Genetics/ Original Article

Transgressive segregations in two pea F_2 populations and their respective $F_{2:3}$ families

Abstract – The objective of this work was to evaluate the variability present in two pea (*Pisum sativum*) F_2 populations and their corresponding $F_{2:3}$ families, as well as to determine, in both generations, the frequency of transgressive segregants in order to isolate early superior families. The study was conducted from a cross of green pea varieties (Ilca 5115 and Turf) and a cross of yellow pea varieties (Zavalla 15 and Amarilla). In both generations, morphological traits were evaluated. Phenotypic and genotypic variances, experimental error variance, genotypic and phenotypic coefficients of variation, broad-sense heritability, and transgressive segregants were determined. The green F_2 population showed greater variation, whereas the yellow $F_{2:3}$ families had higher average values for most traits. In the green $F_{2:3}$ population, the percentage of transgressive segregants was greater or equal to 20, while, in the yellow one, no traits had a percentage greater than 20. High heritability values were obtained for most traits in both generations. Considering all traits, 45% of the transgressive segregants are found in the F_2 populations and 42% of the F_2 transgressive segregants in the $F_{2:3}$ generation. The distribution of $F_{2:3}$ families allows to select promising families according to the breeding program objectives.

Index terms: *Pisum sativum*, genetic variability, heritability, principal component analysis.

Segregações transgressivas em duas populações F_2 de ervilha e suas respectivas famílias $F_{2:3}$

Resumo – O objetivo deste trabalho foi avaliar a variabilidade presente em duas populações F_2 de ervilha (*Pisum sativum*) e suas famílias $F_{2:3}$ correspondentes, bem como determinar, em ambas as gerações, a frequência de segregantes transgressivos para isolar as primeiras famílias superiores. O estudo foi realizado a partir de um cruzamento de variedades de ervilha verde (Ilca 5115 e Turf) e um cruzamento de variedades de ervilha amarela (Zavalla 15 e Amarilla). Nas duas gerações, foram avaliadas características morfológicas. Foram determinadas as variações fenotípica e genotípica, a variação do erro experimental, o coeficiente das variações genotípica e fenotípica, a herdabilidade no sentido amplo e os segregantes transgressivos. A população verde F_2 mostrou maior variação, enquanto as famílias amarelas $F_{2:3}$ apresentaram valores médios mais altos para a maioria das características. Na população verde $F_{2:3}$, a percentagem de segregantes transgressivos foi maior ou igual a 20, enquanto, na amarela, nenhuma característica teve percentagem maior que 20. Valores altos de herdabilidade foram obtidos para a maioria das características nas duas gerações. Ao se considerar todas as características, 45% dos segregantes transgressivos ocorrem nas populações F_2 e 42% dos segregantes transgressivos da F_2, na geração $F_{2:3}$. A distribuição das famílias $F_{2:3}$ permite selecionar famílias promissoras de acordo com os objetivos do programa de melhoramento.

Termos para indexação: *Pisum sativum*, variabilidade genética, herdabilidade, análise de componentes principais.

Federico Cazzola[1] (✉) (iD),
Carolina Julieta Bermejo[1] (iD), and
Enrique Cointry[1] (iD)

[1] Instituto de Investigaciones en Ciencias Agrarias de Rosario, Campo Experimental Villarino, C.C. 14 (S2125ZAA) Zavalla, Santa Fe, Argentina.
E-mail: cazzola.f@gmail.com, bermejo@iicar-conicet.gob.ar, ecointry@unr.edu.ar

✉ Corresponding author

Introduction

Pea (*Pisum sativum* L.) is the second most cultivated legume worldwide with a production of 16.205 million tons in 2017 (FAO, 2019), being an interesting protein source for both human and animal consumption (Dahl et al., 2012). The demand for pea is high and sustained given the high consumption in Asian countries such as India, China, and Bangladesh, which are the main consumers in the world. Globally, the largest exporter is Canada, followed by Russia and the United States and, at a lower scale, France and Australia. In South America, the main pea producer and exporter is Argentina (Janzen et al., 2014). Besides its importance as a food, the legume contributes to a more sustainable agriculture, being a source of biological nitrogen fixation, which allows increasing the nutrient's supply to winter crops and efficient use when obtained from organic matter by the successive crop.

