A DIALLEL CROSS-BASED ANALYSIS OF THE GENETIC BASIS OF POD QUALITY AND POD YIELD IN SNAP BEAN

Njau SN[1]*, Arunga EE[1] and R Otsyula[2]

Serah Njau

*Corresponding author: njauserah23@gmail.com

ORCID: https://orcid.org/0000-0001-8797-4622 - Njau SN
ORCID: https://orcid.org/0000-0001-5265-9075 - Arunga EE

[1]Department of Water and Agricultural Resource Management, University of Embu, P.O Box 6-60100 Embu, Kenya

[2]Grain Legumes Section, Non-Ruminant Research Institute, Kenya Agricultural and Livestock Research Organisation, P.O Box 169-500100, Kakamega, Kenya

https://doi.org/10.18697/ajfand.132.24675   24020

ABSTRACT

Snap bean (*Phaseolus vulgaris* L.) is among the leading vegetables in Kenya that is mainly grown for export with the potential to increase household income. There are few programs in Kenya that focus on breeding new cultivars for increased production. The development of snap bean varieties that are resilient to the changing climate is crucial for sustainable agriculture in Kenya. To achieve this, knowledge of gene action, trait expression, and heritability is vital in effective breeding for quantitative traits like pod quality and yield. A study was conducted to investigate the inheritance of pod quality and yield traits in snap beans, which can inform the breeding of snap beans. A half diallel cross involving two indeterminate dry beans (G2333 and MCM 5001) and five determinate snap beans (Amy, Moonstone, Seagull, Serengeti and Vanilla) varieties was conducted. Data on pod traits (pod weight per plant, pod number per plant, pod length, pod diameter, pod wall fiber and pod suture string) were collected from 21 F_1s and 7 parents grown in two locations (Embu and Kirinyaga Counties) in Kenya. The results showed significant genotypic and environmental effects ($P < 0.001$) for all traits, with significant genotype by environment (G × E) interactions for most traits. Additionally, general combining abilities (GCA) and specific combining abilities (SCA) were significant for all traits evaluated. The significance of GCA and SCA indicated the importance of both additive and non-additive gene effects in controlling the traits, although the additive gene effects were predominant. The study revealed that Vanilla and Serengeti had the highest GCA estimate for pod quality traits, while G2333 and MCM5001 had the highest GCA estimate for pod yield traits. Snap bean pod yield and quality are quantitative traits controlled by multiple genes and influenced by the environment. Therefore, the predominance of additive gene effects suggests that selection for these traits in segregating generations could yield satisfactory gains. The results of this study could impact the development of snap bean varieties that are more resilient to the effects of climate change. Thus, improving the sustainability and productivity of the agriculture sector in Kenya.

Key words: Snap bean, GCA, SCA, gene action, heritability, combining ability

24021

INTRODUCTION

Agriculture is the cornerstone of most African economies, contributing as much as 55% to the continent's gross domestic product [1]. Agriculture serves as the foundation for food security in Africa and acts as the primary livelihood for about 85% of the population, who depend on rain-fed farming [2]. According to Omotoso *et al.* [3], agricultural output in sub-Saharan Africa has declined consistently over the past five decades. The diminishing performance of agriculture in sub-Saharan Africa can be attributed to factors such as climate change, limited incentives for intensification, challenges in accessing markets, unfavourable geographical features, soil quality issues, and insufficient policy frameworks [4].

Snap beans (also referred to as either French or green beans) are the immature pods of the common bean (*Phaseolus vulgaris* L.), which are either consumed as a fresh produce or processed for canning [5]. The immature green snap bean pods are tender and contain protein, carbohydrate, vitamin C, vitamin K, and carotenoids, which are lacking in the dry common bean [6]. The snap bean sub-sector has been a major contributor to the growth of the Kenyan economy due to its potential to generate foreign exchange and create employment opportunities for women and the youth [7]. The crop holds the second position in vegetable export in Kenya after Asian vegetables supported by over 1 million people. Snap bean is grown for both the local and export markets with 34 percent of the produce exported to the European Union export market [8]. To date, publicly funded snap bean improvement has been less successful in Kenya than equivalent programmes focusing on dry bean. This relative lack of success reflects a poor level of understanding of the genetic basis of both pod quality and pod yield traits [9].

