# TOWARDS THE DEVELOPMENT OF A GENE-BASED ECO-PHYSIOLOGY MODEL

# FOR COMMON BEAN: GENOTYPE BY ENVIRONMENT INTERACTIONS

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# TOWARDS THE DEVELOPMENT OF A GNE-BASED ECO-

# PHYSIOLOGY MODEL FOR COMMON BEAN:

## GENOTYPE BY ENVIRONMENT INTERACTIONS

Ву

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## DOCTOR OF PHILOSOPHY

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### ABSTRACT

Genotype by environment interactions (GxE) complicate selection in common bean (Phaseolus vulgaris L.). Crop models can play a valuable role by helping plant breeding programs to better understand GxE. The objectives of this study were to evaluate agronomic, morphological, and phenotypic traits of a recombinant inbred lines population derived from the inter-gene pool cross [Jamapa (Mesoamerican) x Calima (Andean); RIJC] across five environments and generate data to validate a gene based eco-physiology model using an independent population (RISR) from the cross of Stampede x Redhawk. Field trials were conducted across North Dakota, Florida, Puerto Rico, Colombia (Popayan and Palmira), and Nebraska from 2011 to 2013. Resolvable row-column designs and RCBD with three replications and two-row plots were used to evaluate the populations. Analysis of variance was performed using the PROC MIXED procedure of SAS. Genotype main effect and GxE interaction (GGE) biplots were assessed for seed yield components and RISR were compared to the RIJC population. The results suggested different mega-environments depending on the trait of interest. Locations relatively more homogenous can be clustered and North Dakota usually stands alone. The biplots allowed detecting stable genotypes or subsets which were best adapted to mega-environments. Moderate to high narrow-sense heritability estimates (0.55 to 0.87, 0.25 to 0.76 and 0.56 to 0.69 for phenological traits, seed yield components and other agronomic traits, respectively), were observed suggesting various traits such as flowering time, physiological maturity, seeds per pod, plant height, among others, may be used as selection criteria to improve common bean. The populations responded relatively more similar for most of the traits assessed in North

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Dakota. However means across locations for RIJC differ significantly from RISR grown alone in North Dakota. Seed yield losses for RISR population in drought conditions were 54.3% and 59.0% in 2012 and 2013, respectively. This study will help developing the next generation gene-based crop model along with a high-resolution linkage map and identification of potential candidate genes controlling various traits. Ideal genotypes suited for specific mega-environments can be designed. These new techniques should shorten the cycle needed to develop superior varieties by implementing efficient early generation selection.

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# DEDICATION

To my family, I thank you for all of your support along the way.

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### **1. LITERATURE REVIEW**

Common bean (Phaseolus vulgaris L.) is one of the most important food legume consumed worldwide. It is an important source of calories, proteins, vitamins and minerals (Broughton et al., 2003). This legume is the staple food in Latin America, the Caribbean, and some countries in Africa, where it plays a major role in the daily diet as a meat substitute. Even though the world production cannot be calculated with certainty because of confusion with the production of other grain legumes, global estimates of dry bean in 2012 (includes *P. vulgaris*, some beans of other species, including *P. lunatus*, and Vigna sp. except green beans) exceeded 23 million tons on a harvested area of more than 29 million ha (FAOSTAT, 2014). The estimated value of world production for 2008 was over \$12 billion USD. In the western hemisphere, the United States is the third leading common dry bean producer after Brazil and Mexico (Beebe et al., 2010). The United States planted almost 0.7 million ha in 2012. North Dakota and Minnesota lead with 40% of the US dry bean production and approximately 42% of the total area planted in 2013 (USDA-NASS, 2014a). In 2012, total bean production was valued at approximately \$409 million in North Dakota and \$132 million USD in Minnesota (USDA-NASS, 2014b).

Common bean cultivars are classified according to agronomic and morphologic traits as well as cultural preferences. Cultivars can vary in growth habit, duration of growth period, and seed characteristics (size, color, shape, and surface texture) depending on the growing region (Voysest and Dessert, 1991). The United States Department of Agriculture recognizes 21 bean classes (USDA-FGIS, 2008). However,

most of the production in the country is focused in only seven classes including pinto, navy, black, great northern, kidney, small red and pink beans (Figure 1).



Figure 1. U.S. dry beans production by class from 2008 to 2012 (Thousands of tons; adapted from USDA-NASS, 2014a).

Better strategies are needed to improve seed yield and quality in order to satisfy the consumer's market and also increase grower's profit. However, one of the major limitations in the development of improved cultivars is variable genotypic (G) performance across environments (E) or, in other words, the GxE interactions (Ceccarelli, 1996). In order to obtain greater or more stable seed yields from the genotypes with specific desired characteristics, an appropriate balance among physiological processes and yield components is needed. The incorporation of genotypic variables or associated plant traits into an improved crop model can help plant breeders to understand and manage the complexity of GxE interactions (Beaver and Osorno, 2009). Phenotypic data are useful in identifying traits that control common bean growth and development.

### **1.1. Genotype by Environment Interactions**

Genotype by environment interaction can reduce genetic variation of the crop, reduce heritability estimates, and result in lower seed yields due to a lack of adaptation to a wide range of environments (Ceccarelli, 1996). A landrace cultivar growing in the environment where it was selected will often express high productivity but will not necessarily perform well in a contrasting environment. A genotype by environment interaction is the result of a differential response of genotypes (G) to environmental (E) factors (Comstock and Moll, 1963). Depending on the agro-ecologic zone and cropping practice, the E components represent location and season effects. If unpredictable E effects such as climate are recurrent, significant GxE interactions can occur. The interrelationship between genetic and environmental factors affecting the expression of specific traits is complex. GxE interactions are considered a major factor limiting an efficient and predictable response to selection and a significant challenge facing plant breeders.

These interactions become important when the rank of breeding lines changes over a range of environments. Baker (1988) defined this change in genotypic response in terms of rank (qualitative) as crossover GxE interactions. If this change is observed in term of scale (quantitative), the non-crossover is not an issue for breeders because genotypes with superior characters will also perform well in other environments. Selection for broad adaptation has been an important goal of most agricultural breeding programs. However, plants can be bred for disease resistance or tolerance for specific environments, such as drought stress to broaden adaptation.

Crossover interactions may be linked to two or more environmental factors (Nleya et al., 2000). Breeding crops for additional traits can reduce the rate of genetic progress. Abebe and Brick (2003) reported that in five dry bean growing environments of Ethiopia, GxE interaction was significant for seed yield, seed weight, days to flower, and plant height. Positive phenotypic correlations between biomass and seed yield were also observed. Plant biomass, often associated with days to maturity and number of pods per plant are two selection criteria used by dry bean breeding programs because these traits are easy to evaluate using a visual scale and have moderate to high narrow sense heritability and low GxE interactions. Heritability estimates of traits associated with dry bean seed yield reported in the literature differ because of the effects of specific environments, the genetic composition of the population, and the method used to estimate the heritability.

In order to improve dry bean yield and quality, the presence and nature of GxE interactions must be estimated in a reliable way to identify key characters that can affect production. Cultivars regionally adapted can be improved genetically by identification of crossover interactions that implies sufficient variability of high heritable traits. A better understanding of how to manage GxE interactions requires consideration of the effects of growth habit and adaptation on the expression of seed yield. According to Kelly et al. (1998b), breeding common bean for increased yield can only be accomplished successfully within the framework of very specific constraints of growth habit, seed size, maturity, and gene pools.

### 1.2. Growth Habit

Common bean is a highly polymorphic species showing considerable variation in growth habit, vegetative traits, flower color, and the size, shape, and color of both seeds and pods (Laing et al., 1984).

Multiple domestication events from the wild ancestor have resulted into two major centers of origin or gene pools for common bean, Middle American and Andean South American. These gene pools could be further divided into races. Middle American gene pool includes four races namely Mesoamerican, Durango, Jalisco and Guatemala which consists only of climbing beans. Nueva Granada, Chile and Peru races originated from the Andean gene pool. These gene pools can be characterized and distinguished by molecular markers (phaseolin, allozymes) along with vegetative and reproductive traits (Singh et al., 1991; Beebe et al., 2000). Genome sequence assembling 473 Mb of the 587-Mb common bean genome confirmed two independent domestications from the genetically differentiated Middle American and Andean gene pools (Schmutz et al., 2014). Among common bean races, different major growth habits are identified. Growth habit can be divided into determinate and indeterminate. In determinate plants the apical growth ceases when an inflorescences appears whereas indeterminate ones continue to develop and the stem apex remains vegetative. Tanaka and Fujita (1979) classified determinate growth habit cultivars as bush and indeterminate as bush, semiclimbing and climbing type. Singh (1982) used the type of terminal bud, stem stiffness, twining ability, and distribution of pod load to characterize the four major growth habits in common bean (Types I, determinate bush; type II, indeterminate bush; type III, indeterminate prostrate; and type IV, indeterminate climbing). Determinate cultivars

usually show less biomass accumulation due to the compact growth habit in comparison with indeterminate types. Seed yield is generally higher in indeterminate types than in determinate types because of better light distribution within the plant canopy (Tanaka and Fujita, 1979). Upright growth habit is desirable for mechanical (direct) harvest (Smith, 2004, Eckert et al., 2011) and can reduce the incidence of diseases (Miklas et al., 2001). Samper and Adams (1985) observed differential effects among dry bean cultivars under drought stress for biomass accumulation and translocation to yield components. Rosales-Serna et al. (2004) reported that indeterminate cultivars yielded more than determinate across locations and treatments. Indeterminacy seems to be an important trait for adaptation under drought stress and the Durango race is a valuable genetic resource for drought. In the Mexican highlands, cultivars with Type III growth habit showed superior performance in terms of adaptation and yield potential under irrigation and stress conditions when compared to Type I (Rosales-Serna et al., 2002). According to Kelly and Adams (1987), a Type II cultivar exhibited the highest yield and stability compared to Type I and Type III growth habits across both rain-fed and irrigated environments in Michigan.

Type III indeterminate cultivars showed high yield potential but less stability because of white mold disease, caused by *Sclerotinia sclerotiorum* (Lib.) de Bary, and harvest difficulties associated with prostrated growth habit. Trials planted every year across the United States and Canada through the Cooperative Dry Bean Nursery reported superior seed yield into the Type III growth habit by comparison with the Type I and II (Stewart-Williams and Myers, 1995; Singh et al., 2007). Phenotypic traits as height, node and leaf number and branching characteristics are positively correlated

with yield for Type I, II and III. In spite of the important role that growth habits plays on yield, adaptation, maturity, and harvest mechanization, North American breeders are still facing growth habit constraints since this trait is also influenced by the environment. Hence, any attempt to breed common bean must be related to G x E interactions and phenotypic characteristics that can affect the yield.

Although growth habit represents a key factor in bean production, various environmental conditions such as disease, water stress or soil nutrient deficiency can affect seed yield. Disease, for example, can be a major factor limiting dry bean production for the northern US Great Plains (Knodel et al., 2008; Schwartz et al., 2005). An upright architecture in beans can contribute to a better air flow within the canopy and help avoid white mold damage. The pinto bean cultivar 'Stampede' which has and erect Type II growth habit and deep roots, performed better than any other genotypes in yield trials conducted across locations [Washington, Idaho, North Dakota (Kandel et al., 2009; Osorno et al., 2008) and Nebraska (Urrea and Porch, 2009)]. These results showed good example of non-crossover G x E interactions that do not affect seed yield.

#### 1.3. Seed Yield and Yield Components

Seed yield is a function of many plant traits and their interrelationships. High yield can be achieved by simultaneously improving the major yield components. Scully and Wallace (1990) reported that yield is linearly and positively correlated with growth rate, biomass and pod filling duration. The duration of the vegetative and reproductive stages play an important role in the expression of dry bean seed yield. A better understanding of these traits should help to develop different physiological plant models that can be used to increase the yield potential of common bean. White and Izquierdo (1991)

studied the physiology of yield potential and stress tolerance. They concluded that adaptation to abiotic stress in common bean is probably due, in large part, to remobilization of carbohydrate or nitrogen reserves and an indeterminate growth habit. Similarly, Nielsen and Nelson (1998) reported that yield components with high correlation to seed yield were number of pods per plant and number of seeds per pod for black beans in the presence of water stress. Abebe and Brick (2003) used a multiple regression model in a non-stress environment to predict seed yield and showed that only pods per plant, plant biomass, and plant height contributed significantly to the expression of seed yield. These three components accounted for 65% of the variation in seed yield. In a moderate stress environment, pods per plant, biomass, and plant height were correlated to seed yield and 44% of the seed yield variation was due to number pods per plant. The overall results confirm that selection for seed yield as sole selection criterion in a single environment may not result in improved seed yield across a range of environments.

Tanaka and Fujita (1979) reported a variation in number of seeds per pod from 3.0 to 5.4 in two bean cultivars planted at different plant densities. The number of seeds per pod had a significant linear relationship with seed yield. Fageria and Santos (2008) reported that dry bean genotypes grown on a Brazilian Oxisol had seed number per pod varying from 3.1 to 6.0, with an average value of 4.4 per pod. In this study, hundred-seed weight had significant positive linear relationship with seed yield, with 49% of yield variability due to this component. Seed size is controlled genetically but also is influenced by environmental conditions (GxE interactions). For instance, moderate to severe drought stress can reduce seed weight and seed yield by 41 to 92%,

respectively (Foster et al., 1995). Moot (1993) indicated that the analyses of seed yield through assessment of their yield components can be used to describe differences between genotypes. However, selection in breeding programs based on any of the yield components has not produced consistent increases in seed yield, greatly due to the magnitude of GxE interactions.

#### 1.4. Harvest Index

Defined as the ratio of seed yield to aerial dry matter yield, harvest index (HI) is an expression proposed by Donald (1962) to assess the breeding progress towards improved yield potential. Among species and genotypes, large variation has been found for biomass partitioning from vegetative organs to pod and from pod wall to seed. One of the key partitioning indices indicating remobilization of photosyntates is the pod harvest index (PHI) which is positively correlated to seed yield under drought and irrigated environmental conditions (Beebe et al., 2009). Sinclair (1998) revealed that HI is an important trait associated with the dramatic increases in crop yields that have occurred in the twentieth century. At the beginning of the last century, HI of most grain crops was low, usually about 0.3 or less and HI was increased just only with modern plant selections. Based on a study of 23 cultivars of dry bean, Snyder and Carlson (1984) reported that harvest index varied from 0.4 to 0.6. Previous reviews in various crops indicated that selection based on harvest index or grain yield are not necessarily transferable across seasons or environments, because of high GxE interactions. Several authors have been concerned about effectiveness of selections across a wide range of environmental conditions (Deloughery and Crookston, 1979; Johnson and Major, 1979; Whan et al., 1981; Snyder and Carlson 1984). According to Cui and Yu

(2005), harvest index was a larger contributor than biomass to the progress of soybean [*Glycine max* (L.) Merr.] yield improvements in China.

Hedley and Ambrose (1985) studying field peas (Pisum sativum L.) suggested that yield improvement would result from selection of plant types that produced a stable, high plant harvest index. Gifford and Evans (1981) reported that the improvement of yield potential in crops has come largely from increase in the partitioning of assimilates into the harvested organs. Improved HI represents increased physiological capacity (sink capacity) to mobilize photosynthates and transfer to organs of economic value (Wallace et al., 1972). HI varied with the crop genotypes and was also influenced by environmental factors. Dry bean breeding for harvest index has been a major goal through genetic improvement of yield potential and non-biotic stress tolerance. Peet et al. (1977) reported significant positive correlation with HI and seed yield of dry bean cultivars. Variety trials of pinto bean cultivars evaluated under non stressed and intermittent drought-stressed environments in Idaho revealed high significance for year, test environment, genotype, and the year x test environment interaction. The lowest average HI was observed in drought stress in 2003 (0.07) and cultivars Othello and CO46348 had low HI reduction due to severe drought stress (0.34 to 0.28 and 0.33 to 0.26, respectively). The largest HI reduction was observed in Topaz (0.35 to 0.07), Buster (0.31 to 0.14), and a landrace of pinto (0.34 to 0.14) under drought stress in 2003 (Brick et al., 2008). When selection is based on a single parameter or ratio like HI, monitoring the other components which may influence economic yield is very important (Snyder and Carlson, 1984).

### 1.5. Plant Height

Depending on the growth habit, plant height in common bean can be over 3 m in its natural habitat as reported by Singh et al. (1991) for the Jalisco race usually characterized by an indeterminate type IV (also common within Guatemala race and Andean gene pool). Improving the archetype of bean has always been one of the goals for breeders, and it has many advantages associated such as, reducing incidence of diseases or facilitating mechanical harvest. Fuller et al. (1984) reported elevating the canopy of a prostrate highly susceptible indeterminate great northern bean in a semiarid climate reduced white mold incidence and increased seed yield. Increasing plant height was found to be negatively associated with lower white mold incidence (Miklas et al., 2001). In contrast, Kolkman and Kelly (2002) found in a study evaluating resistance traits to white mold that a susceptible parent had a greater canopy height than the resistant parent. The study previously mentioned that plant height reduction in segregating populations was considered an undesirable avoidance mechanism since it will reduce yield potential. The increase in canopy width was a desirable avoidance mechanism in the elite lines, since it reduced disease severity index levels while increasing yield. These contrasting results were due to the extreme differences in resistance between phenotypes evaluated and the environments tested, in other words G x E interactions. Significant G x E interactions were observed by Taran et al. (2002) for plant height, harvest index, and other yield components in a study of genetic mapping of agronomic traits in common bean. Seed yield correlated significantly to numerous phenotypic traits among which are plant height and harvest index.

