genotype ID	Average R1	Average R2	Average R3	LSM estimate
guate1125	1.0	1.0	1.0	3.8
guate1126	4.8	2.5	2.5	1.0
guate1127	5.0	3.5	3.0	3.3
guate1132	2.0	1.0	1.0	3.8
guate1132PMB	2.0	1.0	1.0	1.3
guate1134	1.0	1.8	1.8	1.3
guate1135	1.3	1.3	1.0	1.5
guate1135-1	6.0	5.0	5.3	1.2
guate1136	1.3	1.5	1.0	5.4
guate1137	4.5	6.5	3.5	1.3
guate1142	3.8	1.0	2.3	4.8
guate1143	3.8	1.0	2.3	2.3
guate1147	2.8	2.0	3.0	2.3
guate1148	3.3	2.3	1.3	2.6
guate1149	4.3	4.0	4.8	2.3
guate1150	3.0	2.3	3.8	4.3
guate1151	3.3	3.5	2.8	3.0
guate1152	3.0	2.3	2.0	3.2
guate1154	3.5	4.3	2.0	2.4
guate1159	3.0	2.8	1.8	3.3
guate1161	4.0	3.5	4.0	2.5
guate1161.3PMA	1.5	2.0	1.5	3.8
guate1163	1.0	1.0	1.0	1.7
guate1164	1.0	4.0	3.0	1.0
guate1165	8.5	5.0	3.3	2.7
guate1166	8.0	5.3	8.3	5.6
guate1167	2.5	1.0	3.3	7.2
guate1168	1.0	1.8	2.5	2.3
guate1170	5.0	3.0	4.0	1.8
guate1172	1.0	1.3	2.5	4.0
guate1173	2.5	2.0	2.5	1.6
guate1175	2.8	2.3	3.3	2.3
guate1177	1.0	1.0	1.0	2.8
guate1179	1.5	1.0	1.0	1.0
guate1182	7.3	4.8	5.3	1.2
guate1183	3.0	2.0	2.0	5.8

Table A.3. Climbing bean accession from Guatemala reaction (score 1-9) to race 73 of *C. lindemuthianum*, in three repetitions and the Least Square Means (continued)

Genotype ID	Average R1	Average R2	Average R3	LSM estimate
guate1190	2.0	1.0	1.0	2.3
guate1191	3.3	2.8	3.0	3.0
guate1192	4.0	1.5	3.0	2.8
guate1198	5.5	3.0	6.0	4.8
guate1199	3.3	3.0	1.8	2.7
guate1200	8.0	7.7	5.5	7.1
guate1201	2.3	1.5	2.5	2.1
guate1211	1.8	1.0	2.0	1.6
guate1212	1.0	1.0	1.0	1.0
guate1213	5.5	4.0	3.5	4.3
guate1214	5.5	5.0	4.5	5.0
guate1216	5.0	3.3	2.0	3.4
guate1217	3.5	1.7	2.0	2.4
guate1218	2.3	2.0	1.3	1.8
guate1221	6.8	4.0	3.8	4.8
guate1222	3.8	1.3	2.0	2.4
guate1223	7.0	5.0	4.0	5.3
guate1224	5.0	4.0	4.0	4.3
guate1226	1.5	1.5	1.0	1.3
guate1231	4.0	3.0	3.5	3.5
guate1232	1.0	1.0	1.0	1.0
guate1233	7.8	2.8	5.5	5.3
guate1234	5.8	3.0	4.8	4.5
guate1236	1.3	1.0	1.0	1.1
guate1237	1.5	2.0	2.0	1.8
guate1238	6.0	4.5	4.8	5.1
guate1241	6.5	5.0	4.8	5.4
guate1242	5.3	5.0	2.0	4.1
guate1244	5.3	6.0	4.5	5.3
guate1245	4.5	2.5	3.5	3.5
guate1246	6.8	2.0	2.3	3.7
guate1248	2.3	1.0	1.8	1.7
guate1253	4.3	3.0	3.0	3.4
guate12564PM	2.5	3.0	3.3	2.9
guate1257	4.0	4.8	3.3	4.0
guate12803PM	5.0	4.3	4.5	4.6

Table A.3. Climbing bean accession from Guatemala reaction (score 1-9) to race 73 of *C. lindemuthianum*, in three repetitions and the Least Square Means (continued)