Pod yield, pod quality and stability, which depend on plant architectures, pod traits, and resistance to biotic and abiotic stresses are the most important economic traits in snap bean [10]. A number of aspects of pod morphology including pod length, colour, sieve size, cross-sectional shape, straightness, the length of pod suture strings, the nature of the pod wall fibre and the overall flavour of the product are important for the determination of pod quality [11]. With respect to snap bean breeding for the fresh market and the processing industry, pod quality traits are paramount determinants of marketability, prices consumers are willing to pay and adoption of the new varieties by the farmers [10, 11]. Most of the traits associated with snap bean pod yield and pod quality are quantitative in nature, which is a challenge in the development of new cultivars.

The effectiveness of a crop improvement programme is enhanced when the genetic basis of the key traits under selection is well understood, since this knowledge can be deployed to select the most appropriate breeding strategy [12, 13]. The initial

24022

stage of a breeding program is hybridization of contrasting genitors that display traits of interest. Combining ability estimation can be used to determine the usefulness of the parents in hybrid combinations. Selection of superior parents of hybridization is very crucial because hybrid performance is related to the GCA and SCA of the parents involved in the cross. The diallel cross has proven to be an informative means of evaluating the nature of the gene action underlying a given quantitative trait [14]. In particular, the analysis generates estimates of both the general combining ability (GCA) and specific combining ability (SCA) and heritability from fixed, or non-random parents, which are informative with respect to the genetic basis of trait variation. Bahari *et al*. [15] described how its deployment was able to raise the efficiency and effectiveness of a snap bean improvement programme. The objective of this study was to use this diallel cross method to determine the genetic basis of various key pod quality and pod yield traits, especially in the situation where dry bean germplasm was being introduced to broaden the genetic base of the snap bean genepool. The results of this study will be useful to the snap bean breeding program in Kenya for efficiency and effectiveness in the development of potential and productive varieties with marketable pod quality and yield traits while increasing resilience and productivity despite climate change challenges.

MATERIALS AND METHODS

Plant Materials
A half diallel cross was established using five snap bean commercial varieties (Serengeti, Vanilla, Amy, Seagull and Moonstone) and two dry bean accessions {G2333 and MCM 5001 (Table 1). The purpose of including the dry bean accessions was to assess their potential in snap bean improvement. The Mexican landrace G2333 from the International Centre for Tropical Agriculture (CIAT) is a widely used source of resistance against the fungal disease anthracnose (causative pathogen *Colletotrichum lindemuthianum*), while MCM 5001 which is a breeding line from CIAT has been adopted as a source of resistance against bean common mosaic necrosis virus (a member of the genus *Potyvirus* in the family *Potyviridae*) [16].

Experimental Design
The 21 F_1 hybrids and the seven parental lines were set in an experiment at two different locations in central Kenya at Mwea (Kirinyaga County) and Rupingazi (Embu County). The experimental design was a randomized complete block design (RCBD) with three replicates. The intra-row spacing between plants was 20 cm, and the inter-row spacing was 50 cm. Each plot size was 2 m long and 50 cm wide. Spaces between plots were 50 cm wide. The experimental plots were ploughed and harrowed to achieve a moderate tilth seedbed. Fertilizer application was diammonium phosphate (DAP) of 200 kg ha^{-1} at planting. At flowering, a top-

24023

dressing fertilizer of 100 kg ha^{-1} calcium ammonium nitrate (CAN) fertilizer was applied. Plants were sprayed to control aphids, thrips, and white flies.

Data Collection

Data were collected on plant height, pod length, pod diameter, pods per plant, pod weight per plant, pod suture string and pod wall fiber. Harvesting was done at intervals of two days. Five pods from each variety were randomly selected and boiled in a water bath for 30 min at 100° C to evaluate the pod suture string. After boiling, the pod's strings were gently pulled from the calyx along the adaxial suture of the pod. String length was calculated as a ratio of pod suture string length to total pod length [5]. The average pod suture string ratio values among the five pods were used for analysis. Pod length was measured using a ruler and pod diameter was determined by passing the pods through a ruler (Royal Sluis®) with varied pod diameters. The number of pods per plant was estimated by counting the total number of pods in a plot and dividing the total by the number of plants in the plot. Pod weight per plant was calculated by weighing the pods in a plot and dividing the total pod weight by the number of plants in the plot.