Plant height was positively correlated to days to maturity as well. On the other hand, environmental stress can reduce growth and subsequently yield. For instance, water stress during vegetative stages can delay growth and the immediate phenotypic trait affected will be plant height varying according to growing stage. Nielsen and Nelson (1998) reported in a black bean study in the eastern Midwest (Akron, OH) that yields were most sensitive to water stress during the reproductive growth stage while plant height and leaf area were most sensitive during the vegetative growth stage. Plant height genotypic response is dependent upon the environment for its final expression. Specific environmental factors such as photoperiod, light intensity, temperature, and geographic latitude, among others, can affect plant height.

### **1.6. Heritability**

To estimate or define heritability universally is complicated because of the great diversity found in the natural mode of reproduction of the plant kingdom. Heritability can be considered either in the narrow (h<sup>2</sup>) or the broad (H<sup>2</sup>) sense according to the proportion of phenotypic variance due to genetic effects (Nyquist, 1991). However, Hanson (1963) suggested standardization of the heritability with reference to a selection concept. The heritability both in the broad and narrow sense is important for plant breeding referring to selection process that is only effective for self-pollinated crops when considering additive genetic variance in relation to total variance (Fernandez and Miller, 1985). Based on a single plant selection Allard (1999) noted that seed yield generally shows a low heritability.

Using recurrent selection for improving seed yield in common bean populations, Singh et al. (1999) observed high and moderate heritability estimates for seed weight

and seed yield, respectively. These results indicated that interracial and inter gene pool of common bean populations possess large genetic variance. Wallace et al. (1993) asserted that heritability for biomass is very low while harvest index and days to maturity show high heritability estimates. In common bean, drought is a worldwide production hindrance (Fairbairn, 1993) and breeding for drought resistance is a slow and difficult process (Blum, 1988). Szilagyi (2003) noted the influence of drought on seed yield components of common bean populations and low heritability (broad and narrow sense) in both drought stress and non-stress resulted in medium chances of transmission of the characters to the offspring. Pervin et al. (2007) reported in study of variability of quantitative characters in *Vigna sp.* that low heritability estimates were due to high GxE interaction. The previous authors recommended using a family selection method to increase seed yield in breeding program.

To improve breeding strategies for plant disease resistance it is necessary to have estimates of heritability from diverse sources. Narrow sense heritability estimates for number of pods per plant, plant biomass, plant height, and seeds per pod vary from 0.69 to 0.75, 0.6 to 0.79, 0.80 to 0.85, and 0.78 to 0.81, respectively (Abebe and Brick, 2003). Montoya et al. (1997) reported relatively high narrow sense heritability estimates for common bean populations grown in tropical environments, ranging from 0.61 to 0.79 and mostly due to selection of a resistant parent as source of resistance/tolerance to web blight disease caused by *Rhizoctonia solani* Kuhn, which is the asexual stage of the basidiomycete fungus *Thanatephorus cucumeris* (Frank) Donk.

### 1.7. Crop Models

Different plant genotypes, soil conditions and climate create complex systems where various factors can interact and affect the development and final yield of the crop. Crop models can be used to better understand this complexity. Given that conventional agronomic research requires several years or growing seasons to produce reliable results, the use of genotypic variables or associated traits in crop models can help to expand the knowledge of the plant physiological system. Crop models can be used to estimate risks in order to make better decisions and improve selection efficiency in plant breeding programs (IBSNAT, 1989). A crop model requires a minimum set of inputs such as genetic coefficients, photothermal days (degree days) and weather data such as solar radiation to generate possible outcomes (Jame and Cutforth, 1996). For practical applications of the crop model, an adequate adjustment (calibration) of the system parameters to a given region is needed to provide good predictions. Validation through a wide set of environments is necessary to verify the accuracy of the yield predictions and also to refine the crop model. Computer software has been developed to facilitate the use and applications of crop models. The decision support system for agro technology transfer (DSSAT) is a well-known example (IBSNAT, 1993; Hoogenboom, 2004).

Crop models can be used to simulate various environmental effects (soil water and nitrogen dynamics) on phenologic development and yield. These models also can predict the crop responses to a specific environment. Aggarwal and Penning de Vries (1989) used the CROPGRO model (Hoogenboom et al., 1992) to estimate yield potential in a new environment.

Adikua et al. (2001) simulated common bean growth and development under water and salinity stress in greenhouse. Simulated growth (dry matter) and seed yield was associated with observed values from the crop model producing large coefficients of determination. Whisler et al. (1986) demonstrated the importance of crop models in the measurement of the effects of soil erosion and plant physical damages (insect attacks or herbicide injuries). Crop modeling has the potential to play a valuable role in plant breeding programs. Ritchie and Alagarswamy (2003) used genetic coefficients associated with particular cultivars in a crop model to study GxE interactions. The related parameters are defined as the sum of quantitative response of a specific genotype to environmental factors (IBSNAT 1993). Simulation can be an important tool for developing plant growth information to help manage or exploit GxE interactions. Hoogenboom et al. (1997) predicted effects of days to flowering and maturity on the expression of common bean seed yield using the GenGro model based on effects of genes. This model used linear functions describing the effect of eight genes (three for each growth habit and seed size and two for phenology) instead of standard genotypic parameters of the BEANGRO (Hoogenboom et al., 1992) simulation for common bean. Hoogenboom and White (2003) reported the GenGro model can improve simulation if the genetic control of the expression of quantitative traits is understood. Limitations of using the crop model in agriculture systems are based on the incomplete understanding of the interaction of genotype and environment. Simplifications are made when knowledge is lacking and can result in subjectivity and loss in the ability to predict growth and development of the crop.

# 2. OBJECTIVES

The main objectives of this study are to i) evaluate agronomic, morphological and phenotypic traits of a RIL population (RIJC) from the cross of 'Jamapa' x 'Calima' across five contrasting environments, and ii) generate data to validate a gene based ecophysiology model using an independent population (RISR) from the cross of Stampede x Redhawk. Specific objectives focused on:

- a) Evaluate the agronomic, phenological, and morphologic characteristics of the RIJC population.
- b) Calculate narrow sense heritability of yield components and other variables for the populations.
- c) Compare RIJC with RISR and variety trials from the dry bean breeding program for agronomic and phenological traits.
- d) Evaluate the RISR population in drought and irrigated conditions.

### 3. MATERIALS AND METHODS

#### 3.1. Plant Materials and Field Trials

The performance of 203 lines (recombinant inbred and parents; Table A1) derived from the inter-gene pool cross Jamapa by Calima [RIJC; (Vallejos et al., 2000)] was evaluated in field trials at Prosper, ND; Citra, FL; Isabela, PR and Colombia (Popayan and Palmira) (Table 1). The choice of these parents was based on their contrasting growth habit, seed size, gene pool, high genetic polymorphism, stability, and disease resistance, among other characteristics. Jamapa (SNICS, 2003) is of Mesoamerican origin, indeterminate growth habit and small, black seed (21 g 100-seed<sup>-1</sup>). Calima [also known as Diacol-Calima and ICA-Calima; (Voysest, 2000)], comes from the Andean gene pool, has a determinate growth habit and large, red-mottled seed (57 g 100-seed<sup>-1</sup>).

A second population named RISR of 180 lines (recombinant inbred and parents; Table A2) derived from the cross of 'Stampede' pinto (Osorno et al., 2008) and 'Redhawk' dark red kidney (Kelly et al., 1998a), was evaluated at Prosper, ND and Scottsbluff, NE (Table 2). The RISR population was grown under drought and irrigated conditions in Nebraska in 2012 and the experiment was repeated the following year using a subset of the extreme genotypes and parents. Development of the RISR mapping population has been previously described by Schmutz et al. (2014). Stampede is a high-yielding pinto bean cultivar recently released by North Dakota Agricultural Experiment Station. It has an upright, short vine growth habit (Type II) with brown-mottled seed (38 g 100-seed<sup>-1</sup>). Red Hawk is also a high-yielding dark-red kidney

cultivar released by the Michigan Agricultural Experiment Station. It has an upright, bush growth habit (Type I) and dark-red seed (62 g 100-seed<sup>-1</sup>).

Table 1. Locations and environmental conditions at five testing sites for the RIJC population.

	RIJC Population				
Locations	Citra, FL	Colo Palmira	ombia Popayan	Isabela, PR	Prosper, ND
Coordinates	29° 39' N, 82° 06' W	03° 29' N, 76° 81' W	02° 25' N, 76° 62' W	18° 28' N, 61° 02' W	47° 00' N, 96° 47' W
Altitude (m)	60	1000	1800	128	280
Mean sunlight (h)	13	12	12	12	15
Growing season	Mar-Jun 2011	Nov 2011- Jan, 2012	Mar-Jun 2012	Feb-May 2012	May-Aug 2012
Total rainfall (mm)	290	425	466	672	157
Mean temperature ( <sup>0</sup> C)	25	24	18	24	20
Previous crop	Fallow	Bean	Fallow	Fallow	Wheat
Soil type	Millhoper Fine Sand	Mollisol (fine silty mixed isohypoth ermic Aquic)	Andosol (fine loamy mixed isothermic typic Andic dystropept)	Coto- Aceitunas (Red Acidic fine clay)	Perella sine silty- Bearden clasy loam complex
Irrigation system	Sprinkler	-	-	Drip	-
Density (plant m <sup>-2</sup> )	4	3	4	4	7
Row spacing (cm)	90	120	90	100	76
No.RILs & parents <sup>†</sup>	188	180	179	131	176

<sup>†</sup> Different number of genotypes was planted across locations due to low seed stocks for some lines.

	RISR Population				
Locations	Prosper, ND Scottsbluff, NE				
Coordinates	47° 00' N, 96° 47' W	41.87° N, 103.66° W			
Growing season	May-Aug 2013	May-Aug 2012 May-Aug 20			
Total rainfall (mm)	312	183	331		
Mean temperature ( <sup>0</sup> C)	20	24	22		
Previous crop	Wheat	Corn			
Soil type	Perella sine silty- Bearden clasy loam complex	Coarse-silty, mixed, superactive, calcareous, mesic Ustic Torriorthents			
Irrigation system	-	Sprinkler	Furrow		
Density (plant m <sup>-2</sup> )	11	19	24		
Row spacing (cm)	76	56	56		
No. RILs & Parents <sup>†</sup>	180	182	42		

Table 2. Locations and environmental conditions at two testing sites for the RISR population.

<sup>†</sup> Different number of genotypes was planted across locations due to low seed stocks for some lines.

Resolvable row column designs (Williams et al., 2006) with three replications were used at all locations except for Nebraska (RCBD with split plot arrangement). Experimental units consisted of two row-plots, each 5 to 6 m length, but row spacing varied across locations from 0.76 to 1.2 m, depending on seed availability and planting

equipment. In Nebraska drought trial for RISR population, the plot lengths were 4.6 and 3.7 m, respectively in 2012 and 2013 with row spacing of 0.56 m.

### 3.2. Phenotypic Data Collection

When 50% of the cotyledons have emerged, weekly evaluations started and data were recorded over 48 growth variables and 8 phenological traits for the RIJC population. Many variables are specifically used for the crop model input development and validation of all the components was not possible due to lack of detailed datasets. Therefore, only a subset (18) of the total variables measured for the RIJC population was selected for the purpose of this dissertation (Table 3). For the RISR population, the phenological traits along with seed yield components, pod harvest index, and plant height were collected only in Prosper (ND). Meteorological data including daily maximum and minimum temperature and rainfall were collected from the nearest meteorological station located on the field site and generally web-linked:

http://ndawn.ndsu.nodak.edu/, http://fawn.ifas.ufl.edu/, http://www.nws.noaa.gov/, http://www.wunderground.com/, http://snr.unl.edu/lincolnweather/.

#### 3.2.1. Non-destructive Measurements

The corresponding day-to-events (dates) of the phenological stages from V<sub>E</sub> to  $R_8$  (modified from Gepts et al., 1986) were recorded weekly for six flagged plants within one row of the plot in order to determine the time it takes 50% to reach a given developmental stage. The V stages represent vegetative growth and the number refers to the appearance of the leaf node, V<sub>1</sub> for the first node, V<sub>2</sub> for the second, and V<sub>3</sub> for the third node, etc. The R<sub>1</sub> through R<sub>8</sub> are related to the beginning and the end of the

reproductive stages. Days from planting were recorded for the following phenological traits:  $V_E$ , days to emergence, when cotyledons are visible,

 $V_0$ , primary (unifoliate) leaves are completely open and separated from each other,

V<sub>1</sub>, first tri-foliate has unfolded leaves at the first node above the unifoliate node,

R<sub>1</sub>, blooming time when at least one flower appeared on any node in the plant,

R<sub>3</sub>, first pod is 2.0 cm long on any node in the plant,

R<sub>5</sub>, beginning of seed stage when first pod on plant is fully-elongated,

R<sub>7</sub>, physiologically mature pod, at least one pod with no green coloration,

R<sub>8</sub>, when harvest mature pod on a plant is browning.

Numerical measurements included canopy height and width (cm), number of pods, length of branches and stems (cm).

#### **3.2.2. Destructive Measurements**

Destructive measurements were recorded after harvesting weekly one-plant sample per plot starting at V<sub>0</sub> stage. The plants were partitioned into their different components (Hypocotyl, main stem, branches, petioles and leaves) and dried in the plant dryer at 60°C for 48 hours (dry weight measurement). It should be noted that only leaf areas were collected as destructive measurement for the RISR population grown in Prosper (ND). Leaf areas and dry weight traits included four locations because of missing values for Puerto Rico.

At harvest maturity, the six plants used for non-destructive data collection were hand harvested to determine yield per plant (g), number of seeds per pod, number of pods per plant, and 100-seed weight (g). The effect of temperature on development was

calculated using the formula including three cardinal temperatures (TBase, TMax, TMin).

Trait	Description	Frequency
LA <sup>†</sup> (cm <sup>2</sup> )	Area of successive individual leaves on nodes 1	Weekly
	to 5 of main stem	
LAMS (cm <sup>2</sup> )	Leaf Area of leaves on main stem (other leaves)	Weekly
DW1-5 (g)	Dry Weight of first 5 leaves on main stem	Weekly
LWMS (g)	Dry Weight of leaves on main stem (other leaves)	Weekly
LGTHHI (cm)	Hypocotyl Length	Weekly
LGTHMS (cm)	Total length of main stem	Weekly
MSDW (g)	Dry Weight of main stem	Weekly
PDWMS (g)	Dry Weight of Petioles on main stem	Weekly
PMS	Number of pods on main stem	Weekly
LEAFB	Number of leaves on all branches	Weekly
LABS (cm <sup>2</sup> )	Leaf Area of leaves on branches	Weekly
LWBS (g)	Dry Weight of leaves on branches	Weekly
PDWBS (g)	Dry Weight of petioles on branches	Weekly
PB	Number of pods on branches	Weekly
SHWGT (g)	Shell Dry Weight	Weekly
SDWGT (g)	Seed Dry Weight	Weekly
SDPDV	Number of seeds per pod (n) (10 pod-sample)	Final Harvest
PHI (%)	Pod harvest index [ratio of (seed weight/(seed	Final Harvest
	weight + shell weight)x 100 ]	

Table 3. Subset of destructive sampling and dry weight measurements.

<sup>†</sup> Measured using LI-3100C® meter

Photo-thermal days were derived summarizing temperature responses in terms of (a) the base temperature (TBase) below which there is no metabolic activity and above which development begins, (b) the lowest daily temperature (TMin), (c) the highest daily temperature (TMax), and (d) and the number of solar radiation hourly values (14):

Photo – thermal day = 
$$\frac{\left[\Sigma\left(\frac{TMax + TMin}{2}\right) - TBase\right]}{14}$$

Base temperature for common bean varies over a wide range of values. For this study base temperature was set to 10°C (Guyer and Kramer, 1952; Dickson and Boettger 1984; Scully and Waines 1988) and the most widespread growing degree day method for simulation models (Davidson and Campbell, 1983) was considered if:

$$\left[\frac{(TMax + TMin)}{2}\right] < \text{TBase},$$
$$\left[\frac{(TMax + TMin)}{2}\right] = \text{TBase}$$

It should be noted that an optimum (30°C) would represent the temperature above which metabolic activities decline or cease due to loss of enzyme function. Temperature adjustments were made for the upper threshold [(TUT), McMaster and Wilhelm, 1997] and if:

$$\left[\frac{(TMax + TMin)}{2}\right] > TUT$$
$$\left[\frac{(TMax + TMin)}{2}\right] = TUT$$

Optimum mean temperatures were rarely observed at Citra location during the growing season. The main genotypic coefficients used in the CROPGRO model are summarized below:

EMFL phase is the time interval from the emergence to the appearance of the first flower expressed in photo-thermal days,

FLSH phase is the time interval from production of the first flower until the first pod appears;

FLSD phase is the time interval from the first flower until the appearance of the first seed in the pod;
SDPM phase is the time interval from the appearance of the first seed until the plant has reached the physiological maturity.

