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## GENETICS OF CULTIVATED PLANTS AND THEIR WILD RELATIVES

Original article  
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## Genetic control of yield components in green beans (*Phaseolus vulgaris* L.)

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**Background.** This work aimed at using Hayman's methodology to study the inheritance of some quantitative traits, such as the number of pods per plant, pod length, mean pod weight, and yield per plant in 15 diallel hybrids of six green bean cultivars.

**Materials and methods.** The research was carried out at the Experimental Center of Universidad Nacional de Colombia – Sede Palmira (CEUNP). A randomized complete block experimental design with four replications was used.

**Results.** For most of the traits, except yield per plant, the additive-dominant model was adequate. Non-additive effects with overdominance controlled the number of pods per plant, pod length, and mean pod weight. Most of the characters presented an unequal proportion of positive and negative genes in the loci ( $H_1 < H_2$ ). The asymmetric distribution of genes in the parents ( $H_2/4H_1$ ) was below the maximum value (0.25), except for the character "number of pods per plant". The  $K_D/K_R$  ratio confirmed for most of the traits that there was an excess of recessive alleles over dominant alleles. Dominance effects ( $h^2$ ) for most characters suggested that the substantial contribution of dominance was not due to heterogeneity of loci in these characters. The narrow-sense heritability was moderate to low. The correlation coefficient  $r$  ( $Y_r; W_r + V_r$ ) indicated that dominant genes were responsible for the increased number of pods per plant and recessive genes for increased pod length and mean pod weight.

**Conclusions.** Conventional breeding methods like pedigree selection could be employed to improve the characters "pod length" and "mean pod weight", and for the number of pods per plant, management of segregating populations should employ the single-seeded descent method.

**Keywords:** diallel analysis, additive effects, dominant effects, epistasis, genetic parameters

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# ГЕНЕТИКА КУЛЬТУРНЫХ РАСТЕНИЙ И ИХ ДИКИХ РОДИЧЕЙ

Научная статья

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## Генетический контроль компонентов урожайности овощной фасоли (*Phaseolus vulgaris* L.)

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**Актуальность.** Цель данной работы – изучение с помощью методологии Хаймана наследования некоторых количественных признаков, таких как количество бобов на растение, длина боба, средний вес боба и урожай бобов с растения у 15 диаллельных гибридов шести сортов овощной фасоли.

**Материалы и методы.** Исследования проводились в Экспериментальном центре Национального университета Колумбии – Пальмира (CEUNP). Использовалась рандомизированная полноблочная экспериментальная схема с четырьмя повторностями.

**Результаты.** Для большинства признаков, за исключением урожайности с одного растения, адекватной была аддитивно-доминантная модель. В контроле количества бобов на растение, длины боба и средней массы боба преобладали аддитивные эффекты (наследование по типу сверхдоминирования). Для большинства признаков наблюдалось неодинаковое соотношение генов с положительными и отрицательными эффектами в локусах ( $H_1 < H_2$ ). Неравномерное распределение генов у родителей ( $H_2/4H_1$ ) было ниже максимального значения (0,25), за исключением признака «количество бобов на растение». Отношение  $K_D/K_R$  указывало на преобладание рецессивных аллелей над доминантными для большинства признаков. Эффекты доминирования ( $h^2$ ) для большинства признаков свидетельствуют о том, что существенный вклад доминирования не был обусловлен гетерогенностью локусов по этим признакам. Наследуемость в узком смысле была умеренной или низкой. Значения коэффициента корреляции  $r$  ( $Yr; Wr + Vr$ ) свидетельствовали о том, что доминантные гены отвечают за увеличение количества числа бобов на растение, а рецессивные гены – за увеличение длины боба и его средней массы.

**Выводы.** Традиционные методы селекции, такие как метод педигри, могут быть использованы для улучшения признаков длины бобов и среднего веса бобов, а для числа бобов на растение в работе с расщепляющимися популяциями необходимо использовать метод отбора единичных семян.

**Ключевые слова:** диаллельный анализ, аддитивные эффекты, доминантные эффекты, эпистаз, генетические параметры

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## Introduction

Green beans are unripe fruits of common bean (*Phaseolus vulgaris* L.) which are consumed fresh or processed. They are a good source of nutrients and bioactive compounds, as well as proteins, carbohydrates, fiber, and vitamins (Fabbri, Crosby, 2016). It is the sixth most important vegetable in Colombia, in terms of area (5,584 hectares) and production, (45,124 tons) (Agronet, 2020). A way to increase productivity of this crop is utilization of genetic improvement programs aimed at obtaining high-yielding cultivars (varieties). While there have been huge investments, the success rate has been slow and very low, and therefore the challenge of green bean productivity persists.