Data Analysis

The analysis of variance (ANOVA) of diallel was performed using the DIALLEL-SAS05 program, Zhang *et al*. [17]. This program is considered as an effective method in analyzing and interpreting diallel cross data, which are conducted in multiple environments. Estimates of GCA and SCA effects were achieved using the methodology proposed by Griffing, [18] for analysis of diallel with parents and F$_1$ (Method 2), considering fixed effects of treatments (Model 1), with the genetic statistical model of:

$Y_{ijkl} = \mu + g_i + g_j + s_{ij} + b_k + e_{ijkl}$.. Equation (1)

Where: Y_{ijkl} = observed value of the cross between parent i and j; μ = overall mean; g_i = GCA effect of parent i; g_j = GCA effect of parent j; s_{ij} = SCA of the cross between parents i and j; b_k = effect of the kth block; e_{ijkl} = experimental error associated with the ijklth individual observation.

The magnitude of additive and non-additive effects was determined by the ratio between GCA and SCA mean squares following the general predicted ratio (GPR) GCA/SCA = 2 MSGCA/ (2MSGCA + MSSCA) [19]. The closer this ratio is to 1, the greater the predictability based on GCA.

Furthermore, the broad sense heritability (H^2) of the traits was determined using below formula:

$H^2 = Vg/Vp$……………………………………………………… Equation (2)

Where H^2: broad sense heritability, Vg: genetic variance and Vp: phenotypic variance [20].

RESULTS AND DISCUSSION

The analysis of variance established that significant genotypic and environmental effects ($P < 0.001$) were recorded for each of the traits with a significant genotype by environment (G×E) effect ($P < 0.001$) for all the traits except number of pods per plant and pod weight per plant (Table 2). The presence of significant variations among the genotypes indicated that a considerable genetic diversity existed among the parents for the traits evaluated. The common bean genepool is very diverse, encompassing variation in plant morphology. Intensive selection has greatly narrowed the genetic base of snap beans, although there is much potential for introducing novel variation by making crosses with dry beans [21, 22, 23], which have a much broader genetic base [24, 25]. As is the case for most snap bean varieties, those used for this experiment belong to the Andean genepool, while the two dry bean accessions are both Mesoamerican types; mixing these two distinct genepools is known to release much variability [16, 26]. While the existence of a significant degree of G×E interaction complicates the selection of widely adapted genotypes, the predominance of additive gene effects implies that genetic gain should be relatively easy to achieve [27, 28]. The estimated broad sense heritability (H^2) values for number of pods per plant, pod weight per plant, pod length, pod diameter and pod string were 0.79, 0.80, 0.91, 0.95, and 0.81, respectively. The favourable estimates of the heritability of all of the pod quality and yield traits (ranging from 0.79 to 0.95) were consistent with the findings of Singh *et al.* [29], who also observed high levels of broad sense heritability for pod weight per plant and number of pods per plant; the implication is that early generation selection for these important traits should be effective.

The GCA and SCA effects were significant ($P < 0.001$) for each trait. The closer of the GCA/SCA ratio to the unity (one) implied that additive gene effects predominated. Gomes *et al.* [30] have reported substantially sized GCAs for pod length, pod width and pod thickness. The snap bean market prefers long, slender pods with minimal pod wall fibre and short (if any) suture strings, thus, alleles that favour these traits are important [5, 9, 31, 32]. Vanilla and Serengeti are both important commercial varieties in the Kenyan market. They both displayed the largest GCAs for the pod quality traits. Therefore, they are prime candidates as parents in programmes seeking to breed high quality snap bean varieties to address competitiveness issues in the global market. The two dry bean entries (G2333 and MCM 5001) were the highest pod yielders, but their pods had large pod width and more fibrous. Among the F_1 hybrids, the highest number of pods per plant were largely confined to combinations involving a snap bean variety and a

24025

dry bean accession. The best performing hybrid with respect to number of pods per plant and pod length was the cross Moonstone × Vanilla.