#### 3.3. Statistical Analysis

The software package *CycDesigN* (Whitaker et al., 2002) was used to generate resolvable row-column designs. To determine the statistical significance of differences among genotypes, analyses of variances were performed using the PROC MIXED procedure (SAS Institute, 2013). Environments, replications, rows, and columns were considered as random and genotypes as fixed effects. The linear model for the resolvable row-column design was:

$$Y_{ijkl} = \mu + \beta_j + \gamma_{k(j)} + \lambda_{l(j)} + \alpha_i + \varepsilon_{ijkl}.$$

where  $Y_{ijkl}$  is the observation of the i<sub>th</sub> treatment in j<sub>th</sub> replicate at the k<sub>th</sub> row and the l<sub>th</sub> column.  $\mu$  is the general mean,  $\alpha_i$  is the treatment effect,  $\beta_j$  is the replicate group effect,  $\gamma_{k(j)}$  and  $\lambda_{l(j)}$  are, respectively, the row and column nested in replicate group effect, and  $\varepsilon_{ijkl}$  is the random experimental error.

Even though many traits might be related, it is important to measure the strength of the relationship. The relationship among traits was determined by Pearson's simple correlation analysis (level of probability 0.001, 0.01, and 0.05) computed from means across locations when variances are homogenous. Strong or weak associations were considered based on correlation coefficients ( $r \ge 0.6$  for strong associations or otherwise were considered weak).

For the mean separation tests, *F*-protected LSD at 95% level of confidence was used. Given the mixed model will not output an overall standard error, average standard errors were calculated to estimate significant difference for visual comparisons.

Combined analyses across environments were computed when variances were homogenous. Before performing valid combined analyses, the "10x rule of thumb" procedure for homogeneity of variances was carried out, in order to assess if the largest error variance is no more than 10 times larger than the smallest one (Patterson and Silvey, 1980). Significant GxE interactions were detected among traits. However, when comparing the mean squares if the magnitude (expressed as percent of the total variation) of genotypes is greater than GxE interactions, the analyses focused on specific genotypes across locations. Coefficient of variation (CV%) for each variable and narrow-sense heritability estimates for yield components were calculated on an entry mean basis using the formula  $h^2 = \sigma^2_G/(\sigma^2_G + \sigma^2_{GE}/e + \sigma^2/re)$  where  $\sigma^2_G$  is genetic variance due to genotypes in the RIL population,  $\sigma^2_{GE}$  is genetic variance due to genotypes by environment interaction, e is number of environments, r is number of replicates, and  $\sigma^2$  is experimental error. Given that all genetic variability is due to twice the additive variance in inbred lines, this formula was adjusted and serves to estimate narrow-sense heritability (Hallauer et al. 2010).

As seed yield is one of the most important trait for common bean improvement which is limited by GxE, the statistical software JMP10.0 (SAS, 2012) was used to display genotype main effect and genotype by environment interaction (GGE) biplot (Gabriel, 1971) of the two principal components (PC1 and PC2). The 'which won where' pattern as described by Yan (2003) was graphically shown for seed yield components across locations. Genotypes with unique combination of traits were selected and can be used for future testing. To determine how RIJC population grown across locations and within North Dakota compares to RISR evaluated in North Dakota, t (0.05) tests were

used for population means separation. Genetic coefficients (EMFL, FLSH, FLSD, and SDPM) used in the CROPGRO model were compared as well between populations.

Phenological ( $R_1$  and  $R_7$ ) and seed yield traits of RIJC population were compared [t (0.05) tests] as well to historical data generated from dry bean trials of pinto varieties planted in Carrington, ND from 2008 to 2012 which were grown under similar drought and irrigated conditions than Nebraska. These pinto varieties are commonly grown and economically important in the Minnesota-North Dakota region (http://www.ag.ndsu.edu/varietytrials/dry-bean). Seed yields of RISR population grown under drought and irrigated conditions in Nebraska in 2012 and the subset of extreme genotypes in 2013 were compared as well to North Dakota (Carrington) yield using t (0.05) tests. In order to guantify drought severity, drought intensity index [DII = 1 - Yp/Yi, where Yp and Yi were the mean experimental yield values of all genotypes grown under drought stress and irrigated conditions, respectively (Fischer and Maurer, 1978)] was calculated. DII > 0.7 indicates severe drought conditions and values  $\leq$  0.7 and other than 0 are considered as moderate. Genotype performance under stressed and nonstressed conditions were also calculated using the drought susceptibility index [S = (1-Yd/Yw)/DII where Yd and Yw were means yield of a genotype under stress and irrigated conditions respectively], and geometric mean [GM= (Yd x Yw)<sup>0.5</sup>, Fernández, 1992; Rosielle, and Hamblin, 1981].

## 4. RESULTS AND DISCUSSION

### 4.1. RIJC Phenological Traits

Genotype by environment interactions, locations, and genotypic components were significant (P < 0.001) for all the phenological traits. Some genotypes (15) were photoperiod sensitive and either failed to flower or flowered very late which impacted the variation of the aforementioned traits under North Dakota growing conditions. Large error variances were found for many traits assessed in North Dakota, and to facilitate comparisons, the mean tables included in general a combination of four and the latter locations. Given the fact that for most traits, significant GxE interactions explained a small percentage of the total variation, discussion may be focused mostly on genotypes effect, which explains a larger portion of the variation (Table 4).

2014	Traits <sup>†</sup>								
SOV	VE	V <sub>0</sub>	$V_1$	R₁‡	R₃	R₅	R7	R <sub>8</sub> ‡	
Genotype	5.8	5.7	5.5	129.8 (88.8)	144.7	131.5	74.9	133.4 (25.7 <sup>NS§</sup> )	
GxE	1.3	1.7	1.4	9.0	33.9	33.9	17.3	24.5	
Error	0.4	0.5	0.6	2.9 (13.6)	7.0	8.2	6.9	8.1 (33.7)	
h²	0.62	0.55	0.60	0.87 0.73	0.62	0.59	0.63	0.69 (NA¶)	

Table 4. Phenological traits mean square values (significant at  $P \le 0.001$  level) and narrow-sense heritability (h<sup>2</sup>) across five or four locations.

<sup>+</sup> Emergence (V<sub>E</sub>), unifoliates (V<sub>0</sub>), first trifoliate (V<sub>1</sub>), flowering (R<sub>1</sub>), pod (R<sub>3</sub>), seed (R<sub>5</sub>), physiological maturity (R<sub>7</sub>), harvest maturity (R<sub>8</sub>).

<sup>‡</sup>Four locations (without North Dakota) and North Dakota (second value in parentheses).

§ Non-significant.

<sup>¶</sup>Could not be computed due to many photoperiod-sensitive genotypes.

The results have shown that most of the phenological traits appear to have high narrow-sense heritabilities ranging from 0.55 to 0.87 (Table 4). Across four locations, high narrow-sense heritability estimates for days to flowering (R<sub>1</sub>) might be due to the low magnitude of GxE interaction compared to genotype (more than 14 times less). For R<sub>1</sub>, the environmental conditions seem to be more uniform given that North Dakota location could not be part of the combined analysis. The North Dakota location alone exhibited high narrow-sense heritability estimate for R<sub>1</sub> (0.73), indicating that most of the variation observed might be explained by genetic individual differences. In North Dakota, the R<sub>8</sub> phenological stage heritability estimate could not be computed because of too many missing data points from late genotypes, which increased the error mean square. Similar ranking of genotypes within each environment suggested differences in magnitude and not true cross-overs of the phenological traits which might be the main cause of GxE interactions.

For days to flowering (R<sub>1</sub>) across locations (Table 5), the top 10 genotypes, were not significantly earlier than Calima and RIJC011 was the latest genotype with significant differences when compared to Jamapa. Genotypic differential response was more pronounced in North Dakota and within the population, 15 RILs did not reach reproductive stage and remained vegetative during the entire growing season. It should be noted that genotypes within some plots flowered partially and very late in North Dakota. This observation was particularly interesting given the fact that both parents of the population (Calima and Jamapa) are not sensitive to photoperiod and determinate growth habit of Calima might help to control the lateness in its genetic background. In general, segregation at this stage of inbreeding is less likely and photoperiod

insensitivity needs to be assessed for detecting the presence or absence of its genetic control, especially the *Ppd* gene (Gu et al., 1998). The previous genotypes and few others (Table 5) remain at the top 10 earlier when considering physiological maturity as ranking criterion and RIJC309 replaced the last bottom. These results suggested that days to flowering is highly correlated ( $0.84^{***}$ ) to physiological maturity (Table 6). Early flowering may result in early maturity. Sofi et al. (2011), Cerna and Beaver (1990), among others, reported similar correlation values between the same traits. Compared to this study, when considering each phenological trait across five locations, mean values of 9, 12, 19, 50, 58, and 73 DAP was needed to reach respectively emergence (V<sub>E</sub>), unifoliates (V<sub>0</sub>), first trifoliate (V<sub>1</sub>), pod (R<sub>3</sub>), seed (R<sub>5</sub>), and physiological maturity (R<sub>7</sub>). However, phenological stages across five locations can be seen as very early if considered North Dakota alone which needed 16 more days to reach physiological maturity (89 DAP).

Comparing between growth habits, the overall means do not differ significantly for vegetative stages and either determinate or indeterminate growth types need 9, 12, and 18 DAP, respectively for  $V_E$ ,  $V_0$ , and  $V_1$ . However for reproductive stages, significant differences can be observed (48 vs. 52 DAP, 56 vs. 60 DAP, and 71 vs. 74 DAP for determinates vs. indeterminates) respectively for R<sub>3</sub>, R<sub>5</sub>, and R<sub>7</sub>. Emergence can be influenced by seed size, soil-weather conditions (low temperature, compacted soil), and also the optimum planting depth. Large-seed size cultivars have greater stored food reserves to support early seedling and development (Singh et al., 1972). In contrast, the results in this study have shown that Jamapa (small-size seed) emerged earlier than Calima (large-size seed) and other genotypes.

					Tra	its†			
Genotypes		VE	V <sub>0</sub>	V <sub>1</sub>	R₁‡	R <sub>3</sub>	R₅	R <sub>7</sub>	R <sub>8</sub> ‡
						_DAP§			
RIJC257		8	11	18	33	42	54	71	77
RIJC080		8	11	18	33	42	50	68	76
RIJC006		9	11	18	33	43	53	67	76
RIJC244		8	11	18	33	43	53	67	74
RIJC003		9	11	18	33	44	52	69	75
RIJC078	Early	8	11	17	33	41	49	65	75
RIJC217		8	11	18	34	41	48	66	74
RIJC335		10	12	20	34	43	52	68	77
RIJC029		9	11	19	34	43	51	69	76
RIJC015		8	11	18	34	44	55	69	75
RIJC075		10	12	19	47	58	65	81	91
RIJC339		10	13	20	47	59	68	80	89
RIJC221		11	13	19	47	58	65	79	89
RIJC232		9	12	19	47	57	64	79	87
RIJC309	Lata	9	14	20	48	59	68	81	89
RIJC321	Late	10	13	20	48	58	66	79	89
RIJC026		9	12	19	48	58	66	77	88
RIJC262		10	12	20	48	57	66	76	86
RIJC305		10	12	20	48	56	67	81	91
RIJC011		10	13	20	49	56	66	80	92
		g	11	17	11	17	57	73	82
		10	10	12	77 25	41 51	55	70	75
Moon		0	12 10	10	40 20	50	50	70	7 U Q 1
		9 21	12 2 F	19	40	00	10 E	73 50	01
$CV^{0}$		ی. 17 ۸	3.3 15.2	4.0 10.0	4.3 5.4	9.0 10.0	0.0	0.9 1 1	9.Z
UV 70		17.4	15.3	10.9	5.4	10.0	9.2	4.1	<b>0.</b> C

Table 5. Phenological traits mean values across five or four locations of 10 earliest and 10 latest genotypes and parents ranked by days to flowering (R1).

<sup>†</sup>Emergence ( $V_E$ ), unifoliates ( $V_0$ ), first trifoliate ( $V_1$ ), flowering ( $R_1$ ), pod ( $R_3$ ), seed ( $R_5$ ), physiological maturity ( $R_7$ ), harvest maturity ( $R_8$ ). <sup>‡</sup>Four locations (without North Dakota).

<sup>§</sup> Days after planting.

The same trend can be observed within the RIJC population where small-size seeds emerged earlier than large-size seed genotypes. Low temperature seems to be the main limiting factor delaying emergence. As observed in North Dakota, geographically localized in the temperate zone, emergence was delayed by one week compared to values found across locations in the tropical zone including Puerto Rico. For instance, Colbert and Osorno (2012) reported that even with adequate air temperature (24°C) after planting at Prosper ND, delayed rainfall favored a dry and crusty soil surface which negatively impacted plant emergence. Scully and Waines (1987) suggested that optimum temperature for common bean germination ranges from 20 to 30°C and at 10°C, no emergence was observed after 25 days. Knowledge of the phenological stages influencing common bean growth and development is crucial to obtain reliable seed yield estimates and help optimizing management and production practices.

Strong significant correlation exists between the vegetative stages ( $r \ge 0.7$ ) and between the reproductive stages( $r \ge 0.8$ ). However, weak relationships were observed between vegetative and reproductive stages [ $r \le 0.4$ , (Table 6)]. The weak relationships might be explained by changes in plant developmental stages and the transition in phenology from vegetative to reproductive stages. North Dakota alone showed similar relationships trends albeit lower values ( $r \le 0.2$ ) were observed between R<sub>1</sub> and vegetative stages and weak correlation between R<sub>8</sub> and the other reproductive stages. No relationships were observed in North Dakota between R<sub>8</sub> and any of the other vegetative stages.

Leaf appearance from unifoliates to first trifoliates has shown little variation between the maximum and the minimum number of days required to reach both stages. Among the genotypes with earliest leaf appearance, approximately the same early emergent set of genotypes remains at the top, except the parents which showed intermediate mean values (11 vs.12 DAP; 17 vs. 18 DAP for respectively V<sub>0</sub> and V<sub>1</sub> for Jamapa and Calima). Early vigor characteristics could be used as earliness selection criterion for common bean breeding. Days to flowering (Table 7) is among the traits associated with days to maturity and knowledge of its heritability and the different genetic relationships might ease earliness selection which is suitable for breeding common bean. Coyne (1966), Padda and Munger (1969), Wallace and Enriquez (1980), reported the relationship between early maturity and days to first flower. When compared North Dakota days to flowering to the other four locations, three lines (RIJC078, RIJC080, and RIJC217) were consistently on top 10.

From flowering to harvest maturity ( $R_1$  to  $R_8$ ) RIJC078 and RIJC217 are two early genotypes consistently observed across locations and North Dakota ( $R_1$  and  $R_8$ ). Pod appearance ( $R_3$ ), Seedling ( $R_5$ ), and physiological maturity ( $R_7$ ) mean values across five locations were reached respectively after 50, 58, and 73 DAP. Harvest maturity ( $R_8$ ) excluding North Dakota needed 81 DAP.

In this study, significant differences between growth habits have been found across five locations for physiological maturity. Similar results between growth habits have been reported by Beaver et al. (1985) where indeterminate genotypes tend to have later physiological maturity than determinate ones. It should be noted that in North

Dakota, indeterminate and determinate growth habits did not show significant differences for R<sub>1</sub> when compared to the other four locations.

	Traits <sup>†</sup>							
V <sub>0</sub>	V <sub>E</sub> 0.90***	V <sub>0</sub>	V <sub>1</sub>	R₁‡	R <sub>3</sub>	R₅	R <sub>7</sub>	
$V_1$	0.67***	0.69***						
R1	0.35*** (0.21***)	0.32*** (0.17***)	0.38*** (0.12***)					
R₃	0.37***	0.31***	0.32***	0.88*** 0.79***)				
R₅	0.35***	0.32***	0.33***	0.88*** (0.71***)	0.94***			
R7	0.39***	0.35***	0.38***	0.84*** (0.51***)	0.88***	0.91***		
R <sub>8</sub> ‡	0.35*** (0.14 <sup>NS§</sup> )	0.29*** (0.07 <sup>NS</sup> )	0.38*** (0.07 <sup>NS</sup> )	0.82*** (0.41***)	0.82*** (0.47***)	0.83*** (0.44***)	0.89*** (0.79***)	

Table 6. Correlation coefficients among phenological traits across five or four locations.

\*\*\* Significant at the *P* < 0.001 level.

<sup>+</sup>Emergence (V<sub>E</sub>), unifoliate (V<sub>0</sub>), first trifoliate (V<sub>1</sub>), flowering (R<sub>1</sub>), pod (R<sub>3</sub>), seed (R<sub>5</sub>), physiological maturity (R<sub>7</sub>), harvest maturity (R<sub>8</sub>).

<sup>‡</sup>Four locations (without North Dakota) and North Dakota (second value in parentheses). <sup>§</sup>Non-significant.

These results suggested a lack of adaptation for the RIJC population in North Dakota. As common bean was initially domesticated in tropical-subtropical, Middle American and Andean-South-American regions (Gepts and Debouck, 1991; Bitocchi et al., 2012; Schmutz et al. 2014), selection for longer day length or photoperiod insensitive genotypes is a requirement for temperate climates.