Genotype ID	Average R1	Average R2	Average R3	LSM estimate
guate1317	5.0	4.0	5.0	4.7
guate135	1.0	1.7	1.0	1.2
guate1375	1.0	1.0	1.0	1.0
guate1376	1.3	1.3	1.8	1.4
guate1378	5.0	1.8	1.0	2.6
guate138	8.3	9.0	4.7	7.3
guate13853PMB	6.0	2.0	3.5	3.8
guate1386	2.0	1.0	1.0	1.3
guate1387	3.3	1.8	2.5	2.5
guate1390	5.0	3.5	5.0	4.5
guate1394	2.8	1.7	3.5	2.6
guate1396	1.5	2.0	2.5	2.0
guate1407	2.5	1.3	2.0	1.9
guate1418	5.8	2.7	3.3	3.9
guate1420	1.3	1.0	1.0	1.1
guate1422	2.5	1.7	2.5	2.2
guate1424	3.0	2.0	3.3	2.8
guate1428	4.0	5.8	4.5	4.8
guate1429	1.0	1.0	2.0	1.3
guate143	9.0	7.0	6.0	7.3
guate1430	4.3	2.0	2.0	4.6
guate1434	5.0	4.5	4.3	1.6
guate147	1.8	2.0	1.0	3.7
guate148	2.5	5.5	3.0	5.0
guate1511	4.8	5.3	5.0	3.3
guate1514	2.5	4.3	3.3	3.3
guate1515	4.3	3.0	2.8	1.9
guate1540	2.8	1.0	2.0	3.9
guate1550	6.0	3.5	2.3	3.9
guate156	2.3	1.8	3.0	2.3
guate165	1.0	1.0	1.0	1.0
guate173	2.3	2.5	3.8	2.8
guate180	4.0	2.8	4.3	3.7
guate182	3.3	3.8	3.0	3.3
guate183	3.8	1.7	5.0	3.6
guate186	7.0	5.0	5.0	5.7

Table A.3. Climbing bean accession from Guatemala reaction (score 1-9) to race 73 of *C. lindemuthianum*, in three repetitions and the Least Square Means (continued)

Genotype ID	Average R1	Average R2	Average R3	LSM estimate
guate188	2.5	1.0	1.0	1.5
guate190	2.0	1.0	1.0	1.3
guate192	4.0	4.0	2.5	3.5
guate200	1.0	1.0	1.0	1.0
guate204	4.0	3.5	4.0	3.8
guate205	2.3	1.0	1.8	1.7
guate217	1.0	1.0	1.3	1.1
guate218	1.0	1.0	1.0	1.0
guate219	1.0	1.0	1.0	1.0
guate221	2.8	3.0	5.0	3.6
guate223	4.8	2.5	4.0	3.8
guate230	1.3	2.0	2.0	1.8
guate233	1.5	2.0	2.5	2.0
guate234	1.5	1.0	1.0	1.2
guate237	2.0	1.3	4.3	2.5
guate240	4.0	3.3	3.3	3.5
guate242	5.0	4.0	3.3	4.1
guate245	5.0	5.5	5.0	5.2
guate247	1.0	1.8	1.0	1.3
guate248	1.0	2.5	2.5	2.0
guate251	1.0	1.0	1.0	1.0
guate254	1.0	1.0	1.0	1.0
guate257	4.0	1.7	3.3	3.0
guate258	5.5	4.0	4.5	4.7
guate262	1.0	1.0	1.0	1.0
guate264	3.0	2.0	2.0	2.3
guate266	3.8	2.5	1.0	2.4
guate297	1.0	1.0	1.0	1.0
guate381	2.5	2.0	1.3	1.9
guate385	7.5	3.8	3.0	4.8
guate418	2.5	2.3	1.0	1.9
guate458	6.5	4.3	4.3	5.0
guate578	2.5	1.0	1.0	1.5
guate633	1.0	1.0	1.0	1.0
guate639	1.0	1.0	1.3	1.1
guate647	1.0	1.0	1.5	1.2

Table A.3. Climbing bean accession from Guatemala reaction (score 1-9) to race 73 of *C. lindemuthianum*, in three repetitions and the Least Square Means (continued)