The estimated GCA and SCA for each trait are presented as Table 3. The two dry bean accessions recorded positive and high GCAs for both number of pods per plant and pod weight per plant, while the snap bean varieties Serengeti and Vanilla excelled for both pod diameter and pod length. Based on the SCA, two crosses (Amy × G2333 and Amy × Moonstone) were identified as good combiners for number of pods per plant and five crosses (Amy × G2333, Amy × Moonstone, G2333 × Seagull, G2333 × Vanilla and MCM 5001 × Serengeti) for pod weight per plant. Five of the crosses (Amy × Serengeti, G2333 × Seagull, Moonstone × Serengeti, Moonstone × Vanilla and Serengeti × Vanilla) generated a significant SCA effect for pod length, two crosses (Amy × MCM 5001 and Moonstone × Serengeti) for pod diameter and four (Amy × MCM 5001, Amy × Serengeti, G2333 × Seagull and G2333 × Serengeti) for pod string (Table 3).

The findings of this study are consistent with the observations reported by Trindade *et al.* [33], who showed that, in crosses between dry and snap bean lines, GCAs were significant for all traits except for fibre content. The indeterminate growth habit of the two dry bean accessions used in this study contributed not only to raising pod yield, but also to the plants' resistance to key pathogens. However, they had a negative effect on pod quality, a feature, which will need correction through backcrossing to established snap bean types. The significant SCA effect implies that dominance is also a determining factor of trait expression and that complementarity exists among potential parents [12, 27, 30]. Pod quality traits are vital for snap bean breeding for both the fresh market and the canning industry [10]; thus, selection in the progeny generated from each of the Amy × Serengeti, Moonstone × Serengeti and Moonstone × Vanilla crosses has the potential to identify improved snap bean varieties for sustainable agriculture, food security and poverty alleviation.

CONCLUSION AND RECOMMENDATIONS FOR DEVELOPMENT

Key snap bean traits with respect to both pod quality and pod yield are mainly controlled by multiple genes and are influenced by environmental variations. The quantitative nature of the traits has important implications for the design of snap bean breeding programmes. However, this study demonstrated the predominance of additive gene effects and high heritability estimates for pod yield and quality traits, indicating that significant genetic gains can be achieved during the selection of segregating populations. Moreover, the study identified superior combiners that can serve as parents for enhancing various traits, including dry bean varieties which can be utilized to expand the genetic diversity of snap beans. The findings of

this research have the potential to facilitate the development of snap bean cultivars that can better withstand the impacts of climate change, thereby enhancing the sustainability and productivity of Kenya's agricultural sector while addressing food insecurity and alleviating poverty.

ACKNOWLEDGEMENTS

Conflict of Interest
The authors declare no conflict of interest.

Table 1: Characteristics of the parental genotypes

Genotype	Pod length (Cm)	Pod diameter (mm)	Pod shape & curvature	Pod colour	Maturity
Serengeti	14-16 cm	6-8mm	Circular and straight	Uniform dark green glossy	55 days
Moonstone	13-15 cm	6-9mm	Circular and straight	Uniform dark green glossy	55 days
Seagull	13-14 cm	6.5-9mm	Circular and straight	Medium dark green	65 days
Vanilla	13-14 cm	6.5-9mm	Circular and straight	Uniform dark green	65 days
Amy	10-12 cm	5-6.5mm	Circular and straight	Uniform dark green glossy	55-60 days
G2333	9-12 cm	8.5-9.5 mm	Flat and straight	Uniform light green dull	39 days
MCM 5001	8-10 cm	9-10 mm	Flat and straight	Uniform light green dull	45 days

Source: https://www.royalseed.biz/, http://shamrockseed.com *accessed on 20th March 2023.*

Table 2: Analysis of variance for the various pod quality and yield traits, along with estimates for their heritability