Genotypes		Locations			
Genoty	bes	North Dakota	Combined <sup>†</sup>		
		D/	4P‡		
RIJC217		40	34		
RIJC366		45	35		
RIJC078		45	33		
RIJC316		47	36		
RIJC021		48	36		
RIJC080	Early	48	33		
RIJC020	,	49	36		
RIJC224		49	38		
RIJC251		49	36		
RIJC130		49	40		
RIJC314		69	39		
RIJC261		69	40		
RIJC252		70	38		
RIJC223		70	37		
RIJC358		71	46		
RIJC066	Late	72	37		
RIJC202	2010	72	47		
RIJC071		75	37		
RIJC248		78	35		
RIJC024		83	44		
JAMAPA		52	44		
CALIMA		68	35		
Mean		58	40		
LSD(0.05)		4.7	4.3		
CV%		4.1	5.4		

Table 7. Days to flowering ( $R_1$ ) mean values in North Dakota and across four locations of 10 earliest and 10 latest genotypes and parents (ND ranking).

<sup>†</sup>Four locations (without North Dakota).
<sup>‡</sup> Days after planting.

Considering that both parents of the RIJC population were developed for the tropics, adaptation factors might affect the overall genotype performance in North Dakota. Even though the parents are not photoperiod sensitive, genetic recombination within the RIL population resulted in photoperiod genotypes. In this study, the RIJC population flowered 40 DAP in average across four locations and 58 DAP were needed in North Dakota. However, 73 DAP were observed for physiological maturity across the five locations. Sources of early maturity and its inheritance have been reported among tropical and sub-tropical germplasm (White and Singh, 1991; Cerna and Beaver, 1990). First flower from three early genotypes (Cuarentena, Cuarenteno, and Cincuenteno) were observed 27 DAP and physiological maturity needed 65 DAP (Cerna and Beaver, 1990). Compared to this study, RIJC population flowered 13 days later in average across four locations and 31 more days were needed in North Dakota. However, only seven more days difference were observed for physiological maturity across the five locations.

Previous studies (Wallace, 1985; White and Laing, 1989) described common bean as a short day photoperiodic species and adapted insensitive genotypes have been selected for temperate climate. Genetic controls of photoperiod response and flowering time in common bean have been elucidated by Gu et al. (1998). This finding reported that alleles *Ppd* and *Hr* controlled insensitivity to photoperiod, and enhancing its response, respectively. Since the magnitude of GxE interactions is low, early genotypes found across environments might be the best ones for a mega-environment. Late genotypes observed across locations were among the photoperiod-sensitive RILs found in North Dakota. However care should be taken for selecting genotypes showing

stable performance with low variance and early maturity. Based on the homogeneity of variances, and to cope with GxE and reduce its effect, the mega-environment including five locations can be partitioned into one homogenous group and North Dakota will stand alone considering R<sub>1</sub> and R<sub>8</sub>. Four locations (Palmira, Popayan, Citra, and Puerto Rico) are relatively more homogenous and therefore they can be clustered together and genotype recommendations could be made separately for each subgroup. The previous information obtained from early phenological traits may be paired with seed yield components characters in order to find the right balance and subsequently selecting the best genotypes.

#### 4.2. RIJC Yield Components and Agronomic Traits

#### 4.2.1. Yield components and pod harvest index

Significant (P < 0.001) genotype by environment interactions, locations, and genotypic differences were found for yield components and other agronomic traits. Significant differences were observed for genotype trait means as well as among locations (Table 8). However, the magnitude of GxE was significantly less than genotype main effect except for seed yield per plant. Therefore, moderate to high narrow-sense heritability estimates were observed for seed yield components and pod harvest index, but not for seed yield per plant. It should be noted that seed yield per plant and pod harvest index included four locations because of large error variance in North Dakota and missing values for Citra, respectively for these traits.

Table 8. Seed yield components and pod harvest index (PHI) mean square values (significant at  $P \le 0.001$  level) and narrow-sense heritability estimates (h<sup>2</sup>) across five or four locations.

SOV	100- seed- weight	Seeds pod-1	Pods plant <sup>-1</sup>	Seed yield plant <sup>-1†</sup>	PHI‡
Genotype	156.7	2.9	159.7	120.5 (494.5)	117.9
GxE	21.4	0.6	77.5	72.5	46.3
Error	11.3	0.4	38.0	38.9 (235.3)	32.0
h²	0.76	0.64	0.35	0.25 (0.36)	0.44

<sup>+</sup>Four locations (without North Dakota) and North Dakota (second value in parentheses). <sup>+</sup>Four locations (missing data for Citra).

The low narrow-sense heritability estimate for seed yield per plant (0.25) can be explained by the large GxE magnitude compared to genotype. Considering the North Dakota location alone, the narrow-sense heritability estimate for seed yield per plant was higher (0.36) than the value found across four locations. Selection for this trait might be more effective in detecting improved high-yielding genotypes in North Dakota, albeit accurate estimates are hard to find with one location. Higher heritability estimates have been reported by Abebe and Brick (2003) for number of seeds per pod (0.78) but the estimates for number of pods per plant were higher (0.69) than in this study. Sofi et al. (2011) reported even higher estimates of 0.81 and 0.79, respectively for the same traits. The same authors also reported estimates of 0.83 for both 100-seed weight and seed yield per plant. A weak correlation was observed between phenological and yield components traits (Table 9). Pod harvest index exhibited only negative values when

associated to all the other phenological traits. Negative correlations of PHI with the phenological traits might be explained as well by the fact that cool weather can delay the expression of phenological traits and subsequently slow the rate of biomass accumulation. On the contrary, in warm weather the expression of phenological traits had a reverse effect.

Relationships between seed yield components and phenological traits observed in North Dakota alone followed relatively the same trend found across locations except for R<sub>1</sub> and in some extent R<sub>8</sub>. No relationships were observed between R<sub>1</sub> and seed yield component traits. A weak correlation was observed across locations for number of seeds per pod and R<sub>8</sub>, and for number of pods per plant and R<sub>8</sub> in North Dakota.

Across five locations, mean values for 100-seed weight, number of seeds per pod, and number of pods per plant were 24 g, 4, and 19, respectively. Calima (46 g) and RIJC332 (39 g) are among the top 10 for 100-seed weight (Table 10). Jamapa (6) and RIJC072 (5) are among the best genotypes for number of seeds per pod. Considering the number of pods per plant, RIJC072 (32), RIJC224 (35) and Jamapa (31) expressed the highest mean values suggesting transgressive segregation which might improve seed yield per se. Based on seed yield per plant across four locations, Jamapa (42 g plant<sup>-1</sup>) exhibited the highest value along with genotypes RIJC022 (32 g plant<sup>-1</sup>) but considering North Dakota alone (Table 11) RIJC072 (87 g plant<sup>-1</sup>) and RIJC256 (80 g plant<sup>-1</sup>) expressed the highest mean values. Higher seed yields observed in North Dakota might be due in part, to the longer days compared to the tropics.

Traits <sup>†</sup>	100-seed weight	Seeds pod-1	Pods plant <sup>-1</sup>	Seed yield plant <sup>-1§</sup>	PHI <sup>¶</sup>
VE	0.35***	-0.19**	-0.19**	-0.01 <sup>NS</sup> ‡ (-0.05 <sup>NS</sup> )	-0.13 <sup>NS</sup>
V <sub>0</sub>	0.21**	-0.13 <sup>NS</sup>	-0.11 <sup>NS</sup>	-0.004 <sup>NS</sup> (-0.02 <sup>NS</sup> )	-0.17*
V1	-0.03 <sup>NS</sup>	-0.02 <sup>NS</sup>	-0.12 <sup>NS</sup>	-0.11 <sup>NS</sup> (-0.04 <sup>NS</sup> )	-0.26***
R1 <sup>§</sup>	0.07 <sup>NS</sup> (0.1 <sup>NS</sup> )	0.34*** (0.08 <sup>NS</sup> )	0.17* (-0.1 <sup>NS</sup> )	0.32*** (-0.05 <sup>NS</sup> )	-0.38*** (-0.08 <sup>NS</sup> )
R <sub>3</sub>	0.17*	0.21**	0.06 <sup>NS</sup>	0.23*** (0.01 <sup>NS</sup> )	-0.33***
R5	0.11 <sup>NS</sup>	0.21**	0.06 <sup>NS</sup>	0.22** (-0.02 <sup>NS</sup> )	-0.35***
R7	0.14*	0.21**	0.02 <sup>NS</sup>	0.20** (0.26**)	-0.36***
R <sub>8</sub> §	0.11 <sup>NS</sup> (0.18 <sup>NS</sup> )	0.23*** (0.15 <sup>NS</sup> )	0.07 <sup>NS</sup> (0.31**)	0.22*** (0.38***)	-0.41*** (0.04 <sup>NS</sup> )

Table 9. Correlation coefficients among seed yield components, pod harvest index (PHI) and phenological traits across five or four locations.

\*\*\* Significant at the  $P \leq 0.001$  level.

\*\* Significant at the  $P \leq 0.01$  level.

\* Significant at the  $P \leq 0.05$  level.

<sup>+</sup> Emergence (V<sub>E</sub>), unifoliate (V<sub>0</sub>), first trifoliate (V<sub>1</sub>), flowering (R<sub>1</sub>), pod (R<sub>3</sub>), seed (R<sub>5</sub>), physiological maturity (R<sub>7</sub>), harvest maturity (R<sub>8</sub>).

<sup>‡</sup>Non-significant.

<sup>§</sup> Four locations (without North Dakota) and North Dakota (second value in parentheses).

<sup>¶</sup> Four locations (missing data for Citra).

Pod harvest index exhibited 69% mean value and RIJC246 (82%) was one case of extreme genotype. Significantly low mean values can be observed at the bottom of the tables as across five locations RIJC150, RIJC062 and RIJC227 expressed respectively lowest 100-seed weight (14g), number of seeds per pod (2) and number of pods per plant (11). Comparing North Dakota and the four other locations, the genotype RIJC130 (Table 11) was the lowest significant RIL for seed yield per plant. For PHI, two genotypes [RIJC150, and RIJC339 (58%)] remained at the bottom with lowest mean values.

Significant but weak correlation exists between seed yield per plant and the other seed yield components except for number of pods per plant (Table 12). Weak and negative correlation can be observed between 100-seed weight and number of seeds per pod, and number of pods per plant. These positive correlations suggested that these traits responded similarly across locations indicating that an increase or decrease in one trait may predict the same change for the other trait. However 100-seed weight relationships did not deviate from expectation because negative correlations suggested that an increase in number of pods per plant and/or number of seeds per pod will subsequently reduce seed size.

Pod harvest index showed weak but positive correlation with all the other seed yield component traits. As emphasized by Castañeda-Saucedo et al. (2009), a reduction in number of pods per plant may cause 40% loss in seed yield, suggesting high correlation between these traits. The current results agree with the finding of moderately strong correlation (0.66\*\*\*) between number of pods per plant and seed yield per plant. Similar correlation coefficient values of 0.49, -0.60, and 0.74 have been reported by Gonçalves et al. (2003) for number of pods per plant associated with number of seeds per pod, 100-seed weight, and seed yield per plant, respectively. The same authors concluded that number of pods per plant was the yield component having the strongest association with seed yield. Seed yield per plant was the most important trait for seed yield because

these traits were highly correlated. Indirect selection for traits highly correlated with

seed yield such as yield per plant may be considered.

Table 10. Seed yield components and pod harvest index (PHI) mean values across five or four locations of 10 highest and 10 lowest genotypes and parents (seed yield per plant ranking).

		Traits						
Genotypes		100-seed	Seeds pod <sup>-1</sup>	Pods plant <sup>-1</sup>	Seed	PHI <sup>‡</sup>		
		weight(g)	nur	nber	Yield	(%)		
					plant <sup>-1†</sup>			
					(g)			
JAMAPA		21	6	31	42	76		
RIJC022		27	4	28	32	74		
RIJC332		39	4	17	26	75		
RIJC358		21	4	25	25	72		
RIJC334		26	4	25	25	71		
RIJC312	Hiah	20	5	29	24	70		
RIJC362		23	4	29	23	67		
RIJC072		18	5	32	23	71		
RIJC236		24	4	25	22	70		
RIJC320		24	4	28	22	67		
RIJC210		20	3	15	8	64		
RIJC248		21	3	15	8	71		
RIJC049		17	4	15	8	69		
RIJC131		19	3	15	8	77		
RIJC227	Low	23	3	11	8	65		
RIJC342		21	3	12	8	70		
RIJC149		24	3	13	7	61		
RIJC130		22	3	11	6	61		
RIJC346		23	3	20	6	63		
RIJC150		14	3	15	6	58		
0.4. IN 4.4				. –				
CALIMA		46	4	15	17	74		
Mean		24	4	19	15	69		
LSD(0.05)		4.8	0.8	9.2	8.8	7.9		
CV%		10.1	11.1	24.8	30.8	5.8		

<sup>†</sup> Four locations (without North Dakota).
 <sup>‡</sup> Four locations (missing data for Citra)

	Loc	Locations		
Genotype		North	Combined <sup>†</sup>	
		Dakota		
			g plant <sup>-1</sup>	
		07	00	
		87 00	23	
		80	12	
		80	23	
		78 77	14	
	High	( (	16	
		/4 70	22	
KIJUZJJ		(2	14	
RIJU356		70	14	
RIJC238		67	21	
RIJC373		66	16	
RIJC328		12	9	
RIJC374		11	11	
RIJC239		10	13	
RIJC204		9	16	
RIJC217	LOW	8	13	
RIJC012		8	12	
RIJC252		8	12	
RIJC201		7	11	
RIJC020		5	15	
RIJC130		3	6	
JAMAPA		57	42	
CALIMA		32	17	
Mean		32	15	
LSD(0.05)		24.3	8.8	
CV%		39.0	30.8	

Table 11. Seed yield per plant mean values across four locations of 10 highest and 10 lowest genotypes and parents (ND ranking).

	Seed yield plant <sup>-1‡</sup>	100-seed weight	Seeds pod-1	Pods plant <sup>-1</sup>
100-seed weight	0.20** (0.36***)			
Seeds pod-1	0.53*** (0.53***)	-0.24***		
Pods plant <sup>-1</sup>	0.66*** (0.86***)	-0.24***	0.30***	
PHI §	0.29*** (0.48***)	0.13 <sup>NS†</sup>	0.18*	0.15*

Table 12. Correlation coefficients across five or four locations for seed yield components and pod harvest index (PHI).

\*\*\* Significant at the  $P \leq 0.001$  level.

\*\* Significant at the  $P \le 0.01$  level.

\* Significant at the  $P \leq 0.05$  level.

<sup>†</sup>Non-significant.

<sup>‡</sup> Four locations (without North Dakota) and North Dakota (second value in parentheses).

<sup>§</sup> Four locations (missing data for Citra).

The present study suggests that pod harvest index is a good selection criterion for common bean improvement, assuming a low GxE interaction. Rao et al. (2009), Beebe et al. (2010), among others, reported the efficiency of photosynthate remobilization as an important drought resistance mechanism in common bean. Pod harvest index have been reported by Rao et al. (2009) as a partitioning index indicating the extent of remobilization of photosynthates from pod wall to seeds. Positive correlations of pod harvest index with seed yield components indicated greater photosynthates partition from vegetative to reproductive parts. Assefa et al. (2013) considered pod harvest index as a relatively simple trait integrating essential yield determining factors across environments. In general, genotypes with indeterminate growth habit exhibit greater seed yield potential and more seed yield stability than determinate genotypes (Beaver et al, 1985). In the present study, it should be noted that mean values for most of the traits do not differ significantly when comparing determinate to indeterminate genotypes except for seed yield per plant in North Dakota (27 vs. 37 g plant<sup>-1</sup>, respectively). For pod harvest index, determinate growth habit showed either higher or similar values than indeterminate growth habit. Vegetative traits showed negative correlation coefficient values for seed yield per plant and number of pods per plant. Negative correlation coefficients have been reported by Sofi et al. (2011) for yield component traits associated with flowering and physiological maturity. Number of pods per plant had either negative correlation or non-significant relationships with all the phenological traits except for days to flowering (R<sub>1</sub>). Moreover, number of seeds per pod were significantly correlated with both days to flowering and physiological maturity (0.24 and 0.18), which agree with the present study. The genotypes used by the previous authors were mostly of indeterminate growth habit types.

# 4.2.2. Genotype main effect and GxE interaction (GGE) biplots for seed yield components and pod harvest index

When a large number of genotypes are tested in many environments, it is often difficult to determine the pattern of genotypic responses across locations. The success of phenotypic selection is greatly influenced by the magnitude of genotype by environment interaction component. As emphasized by Yan and Kang (2003), a biplot approach represents a useful option to solve this issue. The first two principal components explained 81.6% of the total GGE variation for 100-seed weight (Figure 2). The first component (PC1) included all the locations but North Dakota and explained 71.6% of the GGE variation. The second component (PC2) explained 10.0% of the

GGE variability and was mostly associated with North Dakota. North Dakota and at least Citra, and Puerto Rico, Palmira, and Popayan tend to form clusters or mega-environments for 100-seed weight. These mega-environments can be interpreted as systems of variables that describe the gradient represented by the two PCs.



Figure 2. Biplot of genotype performance for 100-seed weight across five locations.

The 'which won where' pattern displays genotypes RIJC233, RIJC046, RIJC066, RIJC256, RIJC203, RIJC202, and RIJC021 in the mega-environment North Dakota-Citra. The mega-environment Puerto Rico-Palmira-Popayan includes Calima, genotypes RIJC032, RIJC326, and RIJC067 (Figure 2). The vertex which represents genotypes having the highest seed weight within each environment included Calima, RIJC066, and RIJC233.