Genetic studies to establish the mode of inheritance, gene action and gene effects of major quantitative traits in green bean are scarce in the literature. Knowledge of the nature and magnitude of the genetic effects is essential for the selection process and to know the behavior of segregating generations (Cruz et al., 2004). During the execution of the improvement program, the methods to be followed or the size of the population to be carried out should be taken into account. Therefore, it is necessary to invest in programs that can favor the generation of superior genotypes, increasing the economic benefits for farmers.

Green bean pod yield is a highly complex trait, controlled by hundreds or thousands of genes with very small effects, which makes it difficult to study. However, yield components exhibit simpler heritability and, therefore, the selection progress achieved by selecting these components may be greater than selecting directly for yield. Knowledge of the nature and magnitude of the genetic effects controlling yield components is helpful in planning and executing a breeding program (Venkovsky, Barriga, 1992).

The crossing systems or mating designs allow to know and evaluate the genetic effects of quantitative traits, as well as to identify and select superior genotypes and design the most efficient breeding methods. Regarding diallel analysis methods, C. A. Cruz et al. (2012) mention the method proposed by B. Griffing (1956), C. O. Gardner and S. A. Eberhart (1966), and the method proposed by B. I. Hayman (1954a, 1954b). Hayman's method is based on the knowledge of the environmental and genetical parameters, such as means, variance, and covariance, obtained from the diallel analysis (Cruz et al., 2012). This methodology provides an efficient study of the gene action involved in the control of traits and identifies the presence of epistatic interactions, also estimates the genetic component of genotype determination and selection limit that can be obtained in segregating generations from the evaluated parents. The present study was conducted to investigate the gene effects that control genetic control of yield components in green beans, using the diallel analysis methodology.

## Materials and methods

Six green bean genotypes: two commercial cultivars 'Blue Lake' from Ferry Morse Company (G17723) and 'UNAPAL-Milenio' from Universidad Nacional de Colombia – Sede Palmira (G51158), and four lines from the world bean collection of the Genetic Resources Unit, International Center for Tropical Agriculture (URG-CIAT), previously selected by the Vegetable Program of Universidad Nacional de Colombia – Sede Palmira (G23956, G20400, G18212, and G16806), were subjected to a complete diallel cross design in all possible combinations without reciprocal crosses. The evaluation of

the 21 genotypes (six parents and 15 hybrids) was carried out in the second semester of 2019 and first semester of 2020, at the Experimental Center of the Universidad Nacional de Colombia – Sede Palmira (CEUNP), located in the municipality of Candelaria (26°C; 1,000 m.a.s.l.; annual rainfall 1,028 mm; relative humidity 75%) (Ortiz et al., 2020).

A randomized complete block experimental design with four replications was applied. The experimental unit consisted of eight plants, in furrows 8 m long with a 1.50 m distance between furrows and 1 m distance between plants. Four central plants were evaluated. The following characteristics were analyzed: a) number of pods per plant (NPP), all pods with at least one viable seed on each plant sampled were counted (was recorded from the four selected plants from each plot); b) pod production per plant (PPP), the weight of all pods per plant, expressed in kilograms (based on the pods collected in the experimental unit); c) mean pod weight (MPW), the ratio of pod production per plant over the number of pods per plant, expressed in grams; and d) pod length (PL), the pod measured from its insertion in the pedicel to the free apex end, the average length of ten pods per experimental unit taken and expressed in centimeters.