Source of variation	d.f.	Mean Squares				
		Pods plant^{-1}	Pod weight plant^{-1} (g)	Pod length (cm)	Pod diameter (mm)	Pod suture string (ratio)
Environment (E)	1	11123.15***	64550.64***	3.95***	3.17***	0.04*
Rep (E)	4	1021.92*	16392.16**	0.15ns	0.04ns	0.05**
Genotype (G)	27	1850.93***	25574.02***	5.57***	2.15***	0.11***
G×E	27	429.85ns	5231.01ns	0.48*	0.12**	0.02**
GCA	6	4063.68***	62618.25***	17.80***	8.69***	0.34***
SCA	21	1218.71***	14989.96***	2.08***	0.28***	0.04***
GCA × E	6	799.02*	10010.59*	1.06**	0.16**	0.04**
SCA × E	21	324.38ns	3865.41ns	0.32ns	0.09*	0.01ns
Residuals	108	326.22	3462.70	0.27	0.05	0.01
Heritability (H^2)		0.79	0.80	0.91	0.95	0.81
GCA/SCA Ratio		0.87	0.89	0.94	0.98	0.94
Mean		50.62	154.49	11.39	7.71	0.48
LSD (0.05)		22.34	79.26	0.83	0.44	0.15

***, **, *: means differ significantly from one another at, respectively $P < 0.001$, 0.01 and 0.05.
ns: non-significant

Table 3: Estimated GCA and SCA effects for the various pod quality and yield traits

Genotype	Traits				
	Pods plant^{-1}	Pod weight plant^{-1} (g)	Pod length (cm)	Pod diameter (mm)	Pod suture string (ratio)
GCA effects					
Amy	-5.34*	-22.81**	0.01	-0.27***	-0.01
G2333	11.9***	51.56***	-0.35***	0.54***	0.07***
MCM 5001	10.77***	38.44***	-0.87***	0.62***	0.14***
Moonstone	3.64	10.27	0.16*	-0.12**	-0.03**
Seagull	-6.46**	-29.49**	-0.20**	-0.23***	-0.01
Serengeti	-8.90**	-33.36***	0.27**	-0.32***	-0.07***
Vanilla	-5.60*	-14.60*	0.98***	-0.23***	-0.09***
SCA effects					
Amy × G2333	17.39*	54.00*	-0.08	-0.03	-0.07
Amy × MCM 5001	5.86	12.84	-0.31	-0.22*	-0.12**
Amy × Moonstone	32.49***	108.42***	-0.22	0.59***	0.04
Amy × Seagull	-0.75	-10.77	0.13	-0.13	0.04
Amy × Serengeti	-1.64	4.20	1.37***	0.00	-0.12**
Amy × Vanilla	-6.61	-22.84	0.03	0.12	-0.01
G2333 × MCM 5001	-13.22	-48.42	0.37	0.07	0.08*
G2333 × Moonstone	7.91	24.95	-0.24	0.16	0.03
G2333 × Seagull	2.00	40.96	0.48*	0.12	-0.05
G2333 × Serengeti	12.45	47.07*	-0.35	0.30**	-0.12**
G2333 × Vanilla	12.82	51.64*	-0.52*	0.07	-0.05
MCM 5001 × Moonstone	5.04	18.66	-0.20	-0.12	-0.13
MCM 5001 × Seagull	7.63	33.08	-0.08	-0.05	-0.02
MCM 5001 × Serengeti	13.08	52.51*	-0.10	0.32**	0.00
MCM 5001 × Vanilla	1.12	5.77	-0.63**	-0.06	-0.08
Moonstone × Seagull	-7.07	-37.60	0.22	-0.11	-0.09*
Moonstone × Serengeti	6.21	15.77	0.59**	-0.18*	-0.01
Moonstone × Vanilla	-5.92	-12.07	0.76***	-0.14	0.02
Seagull × Serengeti	4.47	-0.25	0.26	-0.17	0.03
Seagull × Vanilla	11.34	21.90	-0.69**	0.16	0.08*
Serengeti × Vanilla	-10.72	-26.49	0.54*	-0.01	0.05

REFERENCES

1.   **AGRA.** Africa agriculture status report: The business of smallholder agriculture in Sub-Saharan Africa, 2017. https://agra.org/wp-content/uploads/2017/09/Final-AASR-2017-Aug-28.pdf *Accessed 10 March 2024.*

2.   **Kogo BK, Kumar L and R Koech** Climate change and variability in Kenya: a review of impacts on agriculture and food security. *Environment, Development and Sustainability,* 2021; **23(1)**: 23-43.

