

## Differential expression of the genetic variance in F<sub>2</sub> populations of reciprocal crosses of artichoke

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### Abstract

To perform artificial selection, the phenotypic trait of interest is measured on a population and those individuals with the extreme phenotypic values are bred to produce the next generation. Several breeders have recognized reciprocal effects as one source of genetic variability. The objective of this paper was to determine the gene actions, heterosis, and genetic variance present in reciprocal F<sub>2</sub> populations obtained by combining divergent artichoke cultivars. Days to first harvest, number of head per plant, weight of the main head, total yield and marketable yield per plant and the length-diameter ratio of main head were evaluated. For precocity and length-diameter ratio, the means value of F<sub>1</sub> generations were significantly different. The intermediate values between parents for precocity and length-diameter ratio indicate the presence of additive gene action, while for weight of the main head, total and marketable yield dominance effects were detected. For these traits the absolute mean parent heterosis is important but for marketable yield only the best parent heterosis is expressed (13.1%). F<sub>1</sub> reciprocal crosses were not significantly different in any case however, for the reciprocals F<sub>2</sub> all the comparisons indicate unexpected differences between them. The higher genetic variance developed in reciprocal F<sub>2</sub> facilitated the selection.

**Additional key words:** genetic diversity, genetic variance, globe artichoke, heterosis, reciprocal crosses.

### Resumen

#### Expresión diferencial de la variación genética en poblaciones F<sub>2</sub> provenientes de cruzamientos recíprocos en alcachofa

Al efectuar un proceso de selección artificial, se mide el carácter fenotípico de interés sobre una población y los individuos con los valores fenotípicos extremos son apareados para generar la siguiente generación. Distintos mejoradores han reconocido los efectos recíprocos como una fuente de variabilidad genética. El objetivo de este trabajo fue determinar las acciones génicas, la heterosis y la variación genética en poblaciones F<sub>2</sub> recíprocas obtenidas mediante la combinación de cultivares de alcachofa divergentes. Se evaluaron los días a primera cosecha, el número de capítulos por planta, el peso del capítulo principal, el rendimiento total y de mercado por planta y la relación entre longitud y diámetro del capítulo principal. Para la precocidad y la relación longitud-diámetro, el valor medio de las generaciones F<sub>1</sub> mostró valores intermedios entre los progenitores indicando la presencia de acción aditiva, mientras que para las variables peso del capítulo principal, el rendimiento total y de mercado, se encontraron efectos de dominancia. Para estas características la heterosis absoluta sobre el progenitor medio fue importante, pero sólo para el rendimiento de mercado se manifestó heterosis con respecto al progenitor superior (13,1%). Las cruces F<sub>1</sub> recíprocas no fueron significativas para ningún carácter, sin embargo, para las generaciones F<sub>2</sub> recíprocas todas las comparaciones realizadas indicaron diferencias inesperadas entre ellos. La mayor variación genética desarrollada en las F<sub>2</sub> recíproca facilitaría el proceso de selección.

**Palabras clave adicionales:** alcachofa, cruces recíprocas, diversidad genética, heterosis, variancia genética.

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Abbreviations used: ABPH (absolute best parent heterosis), AMPH (absolute mean parent heterosis), ES (Estrella del Sur FCA), FH (days to first harvest), He (broad sense heritability), IS (Imperial Star), MY (marketable yield), NH (number of heads per plant), PCA (principal components analysis), TY (total yield), WH (weight of the main head).

## Introduction

Globe artichoke (*Cynara cardunculus* L. var. *scolymus*) ( $2n = 2x = 34$ ) is a perennial and cross-pollinated vegetable (Pécaut, 1993) native of the Mediterranean basin (Rottenberg and Zohary, 1995; Sonnante *et al.*, 2007). Artichoke heads or capitula, which are immature composite inflorescences, are the edible parts of the plant and are used as a fresh, frozen or canned delicacy all over the world.

Globe artichoke is mainly vegetatively propagated; consequently, many diseases can be transmitted causing considerable losses of heads and even plants and can decrease crop productivity (Cravero *et al.*, 2005). These problems could be avoided if seed-propagated cultivars were available to growers. At the present time, seed propagated varieties of good quality and uniformity are scarce in the market; therefore, the production of seeds of high yielding varieties is an important objective for artichoke breeding programs. On other hand, precocity is an important agronomic trait, which determines the acceptance of the fresh product in the market. The use of precocious cultivars increases the profit because the production arrives at market when best prices are attained. On the other hand, the use of late cultivars can be destined to production plausible to be exported to northern countries in off-season conditions.