The validity of the genetic information of the recorded data was based on the genetic assumptions formulated by B. I. Hayman (1960). To verify whether the data fit the additive-dominant model (absence of epistasis), the sufficiency test was based on linear regression analysis of  $W_r$  on  $V_r$ , testing the significance of the regression coefficient ( $H_0: b = 1$  vs.  $H_a: b \neq 1$ ), the regression should result in a regression coefficient not significantly different than one ( $b = 1$ ). If  $b \neq 1$ , significant epistatic effects were assumed; in this case a second test was applied after weighing the values of  $W_r$  and  $V_r$ , the test ( $t_2$ ) with rotation of the  $W_r$  axis on the  $V_r$  axis at  $45^\circ$ , followed by a new regression coefficient ( $H_0: b = 0$  vs.  $H_a: b \neq 0$ ),  $b$  was expected to be no different from 0 (zero); the nonsignificant value of the  $t_2$  test also confirmed the absence of non-allelic interaction and, therefore, the genes would be independent in their action for the random association. The failure of these tests completely invalidates the additive-dominant model (Mather, Jinks, 1982). The different genetic components and parameters of variation were calculated, based on standard procedures (Hayman, 1954a, b; Singh, Chaudhary, 1999), only for those characteristics that fit the additive-dominant model: we estimated  $D$  (genetic component related to additive effects);  $H_1$  and  $H_2$  (dominance deviations);  $h^2$  (dominant gene action);  $F$  (frequency of dominant and recessive alleles between parents);  $E$  (environmental variance component); and the following genetic parameters:  $(H_1/D)^{1/2}$  (mean degree of dominance);  $H_2/4H_1$  (symmetry of allele distribution between parents);  $K_D/K_R$  (dominant/recessive ratios);  $h^2/H_2$  (number of genes with dominance);  $h^2e$  (narrow-sense heritability); and  $r$  (correlation coefficient). Significance levels of all genetic components were determined by  $t$ -test. All statistical procedures were performed with the help of the Genes program (Cruz, 2020).

## Results and discussion

### Sufficiency test of the additive-dominant model

Table 1 presents the results of the application of the two tests to determine the adequacy of the data to the additive-dominant model for the evaluated characteristics. For the NPP, PL, and MPW, the test results were from partially to non-significant, thus validating the use of the additive-dominant model in the genetic study of these traits. The PPP trait

**Table 1.** Sufficiency test of the additive-dominant model based on linear regression analysis of  $W_r$  on  $V_r$  for mean pod weight, pod production per plant, number of pods per plant, and pod length, among six bean parents and their  $F_1$ s, according to the methodology proposed by B. I. Hayman (1954a, b)

**Таблица 1.** Проверка достаточности аддитивно-доминантной модели на основе линейного регрессионного анализа ( $W_r/V_r$ ) для среднего веса боба, урожая бобов с растения, количества бобов на растение и длины боба среди шести родительских форм фасоли и их гибридов  $F_1$  согласно методологии, предложенной Б. Хейманом (Hayman, 1954a, b)

Character <sup>1</sup>	Regression <sup>2</sup>	Rotation axes <sup>3</sup> $\hat{W}_r$ y $\hat{V}_r$ <sup>3</sup>
	t ( $H_0: b=1$ )	F = t <sup>2</sup> ( $H_0: B=b-1=0$ )
PPP	-6.51*	3.66*
NPP	-2.73*	1.69 ns
LDV	-2.40*	1.57 ns
MPW	-2.48*	1.44 ns

Note: <sup>1</sup> MPW – mean pod weight; PPP – pod production per plant; NPP – number of pods per plant; PL = pod length

<sup>2</sup> t-test, average values of  $W_r$  and  $V_r$ , with a 5% probability level

<sup>3</sup> F-test, average values of  $W_r$  and  $V_r$  by rotation of the axes at 45°, probability level at 5%; ns – not significant

Примечание: <sup>1</sup> MPW – средний вес боба; PPP – урожай бобов с растения; NPP – количество бобов на растение; PL – длина боба

<sup>2</sup> t-тест, средние значения  $W_r$  и  $V_r$  при 5% уровне вероятности

<sup>3</sup> F-тест, средние значения  $W_r$  и  $V_r$  при повороте осей на 45°, уровень вероятности 5%; ns = не значимо

showed statistical significance at 5%, indicating the presence of epistasis; in this case, the analysis cannot be performed using Hayman’s methodology.

### $\hat{W}_r/\hat{V}_r$ Analysis

#### Number of pods per plant (NPP)

The results concerning the trait “number of pods per plant” (NPP) are shown in Table 2. They demonstrate that the components associated with additive effects (D) and dominance effects ( $H_1$ ,  $H_2$ , and  $h^2$ ) are controlling the trait inheritance. However, the values of dominance effects were of higher magnitude ( $H_1 = 3582.89^{**}$ ;  $H_2 = 3008.47^{**}$  and  $h^2 = 8752.56^{**}$ ) compared to additive effects ( $D = 336.65^{**}$ ), indicating that the character “number of pods per plant” (NPP) is more influenced by dominant effects. Similar results were obtained in the studies conducted by M. P. Da Silva et al. (2004), J. H. Chung, E. Stevenson (1973), W. Krause et al. (2012), and E. Y. Owusu et al. (2020) in green beans, kidney beans, and cowpea. However, E. E. Arunga et al. (2010), M. A. A. Barelli et al. (1999), R. Rodrigues et al. (1998), E. V. Rodrigues et al. (2018), E. V. Rodrigues et al. (2016), F. D. Rocha et al. (2014), and N. J. Nayak et al. (2018) reported contradictory results in which additive effects predominated for this trait.