3.   **Omotoso AB, Letsoalo S, Olagunju KO, Tshwene CS and AO Omotayo** Climate change and variability in sub-Saharan Africa: A systematic review of trends and impacts on agriculture. *Journal of Cleaner Production*, 2023; 137487.

4.   **Farooq MS, Uzair M, Raza A, Habib M, Xu Y, Yousuf M and M Ramzan Khan** Uncovering the research gaps to alleviate the negative impacts of climate change on food security: a review. *Frontiers in Plant Science,* 2022; **13**: 927535.

5.   **Hagerty CH, Cuesta-Marcos A, Cregan P, Song Q, McClean P and JR Myers** Mapping snap bean pod and color traits, in a dry bean× snap bean recombinant inbred population. *Journal of the American Society for Horticultural Science*, 2016; **141(2)**: 131-138. https://doi.org/10.21273/JASHS.141.2.131

6.   **Myers JR and K Kmiecik** Economic importance and relevance to biological science research. In the Common Bean Genome; Springer: Cham, Switzerland, 2017; pp. 1–20.

7.   **Mwangi SC, Mbatia O and JM Nzuma** Effects of Exchange Rate Volatility on French Beans Exports in Kenya, 2014.

8.   **HCDA.** Export statistics for horticultural crops, 2011.

9.   **Myers JR and JR Baggett** Improvement of snap bean. In: p 289–329, Singh SP, ed., Common bean improvement in the twenty-first century. Kluwer Academic Publishers, Dordrecht, Netherlands, 1999.

10.   **Singh BK and B Singh** Breeding perspectives of snap beans (*Phaseolus vulgaris* L.). *Vegetable Science,* 2015; **42(1)**:1-17.

11. **Njau SN** Selection for yield potential, disease resistance and canning quality in runner and snap bean lines and populations. *MSc Thesis*, University of Nairobi, 2016.

12. **Cruz Baldissera JN, Bertoldo JG, Valentini G, Coan MMD, Rozeto DS and AF Guidolin** Uso do melhor preditor linear não-viesado (BLUP) na predição de híbridos em feijão. *Bioscience Journal,* 2012; **28**:395-403.

13. **Oghan HA, Vahed MM, Ataei R and M Gholamhosseini** Identification of superior parents and hybrids for improving canola production under optimum and late sowing conditions. *Euphytica,* 2018; **214(6)**: 91. https://doi.org/10.1007/s10681-018-2169-4

14. **Gilbert NEG** Diallel cross in plant breeding. *Heredity*, 1958; **12(4)**: 477-492.

15. **Bahari M, Rafii MY, Saleh GB and MA Latif** Combining ability analysis in complete diallel cross of Watermelon [*Citrullus lanatus* (Thunb.) Matsum. and Nakai]. *Scientific World Journal*, 2012; **Article ID 543158:** 6 pages. https://doi.org/10.1100/2012/543158

16. **Okii D, Mukankusi C, Sebuliba S, Tukamuhabwa P, Tusiime G, Talwana H and P Gepts** Genetic variation, heritability estimates and GXE effects on yield traits of Mesoamerican common bean (*Phaseolus vulgaris* L) germplasm in Uganda. *Plant Genetic Resources*, 2018; **16(3)**: 237. https://doi.org/10.1017/S1479262117000259

17. **Zhang Y and MS Kang** DIALLEL-SAS: A SAS program for Griffing's diallel analyses". *Agronomy Journal*, 1997; **89(2)**:176-182. https://doi.org/10.2134/agronj1997.00021962008900020005x

18. **Griffing B** Concept of general and specific combining ability in relation to diallel crossing systems. *Australian Journal of Biological Sciences*, 1956; **9**: 463-493. https://doi.org/10.1071/BI9560463

19. **Baker RJ** Issues in diallel analysis. *Crop Science*, 1978; **18(4)**: 533- 536. https://doi.org/10.2135/cropsci1978.0011183X001800040001x

20. **Acquaah G** Principles of Plant Genetics and Breeding. UK: Blackwell Publishing, 2007; pp. 128–134.