Being a self-pollinated species, the variability in pea is limited, requiring hybridization and subsequent recombination to obtain segregating materials for use in the selection processes of plants and/or families, resulting in new varieties with higher yields and that are adapted to different environments. In the breeding of domesticated plants, hybridization is used to take advantage of transient hybrid vigor, move desirable variation among lineages, and generate novel phenotypes (Goulet et al., 2017).

For breeding programs, genetic variability is an essential prerequisite (Tiwari & Lavanya, 2012), whose estimation provides the basis for effective selection. Sharma et al. (2003) pointed out that a high hereditary variation increases the possibility of setting a character through appropriate selection methods. As most of the traits of economic importance are polygenic, the estimation of their heritability allows measuring their variability in different populations. Since inheritance acts as a predictive tool to express the reliability of phenotypic traits, a high heritability could help in the effective selection of particular characters and to design future selection programs (Mallu et al., 2014). The generated variability can also be quantified through the ranges of phenotypic variation that depend on the genetic complexity of the evaluated characters (Huang & Han, 2014).

The success of genetic improvement rests on the knowledge and correct use of the available germplasm, in order to identify the varieties to be used as parents in such a way that, when crossed, they generate an F_1 progeny with a high heterotic effect, allowing the appearance of transgressive variants that can be selected in segregating generations. According to Koide et al. (2019), transgressive segregation consists in the production of F_2 progenies or later generations with phenotypes that exceed the range of the parental populations from which they derive. Transgressive segregation, therefore, shows how hybridization can produce novel genotypes and phenotypes. Regarding transgressive phenotypes, Reyes (2019) highlighted that they are a result of a positive or negative complementation of additive alleles, epistatic interactions of unique parental attributes, unmasking of recessive alleles from a heterozygous parent, or any combination of these mechanisms. Cubero (2003) proposed that transgression occurs through the crossbreeding of parents with similar values for the variable under study, but with different genes controlling the character, which allows some F_2 individuals to contain new gene combinations with a greater or lower number of genes that show a more favorable effect than those of the parents. These types of segregations are extremely important in the improvement of self-pollinated species due to the possibility of obtaining superior varieties. Although the transgressive individuals observed in the F_2 generation can be highly heterozygous, heterosis can be fixed or maintained if vigor is caused by the accumulation of dominant alleles (Shreya et al., 2017).

The objective of this work was to evaluate the variability present in two pea F_2 populations and their corresponding $F_{2:3}$ families, as well as to determine, in both generations, the frequency of transgressive segregants in order to isolate early superior families.

Materials and Methods

Pea cultivars were selected from the germplasm collection of Facultad de Ciencias Agrarias of Universidad Nacional de Rosario. For the study, F_2 segregating populations and their $F_{2:3}$ families were developed from: the Ilca 5115 and Turf varieties due to their contrasting characteristics, to obtain a green cotyledon color; and the hybridization between the Zavalla 15 and Amarilla varieties, to obtain a yellow cotyledon color. Turf from Russia and Amarilla from Argentina are semi-leafless varieties, while Ilca 5115

from Spain and Zavalla 15 from Argentina have normal leaflets.

One hundred seeds of each F$_2$ population were sown during June 2017, in the experimental field of Facultad de Ciencias Agrarias of Universidad Nacional de Rosario, located in Santa Fe, Argentina (33°1'S, 60°53'W). The climate is humid subtropical (Cfa) according to Köppen-Geiger's classification. The planting grid was of 70 cm between rows and 10 cm between plants in rows of 30 m in length. The soil was classified as a silty clay loam Vertic Argiudoll by the Roldán series. The soil was prepared using conventional tillage, and the seeds were treated with Metalaxil-M + Fludioxonil – [fludioxonil [4-(2,2-difluoro-1,3-benzodioxol-4-yl)-1H-pyrrole-3-carbonitrile] and metalaxyl [M (N-(2,6-dimethylphenyl)-N-(2'-methoxyacetyl)-D-alanine methyl ester]. A drip-irrigation system was adopted, and the Linuron herbicide (3-(3,4-dichlorophenyl)-1-methoxy-1-methylurea) was applied at pre-sowing and Imazethapyr (5-ethyl-2-(4-isopropyl-4-methyl-5-oxo-2-imidazolin-2-yl) nicotinic acid) after emergence to avoid competition with weeds. Simultaneously, two replicates of 50 plants of each parent were planted. Ninety F$_{2:3}$ families with green and yellow cotyledons were sown in the plots, consisting of a 2-m long row with 10 cm between plants, in a completely randomized design, with two replicates, during 2018. Simultaneously, 100 plants of each of the parental materials were planted in two replicates using the same planting arrangement. Pre-emergence herbicides for weed control were also applied, and drip irrigation was used to supply water when necessary.