No significant environmental effects (E) were found for this trait (Table 2), indicating that the differences were mainly based on genotypic variations. This result corroborates the findings reported by Iqbal et al. (2011).

The difference between  $D-H_1$  estimates also provides information about genetic effects on inheritance of the character. When the estimate is negative, dominance genetic effects predominate; however, positive estimates reveal the presence of additive genetic effects. As shown in Table 2, the  $D-H_1$  estimate ( $-3246.24^{**}$ ) presented a negative and significant value, which indicates the predominance of dominant genetic effects in this trait and is confirmed by the narrow heritability value ( $h^2e = 0.23$ ), suggesting that the simplest breeding method, based on the selection in later segregating generations, when the trait of interest is already fixed, such as the

single seed descent (SSD) method, can be recommended to obtain satisfactory gains in terms of the NPP in future generations. This result corroborates the findings reported by M. P. Da Silva et al. (2004) and M. A. A. Barelli et al. (1999) who observed a genetic advance with intermediate heritability estimates for the trait NPP.

The proportion of genes with positive dominance effects ( $H_1$ ) is shown from the  $H_1$  versus  $H_2$  value. If  $H_1 > H_2$ , genes will be more positive (increase), on the other hand, if  $H_1 < H_2$ , genes will be more negative (decrease). The  $H_1$  value ( $3582.89^{**}$ ) was higher than the  $H_2$  value ( $3008.47^{**}$ ), indicating that genes that increase the trait NPP (dominant genes) were more frequent among the parents than the recessive genes. The distribution of genes among parents expressed by the  $H_2/4H_1$  ratio was symmetrical (0.21) for the trait (see Table 2), indicating a symmetrical distribution of favorable or unfavorable genes among the parents. Similar results were reported by A. M. Iqbal et al. (2011) and M. P. Da Silva et al. (2004). The overall dominance effects of heterozygous loci ( $h^2$ ) were found to be significant ( $8752.56^{**}$ ), indicating that dominance was due to heterozygosity where most of the dominant genes had positive effects.

The proportion of dominant genes in the parents is reflected in the  $K_D/K_R$  value. If  $K_D/K_R > 1$ , there are more dominant genes in the parents. Conversely, if  $K_D/K_R < 1$ , then there are more recessive genes in the parents (Singh, Chaudhary, 1999). In this study, the ratio  $K_D/K_R = 1.53$  showed a higher predominance of dominant genes for the trait NPP (see Table 2) and was confirmed by the positive F value (460.29).

The estimation of the number of genes or gene blocks with dominant effects ( $h^2/H_2 = 2.91$ ) indicated the existence of at least three genes or three gene blocks acting on the genetic control of the trait. However, this estimator underestimates the number of genes with little or no dominance (Cruz et al., 2012).

The estimation of the mean degree of dominance ( $H_1/D$ )<sup>1/2</sup> = 3.26 indicates the existence of overdominance among the genes involved in the genetic control of the trait (see Table 2). Similar results were obtained by M. P. Da Silva et al. (2004) and M. A. A. Barelli et al. (1999). This result can



**Table 2. Genetic parameters and variance components for the traits “number of pods per plant” (NPP), “pod length” in cm (PL), and “mean pod weight” (MPW) in green bean (*Phaseolus vulgaris* L.) using Hayman’s method**  
**Таблица 2. Генетические параметры и компоненты дисперсии для признаков «количество бобов на растение» (NPP), «длина боба» в см (PL) и «средний вес боба» (MPW) у овощной фасоли (*Phaseolus vulgaris* L.), рассчитанные по методу Хеймана**

Genetic parameters <sup>1</sup>	NPP	PL	MPW
D	336.65 **	1.04 **	0.12
H <sub>1</sub>	3582.89 **	1.22 *	0.21
H <sub>2</sub>	3008.47**	0.75	0.05
h <sup>2</sup>	8752.56**	-0.04	-0.05
F	460.29	-0.59	-0.30
E	0.13	0.06	0.13 **
D-H <sub>1</sub>	-3246.24 **	-0.19	-0.09
(H <sub>1</sub> /D) <sup>1/2</sup>	3.26	1.09	1.31
H <sub>2</sub> /4H <sub>1</sub>	0.21	0.15	0.06
K <sub>D</sub> /K <sub>R</sub>	1.53	0.59	0.05
h <sup>2</sup> /H <sub>2</sub>	2.91	-0.05	-1.04
h <sup>2</sup> e	0.23	0.81	0.68
r	-0.66	0.55	0.43