The same genotypes are among the most stable for 100-seed weight. However the best genotypes observed for 100-seed weight are not the same reported in the previous section because high seed weight did not necessarily expressed in high seed yield per plant as it is negatively correlated with number of seeds per pod and number of pods per plant.

The first two principal components explained 67.3% of the total GGE variation for seed number per pod (Figure 3). As seen for 100-seed weight, the first component (PC1) included all the locations but North Dakota and explained 51.9% of the GGE variation. The second component (PC2) explained 15.4% of the GGE variability and was mostly associated with North Dakota. Number of seeds per pod for specific genotypes found in the first quadrant seems to increase gradually in the direction of North Dakota at relatively the same rate than those observed in the opposite mega-environment (second quadrant). Considering only the number of seeds per pod yield component, the biplots suggested that North Dakota environment is more favorable for some genotypes while other specific ones might perform better in Citra and related locations. Genotypes RIJC081, RIJC356, and RIJC205 were among the best in North Dakota. The mega-environment Puerto Rico-Palmira-Popayan-Citra included Jamapa,

RIJC243, and RIJC245 with higher number of seeds per pod. Relationships between mega-environments as well as genotypes facilitated visual comparison. The identification of the vertex and most stable genotypes included Jamapa, RIJC235, RIJC347, and RIJC356. While the biplot provides some insights of best genotypes within mega-environments, identical results are hard to find from generalized combined analysis obtained previously for number of seeds per pod.



Figure 3. Biplot of genotype performance for number of seeds per pod across five locations.

The first two principal components explained 59.1% of the total GGE variation for number of pod per plant (Figure 4). The PC1 included Palmira and North Dakota locations and captured 37.5% of the GGE variation. The PC2 explained 21.6% of the GGE variability and was associated with Citra, Puerto Rico and Popayan (negative). Three mega-environments were observed for number of pods per plant.

Citra-Puerto Rico, Palmira-North Dakota constituted two separate megaenvironments and Popayan was set apart. Genotypes RIJC022, RIJC262, and RIJC142 were among the best in Popayan. The mega-environment Palmira-North Dakota, included Jamapa, RIJC303, and RIJC138 with higher number of pods per plant. Genotype RIJC320 exhibited best performance in Citra-Puerto Rico. Vertex genotypes included RIJC262, RIJC264, RIJC306, and RIJC045. The most stable genotype is RIJC224. As seen previously across locations, Jamapa and other genotypes are among the best for high number of pods per plant and subsequently this trait will be expressed in high seed yield per plant.

The first two principal components explained 67.4% of the total GGE variation for seed yield per plant (Figure 5). The PC1 included all the locations except Citra and captured 40.7% of the GGE variation. The PC2 explained 26.7% of the GGE variability and was associated with Citra. Two mega-environments were observed for seed yield per plant. Puerto Rico-Palmira-Popayan constituted one mega-environment and Citra was set apart. Genotypes RIJC238, and RIJC347 were among the best in the mega-environment Citra. The mega-environment Puerto Rico-Palmira-Popayan, included RIJC334, RIJC142, and RIJC243 with higher seed yield per plant. Vertex and most stable genotypes included RIJC238, and Jamapa. While the results for seed yield per

plant obtained previously are in agreement with the seed yield biplot, care should be taken when making inferences about North Dakota location.



Figure 4. Biplot of genotype performance for number of pods per plant across five locations.

Given data for pod harvest index trait was missing from Citra location, the biplot included only four locations. Figure 6 indicated that the first two principal components explained 75.6% of the total GGE variation for pod harvest index. The PC1 included all

the locations but Puerto Rico and captured 58.4% of the GGE variation. The PC2 explained 17.2% of the GGE variability and was associated with Puerto Rico. Three mega-environments were observed for pod harvest index.



Figure 5. Biplot of genotype performance for seed yield per plant across five locations.

Palmira-Popayan constituted one separated mega-environment and Puerto Rico and North Dakota were set apart. Genotypes RIJC254, and RIJC077 were among the best in Puerto Rico. The mega-environment Palmira-Popayan included RIJC327 and RIJC022 with higher harvest index. Genotypes RIJC142 and RIJC205 exhibited the best performance in North Dakota. Vertex and stable genotypes included RIJC302, Jamapa and Calima. Many genotypes exhibiting high PHI are more efficient in photosynthates partitioning from vegetative to reproductive organ and subsequently contributed to seed yield. As previously reported this trend was generally confirmed by the biplot.



Figure 6. Biplot of genotype performance for pod harvest index (PHI) across four locations (missing data for Citra).

Because more than one trait of interest (seed yield, early maturity, and other traits) needs to be improved simultaneously in a breeding program, multiple-trait selection is usually more appropriated. However, care should be taken for negatively correlated traits since modifying one will automatically affect the other, as usually observed for early maturity and seed yield. As seen previously in this study, early vegetative stage was negatively associated with number of seeds per pod and number of pods per plant. At the same time 100-seed weight was negatively associated with number of seeds per pod and number of pods per plant as well as the relationship between PHI and phenological traits. High yielding cultivars is one of the ultimate goals in plant breeding. Large GxE interactions and low heritability make it uneasy to select best genotype in mega-environments. To fill the gap between potential and realized yield as well as developing stable varieties, GxE interactions which can be explained by biotic and/or abiotic factors should be at low magnitude level. Selection should consider heritability estimates in order to make the best decision. In the present study, low GxE interactions magnitude and relatively high heritability estimates observed across locations for many traits represents an opportunity for selection of best genotypes. As seed yield per se was not the main purpose of this study, seed yield per plot cannot be estimated with precision and extrapolation might be difficult. Seed yield per plant is a selected trait of interest that can be associated with realized yield per plot. Phenotypic variability for this trait was very high and combined analysis excluded North Dakota. Therefore selection in the mega-environment including the other locations might be less reliable in detecting the best genotypes for seed yield per plant. In general, as earliness might be negatively correlated with seed yield, finding a good balance between these

important traits will be suitable for breeding purposes and to develop an improved variety. For example, none of the top ten high-yielding and stable genotypes has matched with the early-maturing ones. For example, when tracking back earliness for the high-yielding genotypes at North Dakota, a good balance between traits was found with genotypes RIJC078 (R7 at 76 DAP and yielded 34 g plant<sup>-1</sup>), RIJC326 (R7 at 78 DAP and yielded 24 g plant<sup>-1</sup>), and Jamapa (R7 at 84 DAP and yielded 56 g plant<sup>-1</sup>). However, across four locations (without North Dakota) genotype RIJC078 yielded 11 g, RIJC326 yielded 15 g and Jamapa yielded 42g. Based on the results from the previous section and the biplots, genotypes of specific interest can be identified with greater precision. Finding equilibrium between early-maturity and seed yield is probably the key factor to focus on when developing selection criteria needed to identify improved common bean genotypes. Reducing GxE interactions effects, the biplots allowed partitioning the target environments into smaller more homogeneous subgroups. When accounting for GxE interaction accurately, stable genotypes and/or subset which best suited to specific mega-environment were identified. Environmental limiting factors affecting the genotypes performance such as soil characteristics, climatic, biotic and abiotic stresses should be considered as well. In this study, plant density and row spacing vary across locations due to site specific factors and environmental conditions. Row spacing, plant density, and environmental conditions across locations might be important factors affecting genotype performance as higher density can increase common bean seed yield.

#### 4.3. RIJC Trait Associated with Destructive Measurements, Plant Height

#### and Width

Significant differences ( $P \le 0.001$ ) among genotypes were observed for plant height and width, leaf area, and dry weight. Across locations, GxE interactions magnitude was lower than genotypes main effects for all the traits. Relatively high heritability estimates were observed for all the traits of interest (Table 13). It should be noted that leaf areas and dry weight traits included four locations because of missing values for Puerto Rico.

Table 13. Mean square values and narrow-sense heritability (h<sup>2</sup>) across five or four locations for plant height (PH), plant width (PW), unifoliate leaf area (LAU), total leaf area (LAT), unifoliate dry weight (DWU), total leaves dry weight (DWL), and total dry weight (DWT).

SOV	PH	PW	LAU <sup>†</sup>	LAT <sup>†</sup>
Genotype	250.1***	195.4***	538.4***	15181.0***
GxE	45.5***	50.3***	100.6***	3989.1***
Error	27.1	24.5	46.9	1249.9
h²	0.69	0.59	0.69	0.58

SOV	DWU <sup>†</sup>	DWL <sup>†</sup>	DWT <sup>†</sup>
Genotype	0.015***	0.328***	0.527***
GxE	0.004***	0.085***	0.151***
Error	0.002	0.035	0.063
h²	0.61	0.59	0.56

\*\*\* Significant at the  $P \le 0.001$  level.

<sup>†</sup> Four locations (missing data for Puerto Rico).

Across locations except Puerto Rico, Calima remained among the top 10 best genotypes having largest leaf areas along with RIJC227, RIJC219, RIJC351, and RIJC081 [(Table 14); These genotypes have indeterminate growth habit except for RIJC081]. The top 10 genotypes including both growth habits are significantly different

than Jamapa and the bottom 10 for LAT. However significant differences can be observed within the top 10 for LAU. Genotypic variation can strongly influence the efficiency of solar energy conversion through photosynthesis into biomass production. Genotypes might utilize photosynthates for greater leaf expansion in lieu of biomass mobilization into reproductive structures (seed yield for instance) and vice versa (Rao et al., 2009). Large leaf area genotypes having low seed yield have been reported under drought stress (Assefa, 2013). In this study, most high yielding and indeterminate genotypes did not have larger leaf areas than determinate ones. For instance RIJC358 was among the top 10 genotypes exhibiting largest leaf area (315.7 cm<sup>2</sup>) and highest seed yield (25.3 g per plant). However, various genotypes having large leaf area expressed very low seed yield (364.8 cm<sup>2</sup> and 8.0 g for RIJC227). Those genotypes expressed contrasting pod harvest index (72 vs. 65) which suggested an increase in photosyntates remobilization efficiency associated with high value and a decrease with low PHI value. Such efficiencies have been reported for genotype adaptation strategy to terminal drought compared to a survival reaction of delaying reproductive stages (Beebe et al., 2008; Beebe, 2012).

Given that leaf expansion is sensitive to environmental factors such as drought, genotypes can respond in different ways and independently of seed yield. Beebe et al. (2010) reported that water limitation at deep rooting stage may result in leaf expansion and seed yield differences. Dry weight measurements (Table 15) followed relatively the same trend as seen for leaf areas. Forty percent of the largest unifoliate leaf area remains at the top 10 for their dry weights. However 60% of the genotypes with largest

total leaf area were observed at the top 10 high yielding, suggesting a positive correlation between leaf area and seed yield.

Table 14. Mean values across four locations of 10 largest and 10 smallest genotypes and parents for leaf area total (LAT), unifoliate leaf area (LAU) (LAT ranking).

-		Tra	its†
Genotype	-	LAT	LAU
		Cr	m²
RIJC227		365	70
RIJC219		351	70
RIJC351		343	60
RIJC234		340	53
RIJC081		334	53
CALIMA	Large	332	61
RIJC241	U	328	46
RIJC246		322	59
RIJC358		316	52
RIJC213		313	52
RIJC205		161	31
RIJC065		159	34
RIJC136		158	35
RIJC138		158	36
RIJC206	Small	158	29
RIJC076	oman	157	30
RIJC049		152	30
RIJC069		151	35
RIJC220		138	34
RIJC212		137	36
JAMAPA		259	44
Mean		237	44
LSD(0.05)		89.4	11.7
CV%		19.2	13.5

<sup>†</sup> Four locations (missing data for Puerto Rico).

			Traits <sup>†</sup>					
Constynes	•	DWU	DWL	DWT				
Genotypes								
		<u>g</u>						
RIJC227		0.39	1.50	2.55				
RIJC241		0.26	1.69	2.28				
RIJC066		0.37	1.57	2.23				
CALIMA		0.30	1.53	2.21				
RIJC240	Large	0.35	1.23	2.19				
RIJC219	Large	0.31	1.59	2.14				
RIJC213		0.27	1.66	2.12				
RIJC130		0.27	1.62	2.10				
RIJC007		0.31	1.65	2.10				
RIJC246		0.31	1.48	2.08				
RIJC049		0.17	0.79	1.18				
RIJC025		0.13	0.80	1.18				
RIJC138		0.18	0.73	1.17				
RIJC079		0.17	0.82	1.16				
RIJC150	Small	0.17	0.83	1.15				
RIJC212	Small	0.19	0.67	1.12				
RIJC069		0.19	0.74	1.12				
RIJC076		0.16	0.74	1.12				
RIJC220		0.18	0.67	1.11				
RIJC206		0.16	0.74	1.10				
JAMAPA		0.20	1.24	1.85				
Mean		0.22	1.11	1.62				
LSD(0.05)		0.06	0.37	0.56				
CV%		14.04	16.89	17.75				

Table 15. Mean values across four locations of 10 largest and 10 smallest genotypes and parents for unifoliate dry weight (DWU), total leaf dry weight (DWL), total dry weight (DWT) (DWT ranking).

<sup>†</sup>Four locations (missing data for Puerto Rico).

Table 16. Correlation coefficient values across five or four locations for pod harvest index (PHI), Emergence ( $V_E$ ), unifoliate ( $V_0$ ), first trifoliate ( $V_1$ ), flowering ( $R_1$ ), pod ( $R_3$ ), seed ( $R_5$ ), physiological maturity ( $R_7$ ), harvest maturity ( $R_8$ ), unifoliate leaf area (LAU), total leaf area (LAT), plant height (PH), and plant width (PW).

	Seed yi plant	eld 100 <sup>1†</sup> w	D-seed eight	Seeds pod <sup>-1</sup>	Pods plar	nt⁻¹ PF	{I <b>‡</b>	VE
LAU	0.14 <sup>NS ¶</sup> ( 0.01 <sup>NS</sup> )		63***	-0.15*	-0.18**	-0.1	-0.10 <sup>NS</sup> 0.32	
LAT	0.18**	, 	39***	0.04 <sup>NS</sup>	-0.10 <sup>NS</sup>	-0.0	8 <sup>NS</sup>	0.26**
PH	0.37**	, * 0	.16*	0.28***	0.21**	-0.3	7***	0.19**
PW	0.43**	) * 0	.26**	0.26**	0.23**	-0.3	1***	0.27***
	V <sub>0</sub>	<b>V</b> 1	R₁†	R <sub>3</sub>	R5	R7		$R_8^{\dagger}$
LAU	0.24**	0.25**	0.23** (0.18*)	0.28***	0.25**	0.28***	0.29*** (0.14 <sup>NS</sup> )	
LAT	0.21**	0.27***	0.19**	0.26**	0.24**	0.28***	0.29*** (0.07 <sup>NS</sup> )	
PH	0.15*	0.15*	0.74***	, * 0.64***	0.65***	0.64***	0.71*** (-0.01 <sup>NS</sup> )	
PW	0.21**	0.20**	0.71***	/ * 0.69*** *)	0.69***	0.72***	0.76*** ( 0.18 <sup>NS</sup> )	
			<u>\</u>	/			( -	- /
	LAU §	LAT §	PH	-				

LAU

LAT 0.81\*\*\*

PH 0.28\*\*\* 0.21\*\*

PW 0.43\*\*\* 0.44\*\*\* 0.83\*\*\*

\*\*\* Significant at the  $P \leq 0.001$  level.

\*\* Significant at the  $P \le 0.01$  level.

\* Significant at the  $P \le 0.05$  level.

<sup>†</sup> Four locations (without North Dakota) and North Dakota (second value in parentheses).

<sup>‡</sup> Four locations (missing data for Citra)

<sup>§</sup> Four locations (missing data for Puerto Rico)

<sup>¶</sup>Non-significant.

Comparing Jamapa to other indeterminate genotypes, RIJC227 and RIJC241 exhibited significant difference and appeared to be transgressive segregants for DWU (0.2 vs. 0.4 g) and DWT (1.9 vs. 2.6 g). However DWU (0.2 vs. 0.3) and DWL (1.2 vs.

1,7g) included RIJC241 having significantly better performance than the parent Jamapa. An 80% of the genotypes with largest leaf area are among the best high yielding. Total dry weight which included main stem, hypocotyl, and petioles followed the same trend as seen for total leaf area where 90% of the best genotypes for this trait were observed at the top 10. Most of the relationships between traits were found to be significant. Strong correlations were observed between plant height and plant width, but weak to strong relationships were observed for vegetative and reproductive phenological stages (Table 16). Weak correlation was observed between plant harvest index (negative) and plant height as well as all leaf areas (LAU and LAT). Plant width showed the same relationship pattern found for plant height with all the traits except for LAT, which exhibited weak correlation coefficient values. LAU did show relatively weak correlation for all the phenological traits, plant height, and width. Surprisingly, no relationship was observed between LAU and seed yield per plant as well as pod harvest index. Negative correlation coefficients were observed for seeds per pod and pods per plant.