Genotype ID	Average R1	Average R2	Average R3	LSM estimate
guate652	3.0	2.3	2.3	2.5
guate660	8.3	4.3	3.8	5.4
guate673	1.0	1.0	1.5	1.2
guate674	4.5	2.5	3.8	3.6
guate675	1.0	1.8	2.8	1.8
guate678	8.5	2.3	3.8	4.8
guate683	1.8	1.3	1.3	1.4
guate684	8.5	6.5	5.5	6.8
guate83	1.0	1.3	1.0	1.1
guate884	5.3	2.3	3.5	3.7
guate886	5.3	2.3	4.3	3.9
guate887	4.0	3.0	3.5	3.5
guate888	2.0	1.0	1.0	1.3
guate891	1.0	1.0	1.0	1.0
guate894	4.3	2.7	2.0	3.0
guate896	1.0	1.0	1.0	1.0
guate898	2.0	1.0	1.8	1.6
guate899	1.8	1.0	1.0	1.3
guate900	3.8	3.0	3.7	3.5
guate902	3.3	2.8	2.8	2.9
guate904	3.0	2.0	1.0	2.0
guate905	4.3	4.0	4.0	4.1
guate906	4.3	3.8	3.3	3.8
guate907	5.3	1.0	5.0	3.8
guate908	1.8	0.0	1.5	1.4
guate908-1	1.5	1.0	1.0	1.2
guate910	2.3	3.0	3.0	2.8
guate911	4.0	1.3	2.0	2.4
guate912	5.5	4.0	4.3	4.6
guate913	6.0	4.0	4.0	4.7
guate914	1.8	1.0	1.0	1.3
guate915	4.3	2.0	3.0	3.1
guate918	3.5	3.3	3.0	3.3
guate919	5.5	3.3	2.5	3.8
guate92	1.0	1.5	1.8	1.4

Table A.3. Climbing bean accession from Guatemala reaction (score 1-9) to race 73 of *C. lindemuthianum*, in three repetitions and the Least Square Means (continued)

Genotype ID	Average R1	Average R2	Average R3	LSM estimate
guate920	4.3	2.0	4.0	3.4
guate923	1.3	1.0	1.0	1.1
guate924	2.5	1.3	1.0	1.6
guate926	6.0	5.0	4.8	5.3
guate927	4.8	2.5	2.0	3.1
guate9282PM	4.3	1.0	1.8	2.3
guate930	4.0	2.7	2.0	2.9
guate931	4.0	1.8	1.3	2.3
guate932	1.0	1.0	1.0	1.0
guate933	3.3	1.8	3.5	2.8
guate935	1.0	1.0	1.0	1.0
guate936	2.3	2.5	3.8	2.8
guate937	3.8	2.8	4.0	3.5
guate938	5.3	3.8	3.5	4.2
guate940	3.0	1.0	1.3	1.8
guate941.3	5.0	3.0	4.8	4.3
guate943	1.0	1.0	1.0	1.0
guate944	5.0	3.3	3.5	3.9
guate945	1.0	1.0	1.0	1.0
guate947	6.3	4.0	2.0	4.1
guate949	2.3	2.3	1.5	2.0
guate950	1.0	1.0	1.0	1.0
guate951	2.5	1.0	1.0	1.5
guate952	1.0	1.0	1.0	1.0
guate953	1.3	1.0	1.0	1.1
guate955	4.0	4.3	2.5	3.6
guate956	4.3	2.8	2.5	3.2
guate958	4.3	2.5	3.8	3.5
guate959	3.0	3.3	2.3	3.5
guate960	2.3	2.5	1.5	2.8
guate961	1.0	1.0	1.0	2.1
guate962	3.5	1.5	1.5	1.0
guate963	4.0	4.0	3.8	2.2
guate966	4.3	1.0	1.5	3.9
guate967	4.8	1.7	3.3	2.3
guate968	1.0	3.0	1.0	3.2