Note: <sup>1</sup>D – additive gene action; H<sub>1</sub> – variance component due to dominance effects of alleles with positive effects; H<sub>2</sub> – variance component due to dominance effects of alleles with negative effects; F – relative frequency of dominant and recessive alleles; h<sup>2</sup> – dominant gene action; E – experimental error; D-H<sub>1</sub> – difference between additive and dominant gene effects; (H<sub>1</sub>/D)<sup>1/2</sup> – mean degree of dominance; H<sub>2</sub>/4H<sub>1</sub> – allele distance (symmetry); K<sub>D</sub>/K<sub>R</sub> – dominant/recessive ratios; h<sup>2</sup>/H<sub>2</sub> – number of genes with dominance; h<sup>2</sup>e – narrow-sense heritability; r – correlation coefficient;

\*, \*\* – significant at the 5% and 1% probability level, respectively

Примечание: <sup>1</sup>D – аддитивное действие генов; H<sub>1</sub> – компонент вариации, обусловленный эффектами доминирования аллелей с положительным эффектом; H<sub>2</sub> – компонент вариации, обусловленный эффектами доминирования аллелей с отрицательным эффектом; F – относительная частота доминантных и рецессивных аллелей; h<sup>2</sup> – доминантное действие генов; E – ошибка эксперимента; D-H<sub>1</sub> – разница между аддитивным и доминантным эффектами генов; (H<sub>1</sub>/D)<sup>1/2</sup> – средняя степень доминирования; H<sub>2</sub>/4H<sub>1</sub> – расстояние между аллелями (симметрия); K<sub>D</sub>/K<sub>R</sub> – соотношение доминантности и рецессивности; h<sup>2</sup>/H<sub>2</sub> – число генов с доминированием; h<sup>2</sup>e – наследуемость в узком смысле; r = коэффициент корреляции;

\*, \*\* – значимы на 5% и 1% уровне вероятности соответственно

be corroborated through graphical analysis in cases where the regression line of Wr on Vr intercepts the ordinate axis below the origin point (Figure 1).

The correlation r (Yr, Wr + Vr) (-0.66) was negative, indicating that genes that increase the trait “number of pods per plant” are predominantly dominant (see Table 2). These results coincide with those found by M. P. Da Silva et al. (2004) and M. A. A. Barelli et al. (1999). The order of dominance is reflected in the covariance (Wr) and variance (Vr) relationship in the graph (see Figure 1). The higher proportion of dominant genes will be found closer to the origin point and will present lower values of Wr and Vr, while those found further from the origin point will present a higher number of recessive genes and higher values of Wr and Vr (Vallejo, Estrada, 2013). In this case, parents 2 (G23956), 3 (G20400), 5 (G16806), and 6 (G51158) were the most suitable for obtaining superior lines, since they carried a higher proportion of dominant genes and were located at the lower limit of the regression line (see Figure 1).

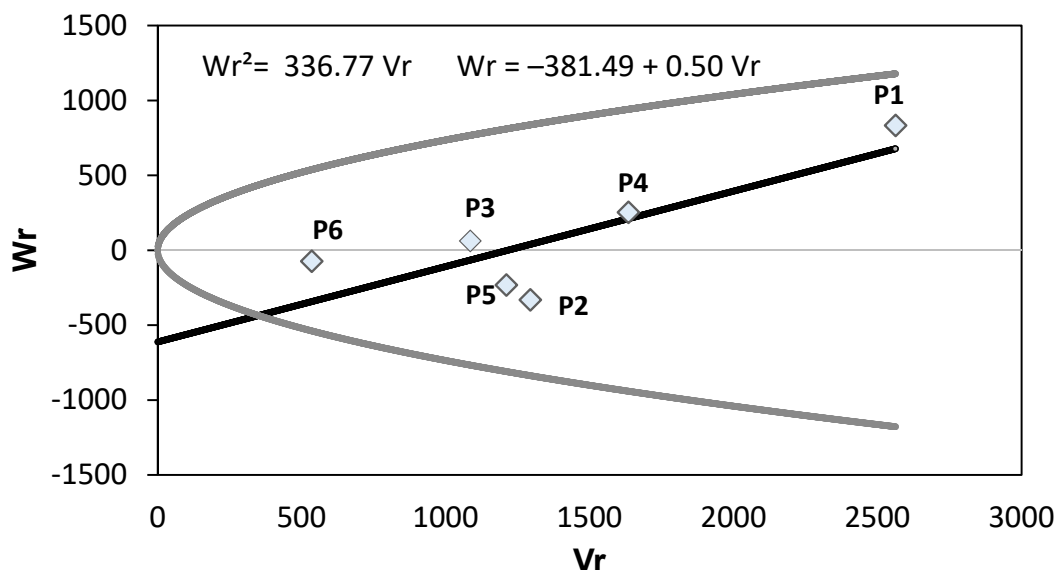
#### Pod length (PL)