In the F$_2$ generations and in the F$_{2:3}$ families, morphological traits were assessed according to International Union for the Protection of New Varieties of Plants (UPOV, 2009). For the F$_2$ populations, the evaluations were carried out at the individual plant level, while, for the F$_{2:3}$ families, the average values per plot were determined.

The following quantitative traits were evaluated: days to the appearance of the first open flower on 50% of the plants of the plot after planting (DAF), plant height at harvest (PH, cm), number of pods per plant (PP), number of grains per plant (NGP), pod length (PL, cm), number of grains per pod (NG), and yield (gram per plant in the F$_2$ population or gram per plot in the F$_{2:3}$ population).

For the F$_2$ populations, the average values, the coefficient of variation (CV), and the maximum and minimum values for each variable were determined as a measure of the current variability. The phenotypic and genotypic variances, experimental error variance, genotypic and phenotypic CVs, and broad-sense heritability were estimated according to Mahmud & Kramer (1951). The CVs were considered: low, if <10%; intermediate, between 10 and 20%; and high, if <20% (Kosev et al., 2012).

The transgressive segregants in the F$_2$ population were identified by counting the number of plants whose mean value was above that of the superior parent or below that of the inferior parent by a critical difference of 5% (Shreya et al., 2017). For the characters plant height and DAF, the segregants with values lower than those of the parents were considered transgressive; the limit was 57 cm for height and 88 days for flowering for the green population, and 47 cm for height and 86 days for flowering for the yellow population. To assess the presence of transgressive segregants in the generation, the transgression index (TI) was calculated as: R / D, where R is the range of variation between F$_2$ for any trait, and D is the difference between the average values of the parents for the same trait (Koide et al., 2019).

Data collected from the F$_{2:3}$ families were subjected to the analysis of variance (Anova) using the Infostat software (Balzarini & Di Renzo, 2013); components of variance between and within families were estimated, broad-sense heritability was calculated following Cahaner & Hillel (1980), and standard error was estimated from the variance of intra-class correlation. The normal distribution of the morphological data evaluated in the different generations was verified by the Shapiro-Wilk test (Shapiro & Wilk, 1965).

The percentage of transgressive F$_{2:3}$ families and the percentage of transgressive families from transgressive F$_2$ plants were also estimated, following the same criteria established for the F$_2$ generation. In order to observe the distribution of the F$_{2:3}$ families and select the superior ones considering all morphological traits, a principal components analysis was performed.

Results and Discussion

The green and yellow pea F$_2$ populations had significant higher average values for PH, PL, NGP, PP,

and DAF (Table 1). The CV was high for all traits in both populations, except for DAF and PL. In addition, the ranges in the two populations were of similar magnitude. Huang & Han (2014) highlighted that the range of phenotypic variation in a quantitative trait depends on genetic complexity. Hybridizations often produce progenies with a wider phenotypic variation than their parents, which is referred to as transgressive segregation (Koide et al., 2019); however, unlike in heterosis, the extreme phenotypes that occur can be fixed after the second generation (F_2).

In relation to the variation generated in the F_2 generation, the TI showed the appearance of transgressive segregants for most of the studied variables (Table 2). PH, PP, NGP, and yield for the green population and PP, NGP, NG, and yield for the yellow population presented the highest values for transgressive segregants; however, a higher percentage of transgression does not always imply a greater index.