To date, in artichoke breeding few studies on the inheritance of a small number of main traits such as precocity, color head, spiny and compacity has been conducted (Pécaut, 1993; López Anido *et al.*, 1998; Mauromicale *et al.*, 2000; Cravero *et al.*, 2005). Most of the traits of economic importance such as yield and precocity are quantitative traits, implying that many genes, along with environmental effects, affect traits. By now, common breeding targets and selection have been based largely on intra-clonal variation (Deidda, 1967; Pécaut, 1993; Mauromicale *et al.*, 2000; Mallica *et al.*, 2004). A few attempts to exploit segregation released by inter-varietal hybridization or selfing have been reported in the literature (Tesi, 1976; Basnizky and Zohary, 1987, 1994). Due to the high level of heterozygosity present in segregating populations is normally possible to identify genotypes with valuable agronomic characters. Then, these selected genotypes can be maintained via vegetative propagation.

To perform artificial selection, the phenotypic trait of interest is measured on a population and the individuals with the extreme phenotypic values are bred to produce the next generation.

Several geneticists and breeders have recognized reciprocal effects as one source of genetic variability (Gonzalo *et al.*, 2007); however, there is little consensus in the literature concerning about the relative importance and systematic exploitation of these effects in practical breeding programs. The presence of reciprocal differences in the evaluation of breeding material has been documented since the early days of modern breeding (Polmer *et al.*, 1979) but in artichoke, no evidence has been presented up to time.

The objective of this paper was to determine the gene actions, heterosis, and genetic variance present in reciprocal  $F_2$  populations obtained by combining divergent cultivars for different traits.

## Material and methods

Two open-pollinated cultivars of artichoke from USA and Argentina were used. Imperial Star (IS,  $P_1$ ) was obtained by California University, Desert Research and Extension Center, with an early (tronco-conical green heads) and very high production (Schrader and Mayberry, 1992; Gil Ortega *et al.*, 1993; Gil and Villa, 2004). Estrella del Sur FCA (ES,  $P_2$ ) was obtained by the Rosario National University, Argentina, with a late (sub-spherical, compact, violet heads) and lower production (García *et al.*, 2006).

Both cultivars were reciprocally crossed using the same parental plants to generate reciprocal  $F_1$  generations and the same plants of  $F_1$  generations were selfed to obtain the reciprocal  $F_2$  populations. All these generations were obtained by the hand pollination technique. Both  $F_2$  populations, the parents, and  $F_1$  generations were sown in plastic plugs in a greenhouse in March 2006 and transplanted when plantlets reached two expanded leaves, approximately 45 days later, in the Experimental Field J. F. Villarino of Rosario National University, located at Zavalla, Argentina ( $33^\circ 01'S$  and  $60^\circ 53'W$ ).

A completely randomized design with three replications for each parental and  $F_1$  generations was used. Each plot was made up of 15 plants. Plant spacing was 140 cm between rows and 80 cm within rows. The  $F_2$  reciprocal populations were implanted in two adjacent plots with 200 plants each one.

In the spring of 2006 the following traits were evaluated: days to first harvest (FH), measured as the number of days from seed sowing to harvest the main head, number of heads per plant (NH), weight of the main

head (WH), total yield (TY), marketable yield (MY) per plant, as TY multiplied by the quality of the head. The quality was evaluated according Asprelli *et al.* (2001), by visual inspection using a scale ranging from 0.2 (poor quality) to 1 (best quality), considering spineless bracts, tightness, color and general aspect of main head. The length and diameter of main head were also evaluated to obtain the length-diameter ratio (R).

The normal distribution of the traits was tested according to Shapiro and Wilk (1965). The mean values were compared by ANOVA and Waller-Duncan multiple comparison test (Sokal and Rohlf, 1969). The distribution of frequency means and variance were obtained for all the traits and evaluated generations. The SAS software was used for all statistical analysis (SAS Institute, 1998).

The following parameters were tested with appropriate two tailed test:

- Absolute MPH (mean parent heterosis):  $AMPH = F_1 - P$ ; being P the mean value between parents.
- Absolute BPH (best parent heterosis):  $ABPH = F_1 - P_{max}$ .
- Reciprocal effect in  $F_1$ :  $Rec(F_1) = (P_1 \times P_2) - (P_2 - P_1)$ .
- Reciprocal effect in  $F_2$ :  $Rec(F_2) = (P_1 \times P_2)s - (P_2 - P_1)s$ .