The genetic variance components for the pod length trait (PL) were significant for D and H<sub>1</sub>, while H<sub>2</sub>, h<sup>2</sup>, F, and E were

not significant (see Table 2). When comparing the magnitude of additive (D = 1.04\*\*) and dominance (H<sub>1</sub> = 1.22\*) components, the non-additive component was revealed to have a greater contribution to the expression of the mentioned character (see Table 2). Similar results were obtained by A. K. Islam et al. (2006) and A. M. Iqbal et al. (2011). It was also observed that the estimates obtained for D-H<sub>1</sub>(-0.19) were negative, revealing that dominant effects are more important in the expression of the trait, as well as indicating overdominance, which can be confirmed by the value of (H<sub>1</sub>/D)<sup>1/2</sup> = 1.09 (see Table 2).

The environmental component (E) estimate was non-significant, suggesting the minimum role of environment in modifying this trait. Similar results were provided by Gangadhara et al. (2019) and Iqbal et al. (2011).

The heritability estimation showed a high narrow-sense heritability (h<sup>2</sup>e = 0.81; > 60%) for the studied trait, indicating that PL is highly heritable. Such magnitude allows the suggestion that desirable genes will be transmitted to the next generations with higher reliability. Considering the dominance components, the magnitude of H<sub>1</sub>(1.22\*) was higher than H<sub>2</sub>(0.75), indicating the predominance of genes with positive effects among the parents for the PL trait, and this



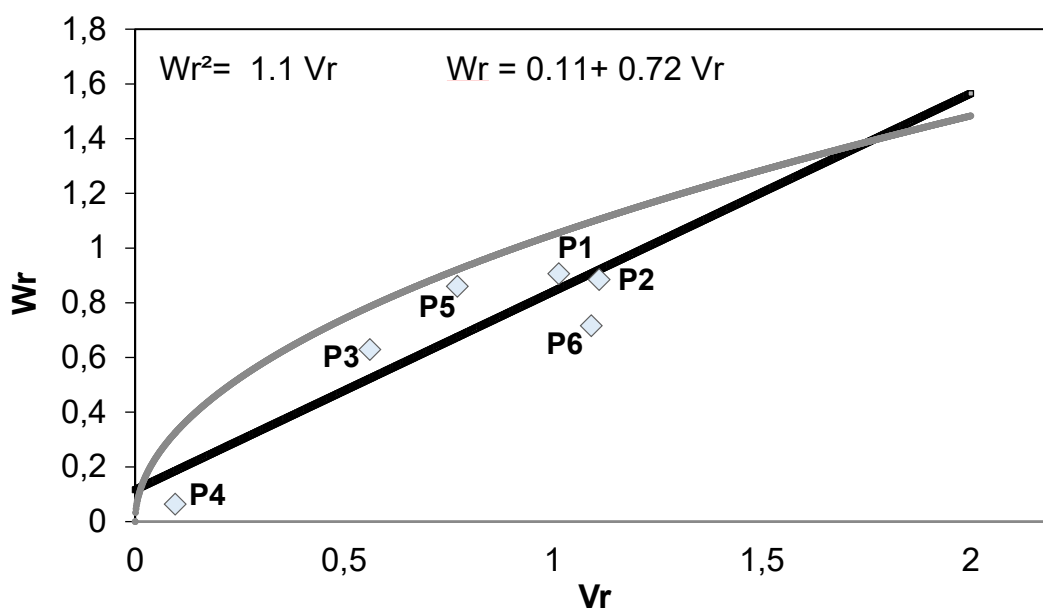
**Fig. 1.** Regression between  $W_r$  vs.  $V_r$  and limiting parabola for the number of pods per plant (NPP) in green bean (*Phaseolus vulgaris* L.). Parents: P1 - G17723; P2 - G23956; P3 - G20400; P4 - G18212; P5 - G16806; P6 - G51158