For the TI analysis, ranges were considered: low, when 0.0< TI <5.0; intermediate, when 5.0 ≤ TI ≤10.0; and high, when TI >10.0. The low TI values may be due

to the great difference between parents regarding PH in both populations and DAF in the yellow population, or to the low variability in the F_2 generation, indicated by the low fluctuation between ranges for PL in the two populations. High TI values were found for NG in the green F_2 population and for PP, NG, and yield in the yellow F_2 population (Table 2), which is attributed to the small but significant difference between the values obtained for the parents and to the wide range of values for their respective F_2. These data agree with those of Koide et al. (2019) for crosses between rice (*Oryza sativa* L.) varieties regarding days to heading; however, they cannot be generalized for all characters. Some characters, for example, such as yield and PP in the yellow population, exhibited high TI although the parents differed significantly, whereas others, as DAF in the green population and NG in both populations, had a high TI but with similar parents.

Transgressive segregants in F_2 may be caused by dominance x dominance and additive x additive interactions, which are fixable, due to the recombination of genes with positive effects, being responsible for the production of transgressive segregants in the $F_{2:3}$ generation.

Anova showed significant differences between the families for all traits in both populations (Table 3).

The analysis of the characters of the green $F_{2:3}$ population showed that, except for PL, the percentage of transgression was greater than or equal to 20, while, in the yellow $F_{2:3}$ population, no character had

Table 1. Average values (AV), coefficient of variation (CV), range, and heritability (H_2) for productive traits of green and yellow pea (*Pisum sativum*) F_2 populations.

Trait[1]	AV	CV	Range	H_2
Green F_2[2]				
PH	68.3*	36.0	33–121	0.83
PL	5.2*	9.5	4.0–6.2	0.84
PP	21.9*	62.8	2–72	0.93
NGP	58.2*	73.0	4–246	0.96
NG	2.6[ns]	22.9	0.7–4.3	0.42
Yield	10.6[ns]	86.9	7.5–25.4	0.96
DAF	95.8*	5.1	86–112	0.95
Yellow F_2[3]				
PH	81.7*	29.8	28–122	0.99
PL	5.53*	8.7	4.3–6.7	0.88
PP	16.6*	62.1	3–58	0.32
NGP	43.7*	61.3	15–203	0.71
NG	2.53[ns]	28.5	1–4.8	0.73
Yield	8.58[ns]	76.8	7.4–31.4	0.79
DAF	94.1*	5.9	85–105	0.86

[1]PH, plant height at harvest (cm); PL, pod length (cm); PP, pods per plant; NGP, number of grains per plant; NG, number of grains per pod; Yield in gram per plant; and DAF, days to the appearance of the first flower. [2]Obtained from a cross between the Ilca 5115 and Turf varieties. [3]Obtained from a cross between the Zavalla 15 and Amarilla varieties. *Significant by the F-test, at 5% probability. [ns]Nonsignificant.

Table 2. Percentage of transgression (T) and transgression index (TI) obtained for productive traits of green and yellow pea (*Pisum sativum*) F_2 populations.

Trait[1]	Green F_2[2]		Yellow F_2[3]	
	T	TI	T	TI
PH	44.1	1.63	13.6	1.57
PL	15.7	3.14	16.8	4.80
PP	51.9	7.10	20.0	11.00
NGP	46.1	8.96	19.2	8.95
NG	21.6	20.1	22.4	10.91
Yield	30.4	3.34	18.4	120.2
DAF	4.9	8.67	3.2	3.33

[1]PH, plant height at harvest (cm); PL, pod length (cm); PP, pods per plant; NGP, number of grains per plant; NG, number of grains per pod; Yield in gram per plant; and DAF, days to the appearance of the first flower. [2]Obtained from a cross between the Ilca 5115 and Turf varieties. [3]Obtained from a cross between the Zavalla 15 and Amarilla varieties.

a percentage greater than 20 (Table 4). As indicated between parentheses (Table 4), the percentage of transgressive F$_{2:3}$ families that came from transgressive F$_2$ individuals and whose values were greater than 20 was higher in the green population for all characters, except for PL; in the yellow families, this was observed for DAF, PH, NG, and yield.