Heterosis was calculated only for traits where dominance effects were present (Falconer and Mackay, 1996). Broad sense heritability ( $H_e$ ) for mean values for each  $F_2$  was calculated following Toker (2004) and Çakmakçý *et al.* (2006) from variance components.

To analyze the internal structure of the reciprocal  $F_2$  populations and to determine which variable contributed more to the total observed variance, principal components analysis (PCA) was performed. The PCA was carried out with the InfoGen software (Balzarini and di Renzo 2003).

## Results and discussion

The comparisons in all the traits indicate significant differences between parents (Table 1).

For FH, WH and R the mean values of  $F_1$  generations were significantly different with intermediate values between  $P_1$  and  $P_2$  indicating the presence of additive gene action for these traits while for TY and MY dominance effects were present. It is widely accepted that heterosis is consequence of dominance or overdominance effects. When gene actions are purely additive, the average phenotypic effects associated with alleles are independent of the genetic background. Hence, heterosis can not occur for traits with a purely additive genetic basis. This is the situation for FH, WH and R traits. Dominance effects are present for TY and MY. For both traits the absolute mean parent heterosis (AMPH) is important but only for MY the best parent heterosis (ABPH) is expressed (13.1%).

Reciprocal effects are due to genetic effects of the parents (*i.e.* maternal and paternal effects, cytoplasmic effects, and parent-of-origin effects) (Gonzalo *et al.*, 2007).  $F_1$  reciprocal crosses were not significantly

**Table 1.** Mean values and standard errors for days to first harvest (FH), weight of the main head (WH), number of heads (NH), total yield (TY), marketable yield (MY) and length-diameter ratio of head (R) in Imperial Star (IS) and Estrella del Sur (ES) cultivars and  $F_1$  and  $F_2$  generations

	FH	WH	NH	TY	MY	R
IS ( $P_1$ )	182.8 ± 1.3 <sup>d</sup>	347.5 ± 13.4 <sup>a</sup>	10.2 ± 0.6 <sup>a</sup>	1,631.8 ± 105.5 <sup>a</sup>	1,386.8 ± 108.4 <sup>a</sup>	1.17 ± 0.01 <sup>a</sup>
ES ( $P_2$ )	204.0 ± 1.2 <sup>a</sup>	288.3 ± 11.8 <sup>b</sup>	9.0 ± 0.5 <sup>ab</sup>	1,251.6 ± 79.4 <sup>b</sup>	1,052.5 ± 70.1 <sup>b</sup>	0.93 ± 0.01 <sup>c</sup>
Mean	193.4	317.9	9.6	1441.7	1219.7	1.05
$F_1$ IS × ES	188.3 ± 1.4 <sup>c</sup>	318.8 ± 8.9 <sup>a</sup>	10.7 ± 0.6 <sup>a</sup>	1,664.4 ± 82.5 <sup>a</sup>	1,526.3 ± 87.8 <sup>a</sup>	1.05 ± 0.02 <sup>b</sup>
$F_1$ ES × IS	190.5 ± 1.7 <sup>c</sup>	312.2 ± 7.4 <sup>a</sup>	10.5 ± 0.7 <sup>a</sup>	1,736.3 ± 109.4 <sup>a</sup>	1,610.4 ± 103.6 <sup>a</sup>	1.04 ± 0.02 <sup>b</sup>
Mean	189.4	315.5	10.6	1700.35	1568.4	1.045
$F_2$ IS × ES	198.1 ± 0.6 <sup>b</sup>	210.6 ± 3.3 <sup>c</sup>	7.5 ± 0.2 <sup>b</sup>	857.8 ± 26.8 <sup>c</sup>	670.4 ± 26.9 <sup>c</sup>	1.17 ± 0.01 <sup>a</sup>
$F_2$ ES × IS	201.5 ± 0.6 <sup>ab</sup>	246.9 ± 4.5 <sup>b</sup>	9.9 ± 0.3 <sup>a</sup>	1,276.5 ± 43.4 <sup>b</sup>	1,094.7 ± 40.6 <sup>b</sup>	1.03 ± 0.02 <sup>b</sup>
Mean	199.8	228.8	8.7	1,067.2	882.6	1.12
Absolute mean parent heterosis	—	—	—	258.7 (17.9%)	174.4 (28.5%)	—
Absolute best parent heterosis	—	—	—	—	90.8 (13.1%)	—