**Рис. 1.** График зависимости  $W_r$  от  $V_r$  и ограничивающая парабола для количества бобов на растение (NPP) у овощной фасоли (*Phaseolus vulgaris* L.). Родители: P1 - G17723; P2 - G23956; P3 - G20400; P4 - G18212; P5 - G16806; P6 - G51158

can also be confirmed by the  $H_2/4H_1$  ratio. When evaluating the proportion of parents that are homozygous dominant or recessive, it is observed ( $H_2/4H_1 = 0.15$ ) that there was no symmetry in the distribution of genes favorable and unfavorable to the increase of this trait among the parents.

The negative F value (-0.59) revealed that recessive genes were more frequent than dominant genes and were in a decreasing position, as confirmed by  $h^2$  (-0.04) (see Table 2). The predominance of homozygous recessive forms was detected by analyzing the ratio of dominant to recessive genes in the studied parents ( $K_D/K_R = 0.59$ ).

A positive correlation ( $r = 0.55$ ) between the order of dominance of the parents ( $W_r + V_r$ ) and their average value ( $Y_r$ ) indicated that recessive genes increased the pod length trait (see Table 2). Figure 2 shows the distribution of parents, according to the proportion of dominant and recessive genes, as follows: parents 1 (G17723), 2 (G23956), and 6 (G51158) were located at the upper limit of the regression line, indicating that these parents have recessive genes for increasing pod length, and at the bottom of the line with the lowest pod length were parents 4 (G18212), 3 (G20400) and 5 (G16806) with the highest number of dominant genes.



**Fig. 2.** Regression between  $W_r$  vs.  $V_r$  and limiting parabola for pod length (PL) in green bean (*Phaseolus vulgaris* L.). Parents: P1 - G17723; P2 - G23956; P3 - G20400; P4 - G18212; P5 - G16806; P6 - G51158

**Рис. 2.** График зависимости  $W_r$  от  $V_r$  и ограничивающая парабола для длины боба (PL) у овощной фасоли (*Phaseolus vulgaris* L.). Родители: P1 - G17723; P2 - G23956; P3 - G20400; P4 - G18212; P5 - G16806; P6 - G51158

### Mean pod weight (MPW)

The additive genetic component ( $D = 0.12$ ) and the component related to dominant gene action with positive effects ( $H_1 = 0.21$ ) indicated that both additive and dominant gene deviations contributed to the expression of mean pod weight, although variation due to dominance deviations had a much greater contribution to the expression of this trait (see Table 2). Similar results were obtained by W. Krause et al. (2012) and E. V. Rodrigues et al. (2018). The value of  $H_1$  was higher than the value of  $H_2$ , indicating unequal gene frequency in the parents, and this was also supported by the ratio of  $H_2/4H_1$  ( $0.06 < 0.25$ ). The environmental component  $E$  was significant and its magnitude was higher than the respective value of  $D$  and  $H_1$  (Table 2), indicating a higher environmental effect in the trait's expression.

Negative values of  $F$  ( $-0.30$ ) and  $h^2$  ( $-0.05$ ) indicated that recessive genes were more frequent than dominant genes with the increasing position. The overall dominance effects of heterozygous loci ( $h^2$ ) were found to be nonsignificant, indicating that dominance was due to homozygosity. Estimation of the number of  $h^2/H_2$  genes with dominance could not be performed because  $h^2$  was not significantly different from zero.