The presence of transgressive segregants has been shown in species such as: wheat (*Triticum aestivum* L.), for yield and yield components (Yadav et al., 1998); lentil (*Lens culinaris* Medik.), for seed yield per plant (Chahota et al., 2007); peanut (*Arachis hypogaea* L.), for characters such as total biomass, crop index, sprout weight, root weight, mature pod weight, and grain weight per plant (Shreya et al., 2017); rice, for flowering days (Koide et al., 2019); and pigeon pea [*Cajanus cajan* (L.) Millsp.], for earliness (Srivastava & Saxena, 2019). In pea, transgressive segregation was analyzed for quality characters (Ubayasena et al., 2011). Recently, a research that analyzed a cross between a variety of green and yellow cotyledon populations showed the presence of transgressive segregants favorable for different quantitative characters (Guindon et al., 2019). Several explanations have been offered to justify the appearance of transgressive phenotypes in segregating populations (Rieseberg et al., 1999), including: a high mutation rate in hybrids, reduced development stability, non-additivity of the allelic effects between loci or epistasis, no additivity of the allelic effects within a locus or over dominance, unmasking of rare recessive alleles that are usually heterozygous in parental taxa, variation of number of chromosomes, and complementary action of the additive alleles that are dispersed between the parental lines. The last explanation assumes that parental lines are often fixed for sets of alleles that have opposite effects within the

Table 3. Analysis of variance for the different quantitative traits evaluated for green and yellow pea (*Pisum sativum*) F$_{2:3}$ populations[1].

Source of variation	DF	PH		PL		PP		NGP		NG		Yield		DAF	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Yellow pea F$_{2:3}$ populations[2]															
Family	95	824.4	10.99*	0.15	1.61*	790.18	3.15*	8879.8	2.06*	0.5	1.45*	299.2	1.94*	24.83	17.59*
Error	96	74.02		0.09		250.79		4315.5		0.35		154		1.41	
Green pea F$_{2:3}$ populations[3]															
Family	95	547.63	9.22*	0.17	1.27*	1218.36	3.16*	1525.4	2.86*	0.71	1.71*	434.6	3.22*	33.01	13.09*
Error	96	59.42		0.14		385.36		5330.9		0.42		135		2.52	

[1]PH, plant height at harvest (cm); PL, pod length (cm); PP, pods per plant; NGP, number of grains per plant; NG, number of grains per pod; Yield in gram per plot; DAF, days to the appearance of the first flower; DF, degrees of freedom; MS, mean squares; and F, Snedecor's F-test. [2]Obtained from a cross between the Ilca 5115 and Turf varieties. [3]Obtained from a cross between the Zavalla 15 and Amarilla varieties. *Significant by the F-test, at 5% probability.
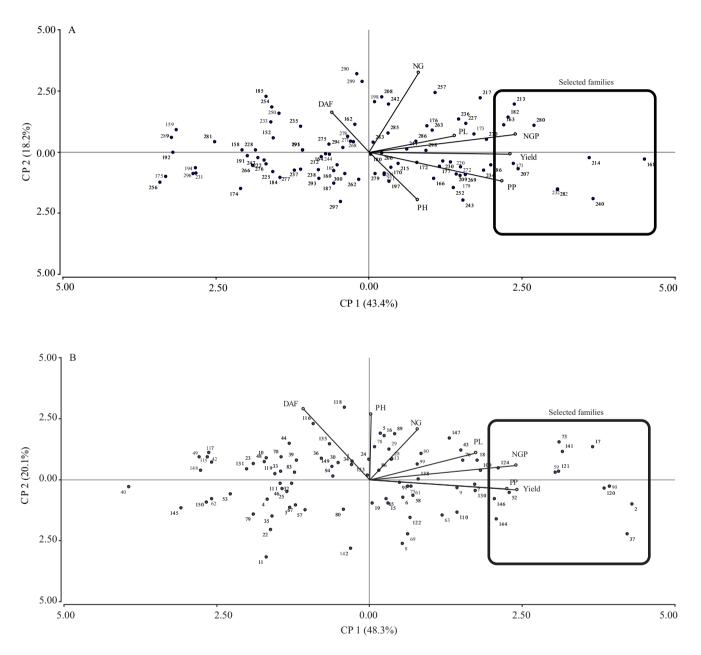
Table 4. Average values (AV), coefficient of variation (CV), range (R), percentage of transgression (T), and heritability (H$_2$) for productive traits of pea (*Pisum sativum*) F$_{2:3}$ families from the green and yellow populations[1].