Weak correlation was found for LAT and seed yield per plant. In contrast, both leaf area traits exhibited weak to strong correlation for 100-seed weight. For the traits which cannot be combined with North Dakota, either no relationships or weak correlation coefficients were observed. Compared to the present study, Taran et al. (2002) reported contrasting results for most of the traits except for pods per plant (0.25\*\*) and plant height. For instance, plant height was weakly correlated with days to maturity (0.43\*\*) while in this study, strong correlation (0.64\*\*\*) was observed. Data presented in this study are more in agreement with the results reported by Sofi et al. (2011) for plant height associated with seeds per pod (0.35), 100-seed weight (0.25)
and seed yield per plant (0.33). As plant height is usually associated with seed yield and it is a highly heritable trait (0.82, Table 13; 0.89, Kolkman and Kelly 2002; 0.85, Sofi et al. 2011), reliable visual selection based on plant height might be done easily to select phenotypes that are good representation of genotypes for common bean improvement. Plant height and width exhibited large variation within and across locations (Tables 17 and 18). These traits were measured over time at different development stages but the results reported in the present study were from 55 to 65 days after planting for consistency in comparison across locations.

Plant height mean values across five locations were 33 cm and ranged from 46 to 21 cm. When comparing with commercial cultivars of different market classes commonly grown in North Dakota, taller genotypes have been reported. For instance pinto and black varieties grown at Prosper ND, in 2013 reached respectively 51 and 53 cm tall in average while kidney beans grown at Park Rapids MN, measured 48 cm (http://www.ag.ndsu.edu/varietytrials/dry-bean). No significant differences were observed within the top tallest and bottom shortest genotypes. However, significant differences between the parents (Jamapa and Calima) were observed. The tallest genotype across five locations was RIJC135 (46 cm). Data presented in Table 18 indicated that plant width mean values were 35 cm across five locations. In contrast to plant height, the parents exhibited no significant difference for plant width. Four genotypes (RIJC135, RIJC305, RIJC339 and RIJC361) were among the top 10 for both plant height and width with significant differences compared to the bottom genotypes.

Plant height and width are desirable characters for common bean improvement. Common bean canopy is determined by genotypes but it can be influenced by the

environment. Relationships of canopy traits associated with disease incidence and direct harvest have been already reported (Fuller et al., 1984; Miklas et al., 2001; Eckert et al., 2011). Higher and narrower canopy can help reduce disease, facilitate mechanical harvest, and subsequently increase seed yield.

		Plant height
Genotypes		cm
RIJC135		46
RIJC129		45
RIJC026		44
RIJC147		43
RIJC361	Tall	43
RIJC030	i an	43
RIJC305		42
RIJC339		42
JAMAPA		42
RIJC346		41
		24
RIJC247		24
RIJC237		24
		20
		23
	Short	23
RUC244		20
RUC078		22
RUC015		21
RIJC201		21
CALIMA		33
Mean		33
LSD(0.05)		8.0
CV%		12.3

Table 17. Mean values across five locations of 10 tallest and 10 shortest genotypes and parents.

		Plant width
Genotypes		cm
RIJC361		46
RIJC031		44
RIJC312		43
RIJC001		43
RIJC339	\\/ido	43
RIJC135	VILLE	42
RIJC357		42
RIJC334		42
RIJC208		41
RIJC305		41
RIJC012		28
RIJC251		27
RIJC223		27
RIJC244		27
RIJC366	Narrow	26
RIJC078		25
RIJC257		25
RIJC201		24
RIJC015		23
RIJC049		22
CALIMA		40
JAMAPA		41
Mean		35
LSD(0.05)		6.0
CV%		8.7

Table 18. Mean values across five locations of 10 widest and 10 narrowest genotypes and parents.

Mean values observed in our study were lower than the results reported by Kolkman and Kelly (2002) except for one year (34 and 32 cm, 35 and 33 cm respectively for plant height and width in elite and RILs). The previous authors reported that common bean elite lines and RILs means vary from 32 to 56 cm and 33 to 59 cm

for plant height and width, respectively. Mean unifoliates leaf area (LAU) and its corresponding dry weight (DWU) ranged respectively from 29 to 70 cm<sup>2</sup> and 0.2 to 0.4 g across four locations (Tables 14 and 15). Highest leaf area and dry weight values were found for RIJC227 while lowest means were observed for RIJC206. Allometric relationships between leaf surface area and dry weight have already been reported for the RIJC common bean population (Clavijo et al., 2013). It was suggested that genotypic variability exists and environmental factors influenced this relationship independently from growth habits. Related to our study, specific leaf area, which describes relationships of dry matter investment and leaf area, is expected to decrease with an increase in leaf area across locations as hypothesized higher photosyntates. Leaf area total (LAT) including the first three tri-foliates along with the corresponding dry weight (DWL) followed a different trend as seen for LAU and DWU. Calima (332 cm<sup>2</sup>) was among the genotypes with largest total leaf area along with RIJC219 (351 cm<sup>2</sup>) and RIJC351 (343 cm<sup>2</sup>). Variation was observed across locations for mean total dry weight (DWT) which includes leaves, petioles, hypocotyl, and main stem (Table 15). Total dry weight followed closely the same trend as seen for DWL (90% of the genotypes stay at the top 10).

Stem dry weight accumulation is important for common bean high seed yield expression. Under drought stress conditions, differences in stem dry weight accumulation or allocation among dry bean cultivars with different growth habits have been reported by Rosales-Serna et al. (2004). Previous studies suggested that plant dry weight showed low GxE interactions and having moderate to high heritability sensitivity to water stress at diverse developmental stages. Data presented in our study showed

relatively high heritability estimates and low GxE for dry weight traits. Our results agreed with Shenkut, and Brick (2003) suggesting that dry weight traits may be used as indirect selection criterion to improve and stabilize seed yield for optimum environments. Under drought stress limitation, dry matter accumulation combined with partitioning vegetative biomass into reproductive structures to a large extent may determine common bean economic yield. Even though common bean dry weight accumulation can be affected by low moisture, it should be noted that some determinate growth habit genotypes might have potential for drought tolerance as emphasized by Emam et al. (2010) for dry-land crop rotation. In contrast, Durango race indeterminate growth habit Type-III has been already reported by Rosales et al. (2012) for superior drought resistance. To maintain seed yield production terminal drought resistant genotypes rely on an early response of stomatal conductance, CO<sub>2</sub> diffusion and an increased in water use, among others mechanisms.

#### 4.4. Comparing RIJC to RISR Population and Variety Trials

#### 4.4.1. RIJC across locations vs. RISR in North Dakota

Comparing population mean values, significant differences were observed for all the genotypic coefficient (EMFL, FLSH, FLSD, and SDPM, Table 19). For the parents of RIJC population, Calima was among the earlier genotypes for EMFL, FLSH whereas later for FLSD and SDPM with respectively 24, 4, 10, and 19 photothermal days (PTD). Jamapa exhibited intermediate values with respectively 31, 4, 9, and 14 for EMFL, FLSH, FLSD, and SDPM. For the RISR population, the parents Stampede and Redhawk expressed intermediate values (34, 7, 13, 15 and 28, 7, 15, 14) respectively for EMFL, FLSH, FLSD, and SDPM.

Table 19. Genotypic coefficients of the CROPGRO-Dry bean model [(emergence-flowering EMFL, flowering-podded (FLSH), flowering-seedling (FLSD), seedling-physiological maturity (SDPM)] for RIJC population grown across five or four locations and RISR in North Dakota.

Genotypic coefficient	Mean (Minimum, Maximum)		
	RIJC PT	RISR D <sup>†</sup>	
EMFL <sup>‡</sup>	28a <sup>§</sup> (22, 36)	35b (20, 51)	
FLSH <sup>‡</sup>	5a (3, 10)	8b (3, 18)	
FLSD <sup>‡</sup>	12a (8, 19)	16b (7, 33)	
SDPM	15a (10, 23)	17b (6, 26)	

<sup>†</sup>Photothermal days.

<sup>‡</sup> Four locations (without North Dakota).

<sup>§</sup> Different letters indicate significance at P < 0.05 between populations for a given trait.

It should be noted that coefficient of variation (20.6, 40.6, 29.8, and 22.0 respectively for EMFL, FLSH, FLSD, and SDPM) was very large in RISR population because of extreme values albeit the RIJC population should not be better adapted than RISR which is derived from parents developed by and for North America.

Relationship between traits indicated that EMFL was negatively associated to FLSH and FLSD in RISR population (Table 20). Contrastingly, no correlations were observed between these traits in RIJC population. Weak correlation coefficient was observed for SDPM and EMFL in RIJC while there was no association between the traits in RISR. Both populations showed a similar strong correlation between FLSD and FLSH. No association was found in both populations between SDPM and FLSH.

Table 20. Correlation coefficients values among emergence-flowering (EMFL), flowering-podded (FLSH), flowering-seedling (FLSD), seedling-physiological maturity (SDPM) for RIJC across five or four locations and RISR in North Dakota (second value in parentheses) populations.

	EMFL <sup>†</sup>	FLSH <sup>†</sup>	FLSD <sup>†</sup>
FLSH	0.09 <sup>NS‡</sup> (-0.69***)		
FLSD	-0.07 <sup>NS</sup> (-0.64***)	0.69*** (0.76***)	
SDPM§	-0.34*** (-0.006 <sup>NS</sup> )	-0.06 <sup>NS</sup> (0.07 <sup>NS</sup> )	-0.21** (0.06 <sup>NS</sup> )

\*\*\* Significant at the  $P \leq 0.001$  level.

\*\* Significant at the  $P \le 0.01$  level.

<sup>†</sup>Non-significant.

<sup>‡</sup>Four locations (without North Dakota)

§ Five locations.

In RIJC, SDPM and FLSH were negatively associated but no correlation was found in RISR. Research carried out by Saliceti et al. (2006) using a population derived from ICA-Pijao x Montcalm reported larger values for all the traits (EMFL, FLSH, FLSD, and SDPM) than what was observed in this study. The previous study also reported that indeterminate growth habit genotypes needed more PTD to reach phenological stages from emergence to physiological maturity. In contrast, no significant differences were detected between growth habits, where indeterminate genotypes expressed similar values than determinate ones within both populations for most of the traits (VE, R1, R3, R5, and R7). This trend is in agreement with the results previously reported in this study. Higher genotypic coefficient (EMFL, FLSH, FLSD, and SDPM) values have been already reported for RIJC population grown in Puerto Rico (Saliceti, 2006). Evaluating F<sub>10</sub> RILs from the RIJC population the mean genotypic coefficients observed were 43, 12, 22, and 24 PTD for respectively EMFL, FLSH, FLSD, and SDPM. When comparing the phenological traits of RIJC population grown across locations and RISR in North Dakota, significant differences were observed (Table 21). In general, RISR population needed significantly more PTD to reach all the phenological stages. These results are in agreement with data previously reported in this study where more calendar days were also needed to complete the different phenological stages. Days to emergence (V<sub>E</sub>) were two (PTD) early across five locations for RIJC population compared to RISR grown in North Dakota.

Table 21. Photothermal days for emergence (V<sub>E</sub>), unifoliate (V<sub>0</sub>), first trifoliate (V<sub>1</sub>), flowering (R<sub>1</sub>), pod (R<sub>3</sub>), seed (R<sub>5</sub>), and physiological maturity (R<sub>7</sub>) of RIJC grown across five or four locations and RISR in North Dakota.

Phenological stage	Mean (Minimum, Maximum)			
	RIJC PT	RISR D <sup>†</sup>		
VE	6a <sup>§</sup> (5, 8)	8b (6, 9)		
R1	35a <sup>‡</sup> (28, 44)	43b (26, 60)		
R₃	42a (33, 52)	51b (34, 71)		
R₅	49a (40, 61)	58b (45, 75)		
R <sub>7</sub>	64a (45, 80)	75b (52, 88)		

<sup>†</sup>Photothermal days.

<sup>‡</sup>Four locations (without North Dakota).

§ Different letters indicate significance at P < 0.05 between populations for a given trait.

Days to flowering, pod initiation, seed filling and physiological maturity were reached respectively, 8, 9, 9, and 11 PTD early across five locations except for the first trait (four locations without North Dakota). In this study, the results were slightly higher when comparing days to flowering with mean historical data of the Pinto variety trial grown at Carrington ND from 2008 to 2010 (30 PTD). Entries in the Pinto variety trials conducted from 2008 to 2012 took relatively less PTD to reach R7. The results suggested that PTD gave in some extent more precise results compared to day after planting for the overall phenological stages. While days after planting provide similar population responses in estimating phenological and developmental stages for most of the traits assessed in North Dakota, PTD can be a more precise option to fine-tune with better estimates. Even though RISR population was not grown in the same environments as RIJC, means across locations for RIJC differ significantly from RISR grown alone in North Dakota. As seen previously in this study, the results did not deviate from expectation by the fact that contrasting environments between tropical and temperate geographic regions.

#### 4.4.2. RIJC vs. RISR in North Dakota

Comparing mean values of the two populations grown in North Dakota showed significant differences for all traits except for EMFL, R<sub>1</sub> and R<sub>3</sub> (Table 22 and 23). Compared to Jamapa, Calima exhibited significantly late EMFL and was observed among the earlier genotypes for the other genotypic coefficients. These results are good evidence of the environment difference where the parents generally observed across the other locations expressed an opposite pattern with Jamapa as the late genotype. Response of both populations for many traits can be observed in Table 23. Means of

days to emergence, R5, and R7 followed the same trend as seen across locations for RIJC population.

Table 22. Genotypic coefficients of the CROPGRO-Dry bean model [(emergence-flowering EMFL, flowering-podded (FLSH), flowering-seedling (FLSD), seedling-physiological maturity (SDPM)] for RIJC and RISR populations grown in North Dakota.

Genotypic coefficient	Mean (Minimum, Maximum)		
-	RIJC PT	RISR D <sup>†</sup>	
EMFL	36a <sup>‡</sup> (19, 60)	35a (20, 51)	
FLSH	10a (6, 22)	8b (3, 18)	
FLSD	20a (4, 33)	16b (7, 33)	
SDPM	10a (5, 17)	17b (7, 26)	

<sup>†</sup>Photothermal days.

<sup>‡</sup>Different letters indicate significance at P < 0.05 between populations for a given trait.

The RISR population has shown late emergence (V<sub>E</sub>) and physiological maturity ( $R_7$ ), but early seed filling compared to the RIJC population. For the RISR population the parents Stampede and Redhawk expressed intermediate values as seen previously. As seen for the number of days after planting needed to reach physiological maturity, a sum of thermal units or PTD is accumulated over time to complete each phenological stage. In this study, the results are in agreement with the fact that phenological development plays a major role in the final outcome of high seed yield. While one of the RIJC parent Jamapa yielded 57g plant<sup>-1</sup> and needed 66 PTD to reach  $R_7$  in North

Dakota, the RISR parent Stampede from similar gene pool exhibited 45 g plant<sup>-1</sup> and 95

PTD.

Table 23. Photothermal days for emergence ( $V_E$ ), unifoliate ( $V_0$ ), first trifoliate ( $V_1$ ), flowering ( $R_1$ ), pod ( $R_3$ ), seed ( $R_5$ ), and physiological maturity ( $R_7$ ) of RIJC and RISR grown in North Dakota.

Phenological stage	Mean (Minimum, Maximum)			
	RIJC PT	RISR D <sup>†</sup>		
VE	6a <sup>‡</sup> (5, 8)	8b (6, 9)		
R1	42a (24, 66)	43a (26, 60)		
R₃	52a (33, 66)	51a (34, 71)		
R₅	61a (42, 71)	58b (45, 75)		
R <sub>7</sub>	69a (58, 77)	75b (52, 88)		

<sup>†</sup> Photothermal days.

<sup>‡</sup> Different letters indicate significance at P < 0.05 between populations for a given trait.

Based on North Dakota weather data, PTD is a useful tool to predict or estimate plant development in absence of adverse climatic conditions such as drought or frost. Accurate estimation of phenological stages influencing common bean growth and development is crucial to optimize management, production practices and yield potential. The ability to predict phenological and developmental stages under field conditions is crucial to the development of crop models. Common bean leaf area development and biomass production are related to phothermal day accumulation.

#### 4.5. Seed Yield of RISR Population Grown under Drought and Irrigated

#### **Environmental Conditions**

Significant differences ( $P \le 0.001$ ) among genotypes were observed for seed yield in RISR population grown under drought and irrigated conditions in Nebraska. Relatively high heritability estimates were observed across environmental conditions (Table 24). These heritability estimates were higher than those reported by Assefa et al. (2013) in similar environmental conditions (0.19 and 0.31, respectively in drought and irrigated). It should be noted that 2013 data represented a sub-sample of the extreme genotypes and the high heritability estimates found in drought conditions might be due to reduced sample size. However, similar values were observed in irrigated environmental conditions for both years. Seed yield means in 2012 in drought and irrigated environmental conditions shown that RISR116 and Stampede were the best genotype following (Table 25). These genotypes (RISR116 and Stampede) were among those which performed almost equally either in drought (stress) and irrigated (non-stress) conditions. Stampede has already been reported for drought tolerance (Kandel, 2009; Osorno et al., 2008; Urrea and Porch, 2009) and this study confirmed the potential of this cultivar. High yielding performance in both environmental conditions suggested stable genotypes with promising potential for drought tolerance adaptation. Compared to Pinto variety trials grown in Carrington, ND between 2008 and 2012 (2770 and 2598 kg ha<sup>-1</sup> respectively in irrigated and drought conditions), lower mean seed yield values were observed for the RISR population [Table 25, (2356 and 1076 kg ha<sup>-1</sup>, respectively)].

Table 24. Mean square values and narrow-sense heritability  $(h^2)$  for seed yield of Stampede x Redhawk population grown in Scottsbluff, NE at two environmental conditions in 2012 and 2013.