21.   **Métais I, Hamon B, Jalouzot R and D Peltier** Structure and level of genetic diversity in various bean types evidenced with microsatellite markers isolated from a genomic enriched library. *Theoretical and Applied Genetics*, 2002; **104(8)**:1346-1352. https://doi.org/10.1007/s00122-002-0901-9

22.   **Krause W, Rodrigues R and NR Leal** Capacidade combinatória para características agronômicas em feijão de vagem. *Revista Ciência Agronômica*, 2012; **43**:522-531.

23.   **Machado JC, Souza JCD, Ramalho MAP and JL Lima** Stability of combining ability effects in maize hybrids. *Scientia Agricola*, 2009; **66**:494-498. https://doi.org/10.1590/S0103-90162009000400010

24.   **Singh SP** Broadening the genetic base of common bean cultivars: a review. *Crop Science,* 2001; **41**:1659-1675. https://doi.org/10.2135/cropsci2001.1659

25.   **De Ron AM, Casquero PA, González AM and M Santalla** Environmental and genotypic effects on pod characteristics related to common bean quality. *Journal of Agronomy and Crop Sciencei*, 2004; **190(4)**:248-255. https://doi.org/10.1111/j.1439-037X.2004.00098.x

26.   **Lobaton J, Miller T, Gil J, Ariza D, de la Hoz J, Soler A, Beebe S, Duitama J, Gepts P and B Raatz** Re-sequencing of common bean identifies regions of inter-gene pool introgression and provides comprehensive resources for molecular breeding. *Plant Genome,* 2018; **11**: 170068. https://doi.org/10.3835/plantgenome2017.08.0068

27.   **Oliveira GHF, Buzinaro R, Revolti LTM and CHB Giorgenon** An accurate prediction of maize crosses using diallel analysis and best linear unbiased predictor (BLUP). *Chil. Journal of Agricultural Research,* 2016; **76**: 294-299. http://dx.doi.org/10.4067/S0718-58392016000300005

28.   **Rocha FD, Stinghen JC, Gemeli MS, Coimbra JLM and AF Guidolin** Diallel analysis as a tool when selecting parents for beans. *Revista Ciência Agronômica,* 2014; **45**: 74-81. https://doi.org/10.1590/S1806-66902014000100010

29. **Singh DK, Singh DP and SS Singh** Studies of genetic variability, heritability and genetic advance for yield and related traits in French bean (*Phaseolus vulgaris* L.). *Journal of Pharmacognosy and Phytochemistry*, 2018; **7**: 236-240.

30. **Gomes ABS, Oliveira TRA, Gravina GA, Cruz DP, Sant'Anna CQSS, Daher RF and IM Pereira** Combining ability in snap bean lines in Brazil. *Genetics and Molecular Research*, 2019; **18(2)**: GMR 18214. DOI http://dx.doi.org/10.4238/gmr18214

31. **Parker TA, Berny Mier Y, Teran JC, Palkovic A, Jernstedt J and P Gepts** Pod indehiscence is a domestication and aridity resilience trait in common bean. *New Phytologist* 2020; **225**:558-570. https://doi.org/10.1111/nph.16164

32. **Parker T, Cetz, J, de Sousa L, Kuzay S, Lo S, Floriani T, Njau S, Arunga E, Duitama J, Jernstedt J, Myers J, Llaca V, Herrera-Estrella A and P Gepts** Loss of pod strings in common bean is associated with gene duplication, retrotransposon insertion, and overexpression of PvIND." *New Phytologist*, 2022; **235**:2454–2465. https://doi.org/10.1111/nph.18319

33. **Trindade RDS, Antonio TDAJ, Rosana R, Jose MSV, Messias GP and SAG Leandro** Combining ability for morpho-agronomic traits in common bean and snap bean. *African Journal of Agricultural Research*, 2011; **6(29)**: 6240-6245. https://doi.org/10.5897/AJAR11.1585