Trait[1]	Green F$_{2:3}$[2]					Yellow F$_{2:3}$[3]				
	AV	CV	R	T	H$_2$	AV	CV	R	T	H$_2$
PH	57.9*	13.3	31–104	51.7 (68.7)	0.80	74.0*	11.6	36–106	16.5 (47.1)	0.83
PL	4.8*	7.3	4.4–5.6	3.3 (12.5)	0.14	5.3*	5.7	4.5–6	7.2 (0.0)	0.37
PP	73.9^{ns}	26.5	26–142	21.9 (24.5)	0.78	76.3^{ns}	20.7	39–143	7.21 (8.0)	0.78
NGP	229.9^{ns}	31.8	70–454	27.5 (31.9)	0.72	237.2^{ns}	27.1	104–403	2.06 (4.2)	0.52
NG	3.1^{ns}	20.7	1.7–4.9	41.8 (36.4)	0.38	3.1^{ns}	18.5	1.5–4.5	16.5 (25.0)	0.26
Yield	31.4*	37	6–66	24.2 (24.8)	0.79	35.5*	34.9	12–69	17.4 (38.7)	0.48
DAF	89.7*	1.7	79–96	29.7 (40.0)	0.86	92.0*	1.2	83–100	6.18 (25.0)	0.89

[1]PH, plant height at harvest (cm); PL, pod length (cm); PP, pods per plant; NGP, number of grains per plant; NG, number of grains per pod; Yield in gram per plot; and DAF, days to the appearance of the first flower. [2]Obtained from a cross between the Ilca 5115 and Turf varieties. [3]Obtained from a cross between the Zavalla 15 and Amarilla varieties. *Significant by the F-test, at 5% probability. ^{ns}Nonsignificant.

lines; therefore, extreme phenotypes are the predicted result.

The hereditary variation determined by heritability estimates would provide a reliable indication of the expected improvement through selection. According to Sight (2005), heritability can be classified as:

low, when ≤0.20; medium or moderate, when 0.20 < heritability <0.50; and high, when ≥ 0.50. In both the green and yellow F_2 populations, high heritability values were obtained for most of the characters, whereas intermediate values were only found for NG for the green F_2 population and PP for the yellow F_2

Figure 1. Principal component analysis of the yellow (A) and green (B) pea (*Pisum sativum*) $F_{2:3}$ families evaluated. The varieties used to obtain the yellow and green populations, respectively, were: Ilca 5115 and Turf and Zavalla 15 and Amarilla. PH, plant height at harvest; PL, pod length; PP, pods per plant; NGP, number of grains per plant; NG, number of grains per pod; Yield in gram per plant; and DAF, days to the appearance of the first flower.

population (Table 1). In the F$_{2:3}$ populations, high values were obtained for most of the evaluated characters, except for NG and PL in the green population and for NG, yield, and PL in the yellow population (Table 4). When comparing the values of the green populations in both generations, it can be seen that NG remains in the intermediate range, while PL is lower in the F$_{2:3}$ population. In the yellow F$_{2:3}$ population, the value of PP was higher than that of F$_2$, but those of NG, yield, and PL were lower. Georgieva et al. (2016) observed similar values of 95 and 61% for grains per plant and yield, respectively, when studying pea. However, Sing & Sing (2006) reported high heritability values for plant height, pod per plant, and yield. High values of heritability indicate that a rapid gain could be achieved by selecting different traits since the presence of additive variance is high, showing the existence of families with different reproductive values. Therefore, these estimates can help researchers in determining an appropriate strategy for crop improvement (Sharma et al., 2003).

The principal component (PC) analysis of the green and yellow F$_{2:3}$ families showed that 68% of the total variation between them is explained by two PCs (Figure 1). For PC1 (48%), the productive variables that contributed the most were PP, NGP, PL, and yield, whereas, for PC2 (20%), they were PH and DAF and, to a lower extent, NG. Considering the NGP, yield, PP, and PL characters, 17 transgressive families in the green population and 13 in the yellow one – shown within the box – would be promising for selection. This is in agreement with Kumar et al. (2017), who concluded that pea grain yield can be increased by choosing genotypes with a larger number of pods per plant and number of grains.

For PH, within the transgressive families, the obtained values were lower than 60 cm and higher than 80 cm. However, these materials were hard to use due to difficulties in mechanical harvesting and lodging. Despite this, their lower flowering days are important for the subsequent sowing of a summer crop. For the green pea population, flowering days were 2, 5, 17, 109, 120, 121, and 124 and, for the yellow pea population, 163, 170, 182, 207, 213, 234, 240, and 280. Taking into account the fixed requirements, green and yellow pea transgressive families were selected when they showed a height within the mentioned range and less than 95 flowering days.