	Year <sup>†</sup>						
	2012		2013				
SOV	Drought	Irrigated	Drought	Irrigated			
Genotype	739983***	1573271***	342150***	312605***			
Error	188813	493327	30372	94068			
h <sup>2</sup>	0.59	0.52	0.84	0.54			

\*\*\* Significant at the  $P \leq 0.001$  level.

<sup>+</sup>182 genotypes grown in 2012 and a subset of 42 genotypes in 2013.

Low GxE combined with high heritability and good yield are desirable traits for dry bean breeding improvement. Assefa et al. (2013), Szilagyi, (2003), Frahm et al., (2004), Beebe et al., (2008), among other authors have reported positive correlation coefficient between seed yield in irrigated and drought conditions. Compared to the results of this study ( $r = 0.62^{***}$  and  $0.58^{***}$ ) observed respectively in 2012 and 2013, relatively low correlation coefficient ( $r = 0.23^{***}$ ) was reported by Assefa et al. (2013).

In 2012, all lines in irrigated conditions yielded higher than drought except for RISR108, RISR153 and RISR154 showing surprisingly opposite mean value which cannot be explained (might be due to human error or poor stands in the irrigated trial for these genotypes). However, only RISR179 yielded higher in drought than irrigated conditions in 2013 (Table 26). Drought intensity indexes (DII) observed in both years were moderate and DSI was higher in 2012 (0.5) than 2013 (0.4). It should be noted that genotypes which yield higher in drought than irrigated conditions exhibited negative values of drought susceptibility index (S). For example RISR108, RISR153, RISR154 and RISR179 exhibited -04, -2.7, -0.7, and -0.4 indicating high susceptibility for drought stress.

Environments					
Genotypes		Drought	Irrigated	Geometric mean <sup>†</sup>	Drought susceptibility index
			Seed yi kg ha <sup>_</sup>	eld 1	
STAMPEDE		3225	4280	3715	0.5
RISR116		3229	4230	3696	0.4
RISR158		2580	3580	3039	0.5
RISR011		2521	3465	2955	0.5
RISR180		2239	3853	2937	0.8
RISR084	High	2455	3494	2929	0.5
RISR111	5	2329	3569	2883	0.6
RISR079		2347	3532	2879	0.6
RISR001		2250	3626	2856	0.7
RISR049		1971	4054	2827	0.9
RISR102		290	1008	540	1.3
RISR103		367	733	519	0.9
RISR177		98	2562	501	1.8
RISR072		253	964	494	1.4
RISR167	Low	182	778	377	1.4
RISR178	2011	114	1102	354	1.7
RISR097		125	945	344	1.6
RISR010		133	619	287	1.4
RISR115		83	864	267	1.7
RISR182		125	412	227	1.3
REDHAWK		1604	2700	2081	0.7
Mean		1076	2356	1565	1.0
LSD(0.05)		968.4	957.6	NA <sup>‡</sup>	NA
CV%		45.9	20.7	NA	NA

Table 25. Mean values of 10 highest and 10 lowest seed yielding genotypes and parents from Stampede x Redhawk population grown in Nebraska at two environmental conditions in 2012 (Geometric mean ranking).

<sup>†</sup> Square root of the product of drought and irrigated yield values.

<sup>‡</sup>Not calculated.

Environment					
Genotypes		Drought	Drought Irrigated		Drought susceptibility index
			Yield kg ha⁻¹		
RISR116		1728	2055	1885	0.4
RISR180		1476	1980	1709	0.6
STAMPEDE		1557	1724	1638	0.2
RISR179		1737	1485	1606	-0.4
RISR111	Hiah	1414	1666	1535	0.4
RISR049	riigii	1112	2003	1493	1.1
RISR045		1044	1755	1353	1.0
RISR137		1071	1525	1278	0.7
RISR018		1011	1603	1273	0.9
RISR032		1182	1362	1269	0.3
RISR019		422	1216	716	1.6
RISR075		561	908	713	0.9
RISR160		445	1065	688	1.4
RISR131	Low	385	901	589	1.4
RISR095	LOW	338	1010	584	1.6
RISR055		343	837	535	1.4
RISR063		415	632	512	0.8
RISR014		143	1696	493	2.2
RISR035		238	839	447	1.7
RISR115		18	680	110	2.4
REDHAWK		815	1587	1137	1.2
Mean		762	1291	992	1.0
LSD(0.05)		267.9	488.1	NA‡	NA
CV%		17.9	19.3	NA	NA

Table 26. Mean values of 10 highest and 10 lowest seed yielding extreme genotypes and parents from the Stampede x Redhawk population grown in Nebraska at two environmental conditions in 2013 (Geometric mean ranking).

<sup>†</sup> Square root of the product of drought and irrigated yield values.

<sup>‡</sup>Not calculated.

As emphasized by Nunez-Barrios et al. (2005) drought yield losses superior to 60% in common beans was linked to a 63% reduction in pods per plant, 29% in seeds per pod and 22% in seed weight. In this study, seed yield losses in drought condition were 54% and 59% in 2012 and 2013, respectively. Previous studies (Rao et al., 2009; Beebe et al., 2008) have reported remobilization of photosyntates capacity as an inherent characteristic found in drought resistant genotypes. When tracking back genotypes from both years (Tables 25 and 26), four lines (RISR049, RISR111, RISR116, and RISR180) along with Stampede remained at the top 10 highest yielding. Among the genotypes assessed in 2013 (Table 26), RISR115 expressed consistently significant low yield and Redhawk showed intermediate value. Water stress caused by drought is a global threat to bean production. Knowledge of specific growth stages most sensitive to drought is crucial because water stress can significantly reduce seed yield components of common bean. Water stress has been found more important during and after flowering but bean was less sensitive at vegetative stage (Manjeru et al., 2007). As previously reported in this study days to flowering play a major role in determining the final outcome of biomass accumulation. The previous genotypes found to be drought resistant might be used as future parents for trait introgression in breeding program for common bean improvement. Stampede pinto bean and other genotypes have confirmed their potential for drought tolerance varieties which can help meeting grower's challenge to increase yield. Matching high yielding and drought tolerance genotypes with early PTD accumulation is already a challenge for common bean breeding. As drought conditions are expected to increase in a warming climate in the near future, the RISR

population will offer a unique opportunity to validate seed yield components for the next generation gene-based crop model.

#### **5. CONCLUSIONS**

The results suggested different mega-environments depending on the trait of interest. Locations relatively more homogenous (Palmira, Citra, and Puerto Rico for instance) can be clustered together and North Dakota usually stand alone or may be associated with Popayan and Citra in some cases. The biplots allowed detecting stable genotypes or subsets which are best suited to each mega-environment. Moderate to high narrow-sense heritability estimates (0.55 to 0.87, 0.25 to 0.76 and 0.56 to 0.69 for phenological traits, seed yield components and other agronomic traits, respectively) were observed suggesting various traits such as days to flowering, physiological maturity, seeds per pod, plant height, leaf area, and dry weights, among others, may be used as selection criterion to improve common bean. Large variation in correlation coefficient estimates has been observed and some traits such as seed yield per plant and early vegetative stages and 100-seed weight, respectively showed negative relationships. When considering days after planting, both RIJC and RISR populations had a similar response for most of the traits assessed in North Dakota. Yield losses for RISR population in drought condition were 54.3% and 59.0% in 2012 and 2013, respectively. When tracking genotypes from 2012 to 2013, four lines (RISR049, RISR12311, RISR116, and RISR180) along with Stampede remained at the top 10 highest yielding. Among the genotypes assessed in 2013 RISR115 expressed consistently low yield and Redhawk showed intermediate value. Genotypes identified in this study need more detailed analysis to uncover genes controlling desirable traits. Based on the phenotypic diversity of both populations, gene mapping using new uncovered single nucleotide polymorphism (SNPs) markers to fast-track common bean

improvement may be developed. If considering the population evaluations as prebreeding screening strategy and the potential parents with ideal characteristics are identified, new gene recombinations can be made through unique backcross hybridization in order to derive variability. Common bean lines can be developed by introgression of desirable traits into improved varieties using appropriated breeding methodologies including marker assisted selection. As the gene base eco-physiology crop model will be developed, these results can be considered as the first steps leading to design ideotypes or ideal genotypes suited for specific mega environments. These new techniques should shorten the cycle needed to develop new superior varieties by implementing efficient early generation selection.

### **6. FUTURE WORK**

Phenotypic data generated across five locations will be also used to estimate the gene-based crop model parameters that are associated with genotypic information extracted from quantitative trait (QTL) analysis. Using a high-resolution linkage map, Bhakta et al. (2013) reported that that phenology and especially flowering time along with growth (plant size) are regulated by quantitative genes located on chromosome *pv1* and *pv3* and *pv8* appeared to control allometric relationships. Further QTL analyses are needed to detect more candidate genes and localization of DNA regions associated with traits of economic importance. Data from the RISR population is expected to be used for validation of the new gene-based crop model in the future. With low GxE interaction magnitude, stable and drought tolerant genotypes identified can be further examined and might be used for future common dry bean improvement. High quality dry bean genotypes with high yield and adaptation to the Northern Great Plains could be developed.

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# APPENDIX

Genotype	Seed Color	Seed Color	Hypocotyl	Growth Habit	Flower
	Pattern		Pigment		Color
Calima	Mottle	Red	No	Determinate	White
Jamapa	Solid	Black	Yes	Indeterminate	Violet
RIJC-001	Mottle	Dark Red	No	Indeterminate	White
RIJC-002	Mottle	Purple	No	Indeterminate	White
RIJC-003	Mottle	Dark Brown	No	Determinate	Violet
RIJC-004	Mottle	Dark Brown	No	Indeterminate	Violet
RIJC-005	Solid	Brown	No	Determinate	White
RIJC-006	Solid	DarkPurple	Yes	Determinate	Violet
RIJC-007	Solid	RedBrown	Yes	Indeterminate	White
RIJC-008	Solid	DarkPurple	No	Determinate	White
RIJC-009	Mottle	Dark Brown	No	Indeterminate	Violet
RIJC-010	Solid	Black	Yes	Indeterminate	Violet
RIJC-011	Mottle	DarkPurple	No	Indeterminate	Violet
RIJC-012	Solid	PurpleBrown	Yes	Determinate	Violet
RIJC-013	Mottle	RedBrown	No	Determinate	Violet
RIJC-014	Solid	DarkPurple	Yes	Determinate	Violet
RIJC-015	Solid	LightBrown	Yes	Determinate	White
RIJC-016	Solid	Black	Yes	Indeterminate	Violet
RIJC-017	Solid	Brown	Yes	Indeterminate	White
RIJC-018	Solid	DarkPurple	Yes	Determinate	White
RIJC-019	Solid	PurpleBrown	Yes	Determinate	Violet
RIJC-020	Solid	DarkPurple	Yes	Determinate	Violet
RIJC-021	Solid	Red	Yes	Determinate	White
RIJC-022	Solid	Black	Yes	Indeterminate	Violet
RIJC-024	Solid	Black	Yes	Indeterminate	Violet
RIJC-025	Mottle	Brown	No	Determinate	Violet
RIJC-026	Mottle	PurpleBrown	No	Indeterminate	Violet
RIJC-027	Mottle	Black	No	Indeterminate	Violet
RIJC-029	Mottle	RedBrown	No	Determinate	White
RIJC-030	Mottle	Purple	No	Indeterminate	Violet
RIJC-031	Mottle	Black	No	Indeterminate	Violet
RIJC-032	Solid	Red	Yes	Indeterminate	White
RIJC-045	Solid	Black	Yes	Determinate	Violet
RIJC-046	Mottle	Purple	No	Indeterminate	White
RIJC-047	Mottle	Black	No	Determinate	Violet
RIJC-048	Mottle	Brown	No	Indeterminate	White
RIJC-049	Solid	DarkPurple	Yes	Determinate	Violet
RIJC-058	Solid	Purple	Yes	Determinate	White
RIJC-059	Mottle	DarkPurple	No	Indeterminate	Violet
RIJC-061	Solid	DarkPurple	Yes	Determinate	Violet
RIJC-062	Mottle	PurpleBrown	No	Determinate	Violet

Table A1. Parents and recombinant inbred line family Jamapa x Calima phenotypes.

Genotype	Seed Color	Seed Color	Hypocotyl	Growth Habit	Flower
51	Pattern		Pigment		Color
	0 "				
RIJC-064	Solid	Brown	No	Determinate	White
RIJC-065	Mottle	DarkPurple	No	Indeterminate	White
RIJC-066	Mottle	DarkPurple	No	Determinate	Violet
RIJC-067	Mottle	RedBrown	No	Indeterminate	White
RIJC-069	Mottle	PurpleBrown	No	Indeterminate	Violet
RIJC-070	Solid	Beige	Yes	Indeterminate	Violet
RIJC-071	Mottle	PurpleBrown	No	Determinate	White
RIJC-072	Mottle	PurpleBrown	No	Indeterminate	Violet
RIJC-073	Solid	RedBrown	Yes	Indeterminate	White
RIJC-074	Mottle	RedBrown	No	Determinate	White
RIJC-075	Mottle	RedBrown	No	Indeterminate	Violet
RIJC-076	Solid	RedBrown	Yes	Indeterminate	White
RIJC-078	Mottle	RedBrown	No	Determinate	Violet
RIJC-079	Mottle	RedBrown	No	Determinate	Violet
RIJC-080	Mottle	Brown	No	Determinate	Violet
RIJC-081	Solid	Black	Yes	Determinate	Violet
RIJC-082	Mottle	DarkPurple	No	Indeterminate	Violet
RIJC-129	Mottle	RedBrown	No	Indeterminate	White
RIJC-130	Mottle	DarkPurple	No	Determinate	Violet
RIJC-131	Solid	Black	Yes	Determinate	Violet
RIJC-133	Mottle	Black	No	Determinate	White
RIJC-135	Solid	Black	Yes	Indeterminate	Violet
RIJC-136	Mottle	RedBrown	No	Indeterminate	Violet
RIJC-137	Solid	Black	Yes	Determinate	Violet
RIJC-138	Solid	Black	Yes	Indeterminate	Violet
RIJC-139	Solid	Black	Yes	Indeterminate	Violet
RIJC-140	Solid	DarkRed	Yes	Determinate	White
RIJC-141	Solid	Black	Yes	Indeterminate	Violet
RIJC-142	Solid	Black	Yes	Indeterminate	Violet
RIJC-144	Solid	Black	Yes	Indeterminate	Violet
RIJC-145	Mottle	RedBrown	No	Indeterminate	Violet
RIJC-146	Solid	DarkPurple	Yes	Indeterminate	Violet
RIJC-147	Mottle	RedBrown	No	Indeterminate	Violet
RUC-148	Mottle	RedBrown	No	Determinate	Violet
RUC-149	Solid	Black	Yes	Indeterminate	Violet
RUC-150	Mottle	RedBrown	No	Determinate	Violet
RUC-151	Solid	Reige	Yes	Indeterminate	White
RUC-201	Mottle	RedBrown	No	Determinate	White
RLIC-202	Solid	Purnle	Yes	Indeterminate	White
RUC-202	Mottle	RedBrown	No	Determinate	Violet
RUC_203	Mottle	Black	No	Determinate	Violet
RUC_204	Solid	Black	Vee	Indeterminate	Violet
RUC_205	Mottle	Brown	No	Indeterminate	Violet
	Mottle	Block	No	Indotorminate	W/bito
RIJU-207	would	DIdCK	INU	muelemmale	vviille

Table A1. Parents and recombinant inbred line family Jamapa x Calima phenotypes (continued).

Genotype	Seed Color Pattern	Seed Color	Hypocotyl Pigment	Growth Habit	Flower Color
	Mattla	DedBrown	No	Determinete	\//bito
RIJC-200	NOLLIE	Reubiowii	INU Voc	Determinate	Violet
RIJC-209	Solid	Black	Yes	Indeterminate	Violet
RIJC-210	Solid	DIACK	Yes	Indeterminate	Violet
RIJC-212	Soliu	DIUWII	res	Determinate	VVIIILE
RIJC-213		DarkBrown	INO	Determinate	VVnite
RIJC-214	Solia	Black	res	Determinate	Violet
RIJC-216	Mottle	Brown	INO	Indeterminate	Violet
RIJC-217	Solia	Black	res	Determinate	Violet
RIJC-218	Mottle	Brown	INO No	Indeterminate	VIOIEt
RIJC-219	Solid	ReaBrown	NO	Indeterminate	vvnite
RIJC-220	Solid	Васк	Yes	Indeterminate	Violet
RIJC-221	Mottle	DarkPurple	NO	Indeterminate	vvnite
RIJC-223	Mottle	DarkPurple	NO	Determinate	vvnite
RIJC-224	Mottle	Brown	No	Indeterminate	Violet
RIJC-225	Mottle	DarkPurple	No	Determinate	White
RIJC-226	Mottle	Brown	No	Indeterminate	Violet
RIJC-227	Solid	RedBrown	Yes	Indeterminate	White
RIJC-228	Solid	DarkPurple	Yes	Determinate	Violet
RIJC-229	Mottle	Brown	No	Indeterminate	White
RIJC-230	Solid	Purple	Yes	Indeterminate	White
RIJC-231	Solid	Black	Yes	Determinate	Violet
RIJC-232	Mottle	DarkPurple	No	Indeterminate	White
RIJC-233	Mottle	Red	No	Determinate	White
RIJC-234	Mottle	Purple	No	Determinate	White
RIJC-235	Solid	DarkPurple	Yes	Indeterminate	Violet
RIJC-236	Solid	Black	Yes	Indeterminate	Violet
RIJC-237	Solid	Black	Yes	Indeterminate	Violet
RIJC-238	Solid	RedBrown	No	Determinate	White
RIJC-239	Solid	Black	Yes	Determinate	Violet
RIJC-240	Mottle	Black	No	Determinate	White
RIJC-241	Mottle	RedBrown	No	Determinate	Violet
RIJC-242	Solid	Purple	Yes	Indeterminate	White
RIJC-243	Solid	Black	Yes	Indeterminate	Violet
RIJC-244	Mottle	Black	No	Determinate	Violet
RIJC-245	Solid	Black	Yes	Determinate	Violet
RIJC-246	Solid	Black	Yes	Determinate	Violet
RIJC-247	Solid	RedBrown	Yes	Determinate	White
RIJC-248	Mottle	RedBrown	No	Determinate	Violet
RIJC-249	Solid	DarkPurple	Yes	Indeterminate	Violet
RIJC-250	Mottle	Black	No	Determinate	Violet
RIJC-251	Solid	Black	Yes	Determinate	Violet
RIJC-252	Solid	Purple	Yes	Determinate	White
RIJC-253	Solid	DarkPurple	Yes	Determinate	Violet
RIJC-254	Mottle	Black	No	Determinate	White

Table A1. Parents and recombinant inbred line family Jamapa x Calima phenotypes (continued).