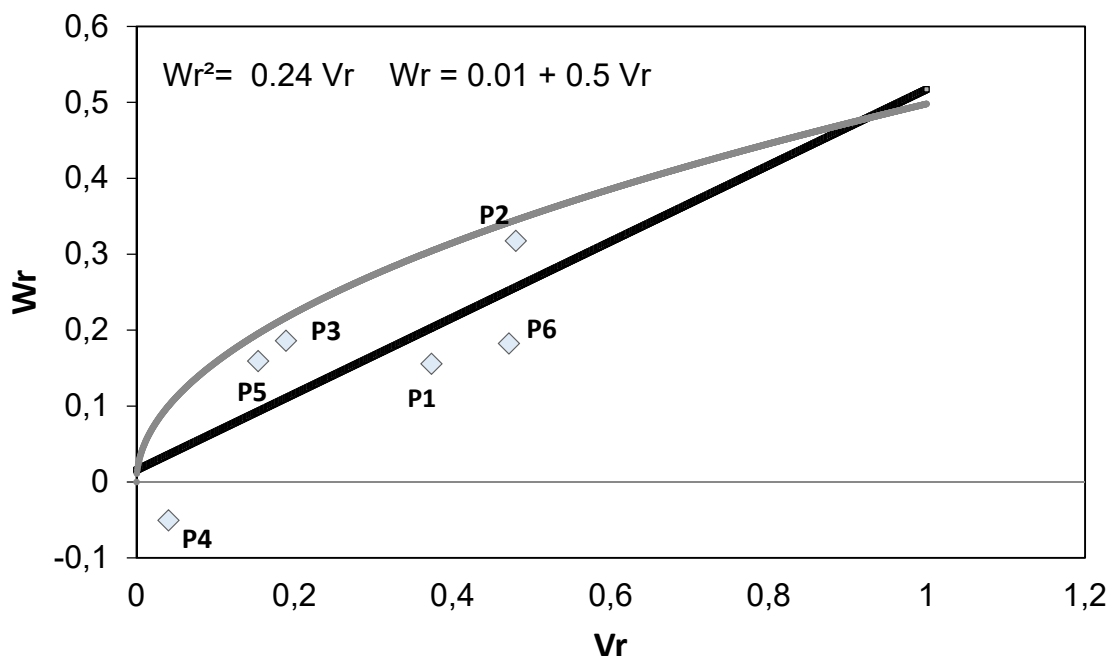
The ratio of dominant to recessive genes in the  $K_D/K_R$  parents ( $0.05$ ) was less than one, indicating that recessive genes drove them. Significant environmental effects ( $E$ ) were found, indicating the influence of the environment on this trait. The negative value of  $D-H_1$  ( $-0.09$ ), indicated overdominance, which could be confirmed by the  $(H_1/D)^{1/2} = 1.31$  value. The heritability value ( $h^2_e = 0.68$ ) indicated some selection possibilities in the segregating generations (see Table 2).

The correlation  $r$  ( $Y_r, W_r + V_r$ ) ( $0.43$ ) was positive, indicating that genes increasing the trait "mean pod weight" were predominantly recessive (see Table 2). The relative ranking of

the parents in terms of the proportions of dominant and recessive genes is presented in Figure 3, suggesting two clearly defined groups: parents 1 (G17723), 2 (G23956) and 6 (G51158) carry the highest proportion of recessive genes for increasing mean pod weight and are therefore located at the upper end of the regression line, while at the lower end near the origin point of the line for lower mean pod weight were parents 4 (G18212), 3 (G20400) and 5 (G16806) with the highest proportion of dominant genes.

### Conclusions

Both additive and non-additive genetic effects were involved in the inheritance of the following traits in hybrids obtained from diallel crosses among six genotypes of *P. vulgaris*: the number of pods per plant, mean pod weight, and pod length. However, for the traits "number of pods per plant", "pod length", and "mean pod weight", the non-additive genetic effect was the major contributor to the expression of the traits. The number of pods per plant is determined by dominant alleles, while the mean pod weight and pod length characters are determined by recessive alleles. The parents P1 (G17723); P2 (G23956) and P6 (G51158) showed higher concentration of alleles favorable for increasing the pod length and mean pod weight characters, and the parents P2 (G23956), P5 (G16806) and P6 (G51158) for the number of pods per plant. The heritability, in the narrow sense ( $h^2_e$ ), was low for the trait "number of pods per plant"; consequently, management of segregating populations should be accomplished by the single-seeded descent method. With the high magnitude of narrow-sense heritability ( $h^2_e$ ) for the pod length and mean pod weight characters, it can be inferred that the most appropriate selection method is the pedigree method.



**Fig. 3.** Regression between  $W_r$  vs.  $V_r$  and limiting parabola for mean pod weight (MPW) in green bean (*Phaseolus vulgaris* L.). Parents: P1 – G17723; P2 – G23956; P3 – G20400; P4 – G18212; P5 – G16806; P6 – G51158

**Рис. 3.** График зависимости  $W_r$  от  $V_r$  и ограничивающая парабола для среднего веса боба (MPW) у овощной фасоли (*Phaseolus vulgaris* L.). Родители: P1 – G17723; P2 – G23956; P3 – G20400; P4 – G18212; P5 – G16806; P6 – G51158



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