Transgressive segregations in two pea F\textsubscript{2} populations and their respective F\textsubscript{2:3} families

Abstract – The objective of this work was to evaluate the variability present in two pea (\textit{Pisum sativum}) F\textsubscript{2} populations and their corresponding F\textsubscript{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\textsubscript{2} population showed greater variation, whereas the yellow F\textsubscript{2:3} families had higher average values for most traits. In the green F\textsubscript{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\textsubscript{2} populations and 42% of the F\textsubscript{2} transgressive segregants in the F\textsubscript{2:3} generation. The distribution of F\textsubscript{2:3} families allows to select promising families according to the breeding program objectives.

Index terms: \textit{Pisum sativum}, genetic variability, heritability, principal component analysis.
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 F1 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 F2 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 F2 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 F2 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 F2 populations and their corresponding F2:3 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, F2 segregating populations and their F2:3 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

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from Spain and Zavalla 15 from Argentina have normal leaflets.

One hundred seeds of each F₂ 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°51'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-pyrole-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 F₂₃ 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 F₂ generations and in the F₂₃ families, morphological traits were assessed according to International Union for the Protection of New Varieties of Plants (UPOV, 2009). For the F₂ populations, the evaluations were carried out at the individual plant level, while, for the F₂₃ 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 F₂ population or gram per plot in the F₂₃ population).

For the F₂ 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 Mahmoud & 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 F₂ 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 F₂ 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 F₂₃ 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 F₂₃ families and the percentage of transgressive families from transgressive F₂ plants were also estimated, following the same criteria established for the F₂ generation. In order to observe the distribution of the F₂₃ families and select the superior ones considering all morphological traits, a principal components analysis was performed.

Results and Discussion

The green and yellow pea F₂ 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 (F₂).

In relation to the variation generated in the F₂ 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 F₂ generation, indicated by the low fluctuation between ranges for PL in the two populations. High TI values were found for NG in the green F₂ population and for PP, NG, and yield in the yellow F₂ 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 F₂. 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 F₂ 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 F₂; generation.

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

The analysis of the characters of the green F₂; population showed that, except for PL, the percentage of transgression was greater than or equal to 20, while, in the yellow F₂; population, no character had

### Table 1. Average values (AV), coefficient of variation (CV), range, and heritability (H₂) for productive traits of green and yellow pea (Pisum sativum) F₂ populations.

| Trait(1) | AV | CV | Range | H₂ |
|----------|----|----|-------|----|
| **Green F₂(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*  | 22.9 | 0.7–4.3 | 0.42 |
| Yield    | 10.6* | 86.9 | 7.5–25.4 | 0.96 |
| DAF      | 95.8* | 5.1  | 86–112 | 0.95 |

| **Yellow F₂(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* | 28.5 | 1–4.8  | 0.73 |
| Yield    | 8.58* | 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 Ica 5115 and Turf varieties. (3)Obtained from a cross between the Zavalla 15 and Amarilla varieties. *Significant by the F-test, at 5% probability. **Nonsignificant.

### Table 2. Percentage of transgression (T) and transgression index (TI) obtained for productive traits of green and yellow pea (Pisum sativum) F₂ populations.

| Trait(1) | Green F₂(2) | Yellow F₂(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 Ica 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 (Shrey 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

| Source of variation | DF | PH | PL | PP | NGP | NG | Yield | DAF |
|--------------------|----|----|----|----|-----|----|-------|-----|
|                    |    | MS | MS | MS | MS | MS | MS    | MS  |
| 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 | 0.09 | 0.90* | 2.507 | 0.56* | 1431.5 | 0.35 | 154 | 1.41  |

| 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 | 0.14 | 1.23* | 385.36 | 5.33* | 5330.9 | 0.42 | 135 | 2.52  |

Table 3. Analysis of variance for the different quantitative traits evaluated for green and yellow pea (Pisum sativum) \( F_{2:3} \) populations\(^{(1)}\).

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* | 26.5 | 26–142 | 21.9 (24.5) | 0.78 | 76.3* | 20.7 | 39–143 | 7.2 (8.0) | 0.78 |
| NGP            | 229.9* | 31.8 | 70–454 | 27.5 (31.9) | 0.72 | 237.2* | 27.1 | 104–403 | 2.06 (4.2) | 0.52 |
| NG             | 3.1*  | 20.7 | 1.7–4.9 | 41.8 (36.4) | 0.38 | 3.1*  | 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; 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.
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 S 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 F2 populations, high heritability values were obtained for most of the characters, whereas intermediate values were only found for NG for the green F2 population and PP for the yellow F2.

Figure 1. Principal component analysis of the yellow (A) and green (B) pea (Pisum sativum) F2.3 families evaluated. The varieties used to obtain the yellow and green populations, respectively, were: Ilica 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$_{2}$ 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.

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