Genotype	Seed Color Pattern	Seed Color	Hypocotyl Pigment	Growth Habit	Flower Color
RUC-255	Solid	Black	Ves	Determinate	Violet
DLC 256	Solid	Black	Vec	Indeterminate	Violet
RIJC-257	Solid	RedBrown	Ves	Determinate	W/hito
RUC-259	Mottle	DarkPurnle	No	Indeterminate	Violet
RUC-260	Solid	Red	Ves	Determinate	White
RUC-261	Solid	RedBrown	Ves	Determinate	White
RUC-262	Solid	Black	Ves	Indeterminate	Violet
RUC-263	Solid	DarkPurnle	Yes	Indeterminate	Violet
RUC-264	Mottle	DarkPurple	No	Determinate	White
RUC-301	Solid	Black	Yes	Indeterminate	Violet
RUC-302	Solid	Black	Yes	Determinate	Violet
RIJC-303	Mottle	RedBrown	No	Indeterminate	Violet
RIJC-304	Mottle	DarkPurple	No	Indeterminate	White
RIJC-305	Mottle	RedBrown	No	Indeterminate	White
RIJC-306	Solid	Black	Yes	Determinate	Violet
RIJC-307	Solid	Brown	No	Indeterminate	White
RIJC-308	Mottle	Brown	No	Indeterminate	Violet
RIJC-309	Solid	LightBrown	No	Indeterminate	White
RIJC-310	Mottle	Black	No	Determinate	Violet
RIJC-311	Solid	Purple	Yes	Determinate	White
RIJC-312	Solid	Black	Yes	Indeterminate	Violet
RIJC-313	Mottle	Brown	No	Determinate	Violet
RIJC-314	Mottle	Brown	No	Determinate	Violet
RIJC-315	Solid	Black	Yes	Determinate	Violet
RIJC-316	Solid	Black	Yes	Determinate	Violet
RIJC-317	Solid	RedBrown	Yes	Indeterminate	White
RIJC-318	Solid	DarkPurple	Yes	Indeterminate	Violet
RIJC-319	Mottle	DarkPurple	No	Determinate	Violet
RIJC-320	Solid	Black	Yes	Determinate	Violet
RIJC-321	Mottle	RedBrown	No	Indeterminate	White
RIJC-322	Mottle	Brown	No	Determinate	White
RIJC-323	Mottle	Brown	No	Indeterminate	Violet
RIJC-324	Solid	Black	Yes	Indeterminate	Violet
RIJC-325	Mottle	Purple	No	Indeterminate	White
RIJC-326	Mottle	Black	No	Determinate	Violet
RIJC-327	Solid	Purple	Yes	Determinate	White
RIJC-328	Solid	Black	Yes	Determinate	Violet
RIJC-330	Mottle	Brown	No	Indeterminate	Violet
RIJC-331	Solid	LightBrown	No	Determinate	White
RIJC-332	Mottle	DarkPurple	No	Determinate	White
RIJC-333	Solid	Purple	Yes	Determinate	White
RIJC-334	Solid	RedBrown	NO	Indeterminate	White
RIJC-335	Mottle	Brown	No	Determinate	White
RIJC-336	Solid	Brown	No	Indeterminate	White

Table A1. Parents and recombinant inbred line family Jamapa x Calima phenotypes (continued).

Genotype	Seed Color Pattern	Seed Color	Hypocotyl Pigment	Growth Habit	Flower Color
RIJC-337	Solid	Brown	Yes	Indeterminate	White
RIJC-338	Mottle	DarkPurple	No	Indeterminate	White
RIJC-339	Mottle	Brown	No	Determinate	White
RIJC-340	Mottle	Brown	No	Determinate	White
RIJC-341	Mottle	Black	No	Determinate	White
RIJC-342	Solid	Black	Yes	Determinate	Violet
RIJC-343	Solid	Purple	Yes	Indeterminate	White
RIJC-344	Mottle	Black	No	Determinate	Violet
RIJC-345	Mottle	Black	No	Determinate	White
RIJC-346	Mottle	Black	No	Indeterminate	Violet
RIJC-347	Mottle	Black	No	Indeterminate	Violet
RIJC-348	Solid	Black	Yes	Determinate	Violet
RIJC-349	Solid	Black	Yes	Indeterminate	Violet
RIJC-350	Solid	Black	Yes	Indeterminate	Violet
RIJC-351	Mottle	Brown	No	Indeterminate	Violet
RIJC-352	Solid	Brown	Yes	Indeterminate	White
RIJC-353	Mottle	DarkPurple	No	Determinate	White
RIJC-354	Mottle	Black	No	Determinate	White
RIJC-355	Solid	Black	Yes	Determinate	Violet
RIJC-356	Mottle	Brown	No	Determinate	Violet
RIJC-357	Solid	Black	Yes	Indeterminate	Violet
RIJC-358	Solid	Brown	Yes	Indeterminate	Violet
RIJC-359	Mottle	DarkPurple	No	Determinate	Violet
RIJC-360	Mottle	DarkPurple	No	Indeterminate	Violet
RIJC-361	Solid	Black	Yes	Indeterminate	Violet
RIJC-362	Mottle	Black	No	Determinate	Violet
RIJC-363	Solid	Black	Yes	Determinate	Violet
RIJC-364	Mottle	Brown	No	Determinate	Violet
RIJC-365	Solid	Black	Yes	Determinate	Violet
RIJC-366	Solid	Beige	Yes	Determinate	White
RIJC-367	Mottle	Brown	No	Determinate	Violet
RIJC-368	Mottle	Purple	No	Determinate	White
RIJC-369	Solid	Black	Yes	Determinate	Violet
RIJC-370	Solid	Black	Yes	Indeterminate	Violet
RIJC-371	Mottle	RedBrown	No	Indeterminate	White
RIJC-372	Mottle	Black	No	Determinate	Violet
RIJC-373	Mottle	Black	No	Determinate	White
RIJC-374	Mottle	Brown	No	Determinate	Violet
RIJC-375	Mottle	DarkPurple	Yes	Determinate	White

Table A1. Parents and recombinant inbred line family Jamapa x Calima phenotypes (continued).
Genotype	Seed Color Pattern	Seed Color	Growth Habit
Stampodo	Mottled	Brown	Indeterminate
	Solid	Dark Ped	Determinate
	Solid	Dark Red	Determinate
	Mottled	Brown	Determinate
	Mottled	Brown	Determinate
	Mottled	Brown	Determinate
	Mottled	Dark Ped	Determinate
	Mottled	Brown	Indeterminate
	Mottled	Brown	Determinate
	Mottled	Dark Red	Determinate
	Mottled	Brown	Determinate
RISR-010	Mottled	Brown	Determinate
RISR-011	Mottled	Brown	Determinate
RISR-012	Solid	Brown	Indeterminate
RISR-013	Mottled	Brown	Indeterminate
RISR-014	Mottled	Brown	Indeterminate
RISR-015	Solid	Dark Red	Indeterminate
RISR-016	Mottled	Brown	Determinate
RISR-017	Mottled	Dark Red	Determinate
RISR-018	Mottled	Brown	Determinate
<b>RISR-019</b>	Mottled	Dark Red	Indeterminate
RISR-020	Solid	Brown	Determinate
RISR-021	Mottled	Brown	Determinate
RISR-022	Solid	Dark Red	Indeterminate
RISR-023	Mottled	Dark Red	Determinate
RISR-024	Solid	Brown	Determinate
RISR-025	Mottled	Brown	Determinate
RISR-026	Mottled	Brown	Indeterminate
RISR-027	Solid	Dark Red	Determinate
RISR-028	Mottled	Dark Red	Indeterminate
RISR-029	Mottled	Dark Red	Determinate
RISR-030	Solid	Brown	Determinate
RISR-031	Mottled	Dark Red	Indeterminate
RISR-032	Mottled	Brown	Indeterminate
RISR-033	Mottled	Brown	Determinate
RISR-034	Mottled	Brown	Indeterminate
RISR-035	Mottled	Brown	Determinate
RISR-036	Solid	Brown	Indeterminate
RISR-037	Mottled	Dark Red	Determinate
RISR-038	Mottled	Brown	Determinate
RISR-039	Mottled	Dark Red	Determinate
RISR-040	Mottled	Brown	Determinate
RISR-041	Mottled	Dark Red	Determinate
RISR-042	Mottled	Dark Red	Indeterminate
RISR-043	Mottled	Brown	Determinate

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Genotype	Seed Color Pattern	Seed Color	Growth Habit
RISR-044	Mottled	Brown	Indeterminate
RISR-045	Mottled	Brown	Indeterminate
RISR-046	Mottled	Brown	Indeterminate
RISR-047	Mottled	Brown	Determinate
RISR-048	Solid	Dark Red	Indeterminate
RISR-049	Mottled	Brown	Indeterminate
RISR-050	Mottled	Brown	Determinate
RISR-051	Solid	Brown	Determinate
<b>RISR-052</b>	Mottled	Brown	-
RISR-053	Solid	Dark Red	Determinate
RISR-054	Solid	Dark Red	-
RISR-055	Mottled	Brown	Indeterminate
RISR-056	Mottled	Brown	Indeterminate
RISR-057	Solid	Brown	Indeterminate
RISR-058	Mottled	Brown	Indeterminate
RISR-059	Solid	Brown	Determinate
RISR-060	Solid	Brown	Determinate
RISR-061	Solid	Dark Red	-
RISR-062	Mottled	Brown	Determinate
RISR-063	Mottled	Brown	Determinate
RISR-064	Mottled	Brown	Determinate
RISR-065	Mottled	Brown	Indeterminate
RISR-066	Mottled	Dark Red	Indeterminate
RISR-067	Mottled	Brown	Indeterminate
RISR-068	Mottled	Brown	Indeterminate
RISR-069	Mottled	Brown	Indeterminate
RISR-070	Mottled	Brown	Determinate
RISR-071	Solid	Dark Red	Indeterminate
RISR-072	Mottled	Brown	Determinate
RISR-073	Mottled	Dark Red	Determinate
RISR-074	Mottled	Brown	Indeterminate
RISR-075	Mottled	Brown	Indeterminate
RISR-076	Mottled	Dark Red	Indeterminate
RISR-077	Mottled	Brown	Indeterminate
RISR-078	Mottled	Brown	Determinate
RISR-079	Mottled	Brown	Indeterminate
RISR-080	Mottled	Dark Red	Indeterminate
RISR-081	Mottled	Brown	Indeterminate
RISR-082	Mottled	Brown	Indeterminate
RISR-083	Mottled	Dark Red	Indeterminate
RISR-084	Mottled	Brown	Indeterminate
RISR-085	Mottled	Brown	Indeterminate
RISR-086	Mottled	Brown	Determinate
RISR-087	Mottled	Brown	Indeterminate
RISR-088	Mottled	Brown	Indeterminate

Genotype	Seed Color Pattern	Seed Color	Growth Habit
RISR-089	Solid	Brown	Indeterminate
<b>RISR-090</b>	Mottled	Brown	Indeterminate
RISR-091	Solid	Dark Red	Determinate
<b>RISR-092</b>	Mottled	Dark Red	Determinate
RISR-093	Mottled	Brown	Indeterminate
RISR-094	Mottled	Brown	Indeterminate
RISR-095	Solid	Dark Red	Determinate
RISR-096	Mottled	Brown	Determinate
RISR-097	Mottled	Brown	Determinate
RISR-098	Mottled	Brown	Indeterminate
RISR-099	Mottled	Brown	Indeterminate
RISR-100	Mottled	Dark Red	Determinate
RISR-101	Mottled	Brown	Indeterminate
RISR-102	Solid	Dark Red	Indeterminate
<b>RISR-103</b>	Mottled	Brown	Indeterminate
RISR-104	Solid	Brown	Determinate
RISR-105	Mottled	Dark Brown	Indeterminate
RISR-106	Mottled	Dark Brown	Indeterminate
RISR-107	Mottled	Brown	Indeterminate
RISR-108	Mottled	Dark Red	Determinate
RISR-109	Mottled	Dark Red	Indeterminate
RISR-110	Mottled	Dark Red	Determinate
RISR-111	Mottled	Brown	Indeterminate
RISR-112	Mottled	Dark Red	Determinate
RISR-113	Solia	Brown	Indeterminate
RISR-114	Nottled	Brown	Determinate
RISR-115	Mottled	Dark Red	Determinate
	Mottled	Dork Brown	Indeterminate
	Solid	Dark Drown	Dotorminate
	Mottled	Dark Brown	Indeterminate
RISR-120	Mottled	Brown	Indeterminate
RISR-121	Mottled	Brown	Indeterminate
RISR-122	Mottled	Brown	Determinate
RISR-123	Mottled	Dark Brown	Indeterminate
RISR-124	Solid	Dark Red	Determinate
RISR-125	Solid	Dark Red	Determinate
RISR-126	Mottled	Brown	Indeterminate
RISR-127	Mottled	Dark Red	Indeterminate
<b>RISR-128</b>	Mottled	Brown	Indeterminate
RISR-129	Mottled	Dark Red	Determinate
RISR-130	Mottled	Brown	Indeterminate
<b>RISR-131</b>	Solid	Dark Red	Determinate
RISR-132	Mottled	Dark Red	Indeterminate
RISR-133	Mottled	Brown	Determinate

Genotype	Seed Color Pattern	Seed Color	Growth Habit
RISR-134	Mottled	Dark Brown	Indeterminate
RISR-135	Mottled	Brown	Determinate
RISR-136	Mottled	Brown	Determinate
RISR-137	Solid	Brown	Determinate
RISR-138	Mottled	Brown	Indeterminate
RISR-139	Mottled	Brown	Determinate
RISR-140	Mottled	Brown	Determinate
RISR-141	Mottled	Dark Red	Determinate
RISR-142	Mottled	Dark Brown	Indeterminate
RISR-143	Mottled	Brown	Determinate
RISR-144	Mottled	Brown	Indeterminate
RISR-145	Mottled	Brown	Indeterminate
RISR-146	Mottled	Brown	Determinate
RISR-147	Mottled	Brown	Determinate
RISR-148	Mottled	Brown	Indeterminate
RISR-149	Solid	Brown	Indeterminate
RISR-150	Mottled	Dark Red	Determinate
RISR-151	Mottled	Brown	Determinate
RISR-152	Solid	Dark Red	Indeterminate
RISR-153	Mottled	Brown	Indeterminate
RISR-154	Mottled	Dark Brown	Indeterminate
RISR-155	Mottled	Dark Red	Indeterminate
RISR-156	Mottled	Brown	Determinate
RISR-157	Mottled	Dark Red	Indeterminate
RISR-158	Mottled	Brown	Determinate
RISR-109	Mottled	Brown	Determinate
RISR-100	Mottled	Brown	Indeterminate
	Solid	Brown	Indeterminate
DISD 163	Solid	Brown	-
RISR-164	Mottled	Dark Red	- Determinate
RISR-165	Solid	Brown	Indeterminate
RISR-166	Mottled	Brown	Determinate
RISR-167	Solid	Brown	Indeterminate
RISR-168	Solid	Dark Red	Indeterminate
RISR-169	Mottled	Brown	Indeterminate
RISR-170	Mottled	Brown	Determinate
RISR-171	Mottled	Brown	Determinate
RISR-172	Solid	Dark Red	Determinate
<b>RISR-173</b>	Mottled	Brown	Determinate
RISR-174	Mottled	Brown	Determinate
RISR-176	Mottled	Brown	Determinate
RISR-177	Mottled	Brown	Determinate
RISR-178	Mottled	Brown	Determinate
RISR-179	Mottled	Brown	Indeterminate

Genotype	Seed Color Pattern	Seed Color	Growth Habit
<b>RISR-180</b>	Mottled	Brown	Indeterminate
RISR-181	Mottled	Brown	Indeterminate
RISR-183	Mottled	Dark Red	Indeterminate
RISR-184	Solid	Brown	Determinate
<b>RISR-185</b>	Mottled	Brown	Indeterminate