Conclusions

1. The hybridization and recombination process produces a wide genetic variability in the green and yellow pea (*Pisum sativum*) F$_2$ populations studied, evidenced by the high heritability values and high coefficients of variation obtained for them and their F$_{2:3}$ families.

2. The F$_2$ populations show 45% of the transgressive segregants considering all traits, and 42% of the F$_2$ transgressive segregants remain in the F$_{2:3}$ generation, which suggests that they could produce superior lines.

3. The distribution of F$_{2:3}$ families allows to select promising families according to the breeding program objectives.

Acknowledgments

References

BALZARINI, M.G.; DI RIENZO, J.A. **Info-Gen**: Software Estadístico para Análisis de Datos Genéticos. 2013. Available at: <http://www.info-gen.com.ar>. Accessed on: Aug. 4 2019.

CAHANER, A.; HILLEL, J. Estimating heritability and genetic correlation between traits from generations F$_2$ and F$_3$ of self-fertilizing species: a comparison of three methods. **Theoretical and Applied Genetics**, v.58, p.33-38, 1980. DOI: https://doi.org/10.1007/BF00264666.

CHAHOTA, R.K.; KISHORE, N.; DHIMAN, K.C.; SHARMA, T.R.; SHARMA, S.K. Predicting transgressive segregants in early generation using single seed descent method-derived micro-macrosperma genepool of lentil (*Lens culinaris* Medikus). **Euphytica**, v.156, p.305-310, 2007. DOI: https://doi.org/10.1007/s10681-007-9359-9.

CUBERO, J.I. **Introducción a la mejora genética vegetal**. Madrid: Mundi-Prensa, 2003. 567p.

DAHL, W.J.; FOSTER, L.M.; TYLER, R.T. Review of the health benefits of peas (*Pisum sativum* L.). **British Journal of Nutrition**, v.108, p.S3-S10, 2012. DOI: https://doi.org/10.1017/S0007114512000852.

FAO. Food and Agriculture Organization of the United Nations. **Faostat**. Available at: <http://www.fao.org/faostat/en/#data/QC/visualize>. Accessed on: Aug. 12 2019.

GEORGIEVA, N.; NIKOLOVA, I.; KOSEV, V. Evaluation of genetic divergence and heritability in pea (*Pisum sativum* L.). **Journal of BioScience and Biotechnology**, v.5, p.61-67, 2016.

GOULET, B.E.; RODA, F.; HOPKINS, R. Hybridization in plants: old ideas, new techniques. **Plant Physiology**, v.173, p.65-78, 2017. DOI: https://doi.org/10.1104/pp.16.01340.

GUINDON, M.F.; MARTIN, E.; CRAVERO, V.; GALI, K.K.; WARKENTIN, T.D.; COINTRY, ENRIQUE. Linkage map development by GBS, SSR, and SRAP techniques and yield-related QTLs in pea. **Molecular Breeding**, v.39, art.54, 2019. DOI: https://doi.org/10.1007/s11032-019-0949-8.

HUANG, X.; HAN, B. Natural variations and genome-wide association studies in crop plants. **Annual Review of Plant Biology**, v.65, p.531-551, 2014. DOI: https://doi.org/10.1146/annurev-arplant-050213-035715.

JANZEN, J.P.; BRESTER, G.W.; SMITH, V.H. **Dry peas**: trends in production, trade, and price. Montana: Agricultural Marketing Policy Center, 2014. (AMPC. Briefing, 57).

KOIDE, Y.; SAKAGUCHI, S.; UCHIYAMA, T.; OTA, Y.; TEZUKA, A.; NAGANO, A.J.; ISHIGURO, S.; TAKAMURE, I.; KISHIMA, Y. Genetic properties responsible for the transgressive segregation of days to heading in rice. **G3: Genes, Genomes, and Genetics**, v.9, p.1655-1662, 2019. DOI: https://doi.org/10.1534/g3.119.201011.