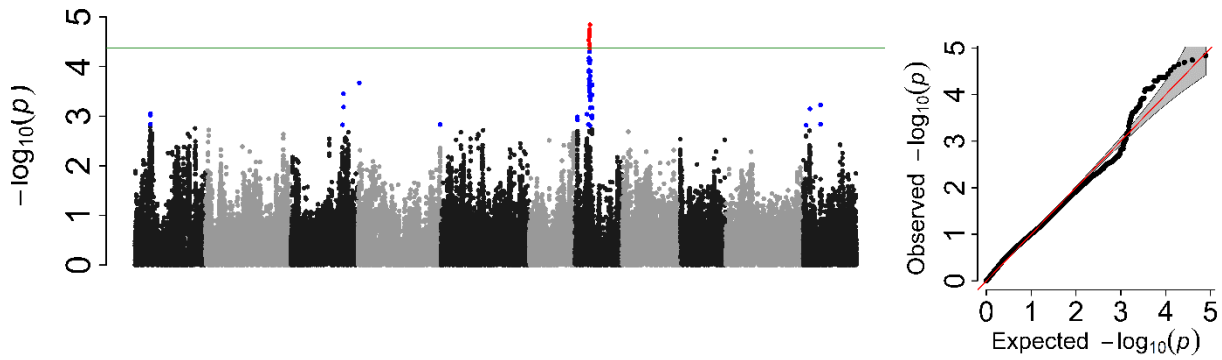
Table A.3. Climbing bean accession from Guatemala reaction (score 1-9) to race 73 of *C. lindemuthianum*, in three repetitions and the Least Square Means (continued)

Genotype ID	Average R1	Average R2	Average R3	LSM estimate
guate969	2.0	1.0	1.3	1.7
guate970	1.0	1.3	1.0	1.4
guate971	4.5	2.3	4.5	1.1
guate972	2.8	2.0	1.5	3.8
guate973	3.0	2.8	4.8	2.1
guate974	3.3	3.8	4.0	3.5
guate977	3.5	1.8	3.3	3.7
guate978	1.5	1.0	1.0	2.8
guate979	3.0	3.0	2.0	1.2
guate980	1.0	1.0	1.0	2.7
guate982	2.5	1.0	1.8	1.0
guate984	6.8	3.0	4.3	1.8
guate985	3.3	3.3	4.0	4.7
guate986	2.3	1.8	2.0	3.5
guate988	2.3	4.0	2.0	2.0
guate992	1.3	1.0	1.8	2.8
guate993	6.5	6.0	5.0	1.3
guate995	2.0	1.5	1.0	5.8
guate997	2.0	1.0	1.5	1.5
jardinero	6.8	7.0	4.8	6.2
LaborOvalle	4.0	2.3	4.0	3.4
LaSonrisa	1.5	1.0	1.0	1.2
LCH86V11	3.3	2.0	2.5	2.6
LCH86V13	5.3	3.0	3.5	3.9
LCH86V17	3.8	2.0	1.5	2.4
LCH86V19	2.0	2.0	2.3	2.1
LCH86V23	3.3	2.0	3.3	2.8
LCH86V31	2.8	1.3	1.5	1.8
LCH86V41	3.8	4.8	5.5	4.7
LCH86V69	3.5	3.3	3.8	3.5
LCH86V71	5.5	6.3	3.8	5.2
LCH86V77	5.5	4.8	2.0	4.1
LCH86V83	5.0	4.0	3.3	4.1
LCH86V87	6.0	4.0	6.0	5.3
LCH86V9	2.8	1.8	2.5	2.3
lineach86B39	2.5	1.0	2.8	2.1

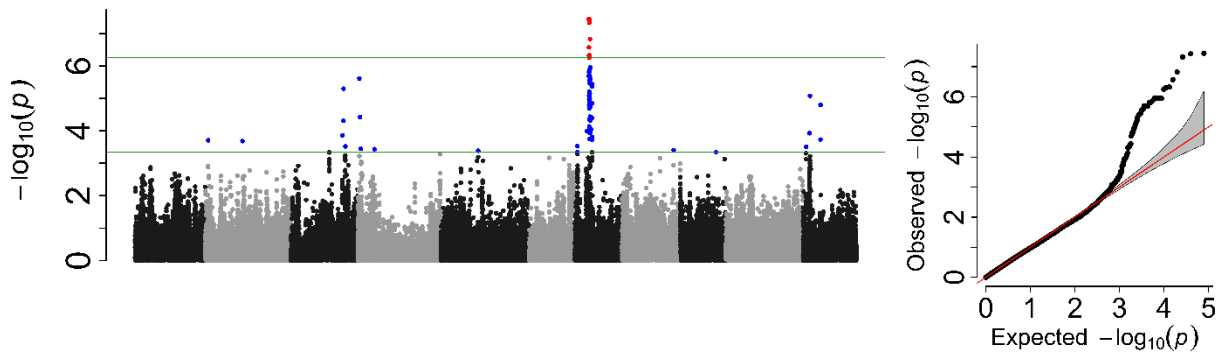
Table A.3. Climbing bean accession from Guatemala reaction (score 1-9) to race 73 of *C. lindemuthianum*, in three repetitions and the Least Square Means (continued)

Genotype ID	Average R1	Average R2	Average R3	LSM estimate
mediamilpa1	3.0	1.5	1.5	2.0
mediamilpa2	3.3	3.0	1.8	2.7
Michellite	8.0	9.0	8.7	8.6
Montcalm	1.0	1.0	1.0	1.0
Pascueno2	3.0	2.7	4.0	3.2
V4609.318	6.3	3.5	4.8	4.8
V4614315	4.0	0.0	6.8	4.5
V4616320	4.5	2.0	2.3	2.9
V4616324	7.0	3.0	3.8	4.6
V461634	3.3	2.5	2.0	2.6
V5746313	4.5	1.3	2.0	2.6
V7966	4.5	2.5	3.0	3.3
vainamorada1	3.0	2.8	2.5	2.8
xenimajuyu	5.8	7.5	7.3	6.8

PCA 1.37E-01



2PC-EMMA 0.167147



EMMA 0.168639

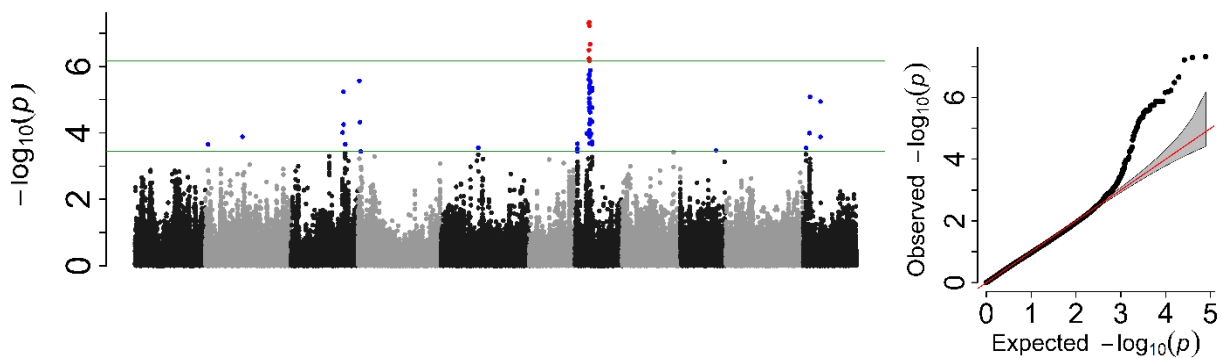


Figure A.1. Manhattan plots using different models for *C. lindemuthianum* resistance to race 73 and QQ-plots using GenABEL software, the MSD value is on the top left. From bottom the first green line is for 0.1 percentile and the second is for 0.01. The green line is the cut-off value to call a peak significant. SNPs above the 0.01 percentile are highlighted in red, while those above 0.1 are highlighted in blue.

Table A.4. SNPs significantly associated, chromosome, position, minor allele frequency (maf) and significant P-values for the trait anthracnose on 369 climbing bean accessions from Guatemala for PCA model, sorted by lowest P-value, using GenABEL software.