KOSEV, V.; PACHEV, I.; ANGELOVA, S.; MIKIĆ, A. Inheritance of quantitative traits in crosses between two *Pisum sativum* subspecies with particular reference to their breeding value. **Russian Journal of Genetics**, v.48, p.41-46, 2012. DOI: https://doi.org/10.1134/S102279541111010X.

KUMAR, M.; JEBERSON, M.S.; SINGH, N.B.; SHARMA, R. Genetic analysis of seed yield and its contributing traits and pattern of their inheritance in fieldpea (*Pisum sativum* L). **International Journal of Current Microbiology and Applied Sciences**, v.6, p.172-181, 2017. DOI: https://doi.org/10.20546/ijcmas.2017.606.021.

MAHMUD, I.; KRAMER, H.H. Segregation for yield, height, and maturity following a soybean cross. **Agronomy Journal**, v.43, p.605-609, 1951. DOI: https://doi.org/10.2134/agronj1951.00021962004300120005x.

MALLU, T.S.; MWANGI, S.G.; NYENDE, A.B.; GANGA RAO, N.V.P.R.; ODENY, D.A.; RATHORE, A.; KUMAR, A. Assessment of genetic variation and heritability of agronomic traits in chickpea (*Cicer arietinum* L.). **International Journal of Agronomy and Agricultural Research**, v.5, p.76-88, 2014.

REYES, B.G. de los. Genomic and epigenomic bases of transgressive segregation – new breeding paradigm for novel plant phenotypes. **Plant Science**, v.288, p.110-213, 2019. DOI: https://doi.org/10.1016/j.plantsci.2019.110213.

RIESEBERG, L.H.; ARCHER, M.A.; WAYNE, R.K. Transgressive segregation, adaptation and speciation. **Heredity**, v.83, p.363-372. 1999. DOI: https://doi.org/10.1038/sj.hdy.6886170.

SHAPIRO, S.S.; WILK, M.B. An analysis of variance test for normality (complete samples). **Biometrika**, v.52, p.591-611, 1965. DOI: https://doi.org/10.1093/biomet/52.3-4.591.

SHARMA, A.K.; SINGH, S.P.; SHARMA, M.K. Genetic variability, heritability and character association in pea (*Pisum sativum* L.). **Crop Research**, v.26, p.135-139, 2003.

SHREYA; AINMISHA; VASHANTI, R.P. Transgressive segregation study in F3 population of four groundnut crosses. **International Journal of Current Microbiology and Applied Sciences**, v.6, p.2054-2059, 2017. DOI: https://doi.org/10.20546/ijcmas.2017.604.243.

SING, J.D.; SING, I.P. Genetic variability, heritability, expected genetic advance and character association in field pea (*Pisum sativum* L.). **Legume Research: an International Journal**, v.29, p.65-67, 2006.

SRIVASTAVA, R.K.; SAXENA, K.B. The earliest maturing pigeonpea [*Cajanus cajan* (L.) Millspaugh] germplasm bred at ICRISAT. **Genetic Resources and Crop Evolution**, v.66, p.763-766, 2019. DOI: https://doi.org/10.1007/s10722-019-00743-3.

TIWARI, G.; LAVANYA, G.R. Genetic variability, character association and component analysis in F_4 generation of fieldpea (*Pisum sativum* var. arvense L.). **Karnataka Journal of Agricultural Sciences**, v.25, p.173-175, 2012.

UBAYASENA, L.; BETT, K.; TAR'AN, B.; WARKENTIN, T.D. Genetic control and identification of QTLs associated with visual quality traits of field pea (*Pisum sativum* L.). **Genome**, v.54, p.261-272, 2011. DOI: https://doi.org/10.1139/g10-117.

UPOV. Internacional Union for the Protection of New Varieties of Plants. **Guidelines for the conduct of tests for distinctness, uniformity and stability**: Pea: UPOV code: Pisum_SAT: *Pisum sativum* L. 2009. Available at: <https://www.upov.int/edocs/tgdocs/en/tg007.pdf>. Accessed on: Aug. 1 2019.

YADAV, B.; TYAGI, C.S.; SINGH, D. Genetics of transgressive segregation for yield and yield components in wheat. **Annals of Applied Biology**, v.133, p.227-235, 1998. DOI: https://doi.org/10.1111/j.1744-7348.1998.tb05823.x.