SNP	Chromosome	Position	P.value	maf
S07_8954263	7	8954263	1.44E-05	0.121951
S07_8767491	7	8767491	1.79E-05	0.128726
S07_8711204	7	8711204	2.02E-05	0.078591
S07_8711208	7	8711208	2.23E-05	0.079946
S07_8726264	7	8726264	2.49E-05	0.130081
S07_8507679	7	8507679	2.95E-05	0.069106
S07_8875287	7	8875287	3.58E-05	0.121951
S07_8875263	7	8875263	4.21E-05	0.123306
S07_8875341	7	8875341	4.21E-05	0.123306
S07_8875373	7	8875373	4.21E-05	0.123306
S07_8875375	7	8875375	4.21E-05	0.123306
S07_8875274	7	8875274	4.96E-05	0.124661
S07_8711251	7	8711251	5.01E-05	0.082656
S07_8875249	7	8875249	5.03E-05	0.126016
S07_8590734	7	8590734	6.71E-05	0.070461
S07_8879902	7	8879902	7.13E-05	0.119241
S07_9298239	7	9298239	7.48E-05	0.073171
S07_9298287	7	9298287	7.48E-05	0.073171
S04_527782	4	527782	0.000213	0.330623
S04_47695582	4	47695582	0.001475	0.165312
S04_47695850	4	47695850	0.004419	0.161247
S04_1022377	4	1022377	0.004852	0.181572
S04_47712717	4	47712717	0.005006	0.155827
S04_47163814	4	47163814	0.005608	0.055556
S04_47695703	4	47695703	0.005663	0.166667
S04_47695774	4	47695774	0.005663	0.166667
S04_47695809	4	47695809	0.005929	0.168022
S04_47695831	4	47695831	0.006393	0.169377
S04_47709078	4	47709078	0.007845	0.173442
S04_8236887	4	8236887	0.008154	0.348238
S04_47695783	4	47695783	0.0082	0.173442
S04_47695868	4	47695868	0.008606	0.173442
S04_1276626	4	1276626	0.009012	0.079946
S04_1431968	4	1431968	0.009156	0.318428
S04_467709	4	467709	0.010308	0.172087
S04_8986235	4	8986235	0.01034	0.079946

Table A.5. Reaction of different Andean sources of resistance to race 556 and 3981 of *C. lindemuthianum*

Cultivar/line	Pool	Gene	556	3981
Amendoim Cavalo	A	<i>Co-AC</i>	S	S
AND 277	A	<i>Co-1⁴</i>	R	R
Jalo Vermelho	A	<i>Co-12</i>	NA	R
Jalo Listras Pretas	A	<i>Co-13</i>	NA	S
Pitanga	A	<i>Co-14</i>	NA	R
Corinthiano	A	<i>Co-15</i>	NA	S
Paloma	A	<i>Co-Pa</i>	S	S
Jalo Pintado 2	A	<i>Co-18</i>	R	R
Perla	A	<i>Co-Pe</i>	NA	S
BGF20	A	<i>Unknown</i>	R	R

R: Resistant (score 1-3) S: Susceptible (score 4-9) NA: Not available

Table A.6. Reaction of the differential cultivar of anthracnose to isolates of *C.lindemuthianum*

	Race 556					Race 585					Race 897				
Michelite	1	1	1	1	1	9	9	9	9	9	9	9	9	9	9
MDRK*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Perry Marrow	7	7	7	7	7	1	1	1	1	1	1	1	1	1	1
Cornell 49242	9	9	9	9	9	9	9	9	9	9	1	1	1	1	1
Widusa	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Kaboon	9	9	9	9	9	1	1	1	1	1	1	1	1	1	1
Mexico 222	1	1	1	1	1	7	7	7	7	7	1	1	1	1	1
PI 20762	1	1	1	1	1	1	1	1	1	1	7	7	7	7	7
TO	1	1	1	1	1	1	1	1	1	1	9	9	9	9	9
TU	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
AB 136	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
G2333	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

	Race 1609					Race 1993					Race 3981				
Michelite	9	9	9	9	9	9	9	9	9	9	5	5	6	5	5
MDRK*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Perry Marrow	1	1	1	1	1	1	1	1	1	1	6	6	6	6	6
Cornell 49242	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
Widusa	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Kaboon	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Mexico 222	7	7	7	7	7	7	7	7	7	7	3	3	3	3	3
PI 20762	1	1	1	1	1	8	8	8	8	8	9	9	9	9	9
TO	1	1	1	1	1	9	9	9	9	9	9	9	9	9	9
TU	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
AB 136	8	8	8	8	8	8	8	8	8	8	7	7	7	7	7
G2333	1	1	1	1	1	1	1	1	1	1	5	5	5	5	5

MDRK: Michigan dark red kidney; Scale (1-3) resistant and (4-9) susceptible.