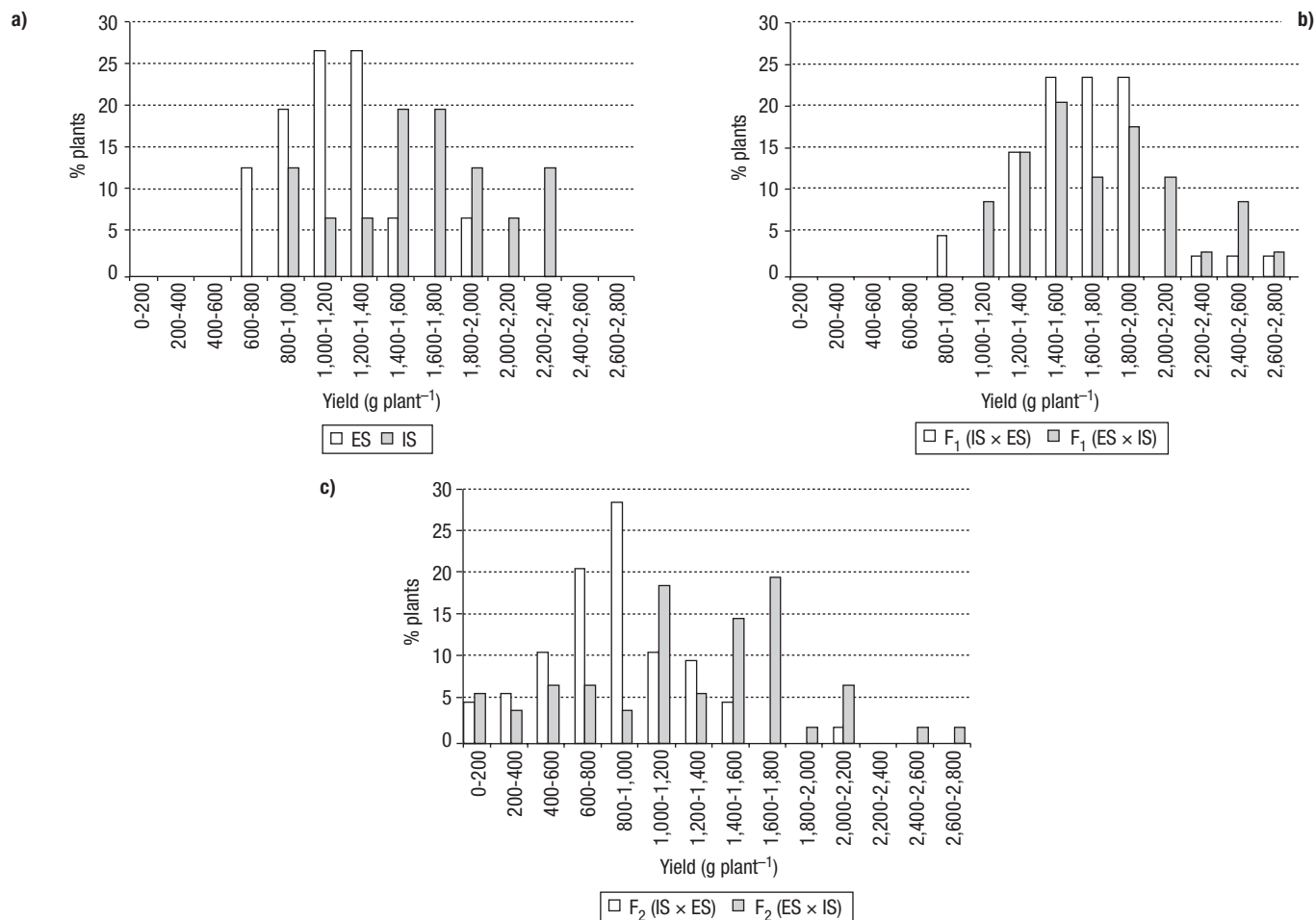
different in any case indicating that for the evaluated traits these crosses were controlled mostly by the genotype of the embryo and not by the genotype of maternal parent. However, for the reciprocal  $F_2$  all comparisons indicate unexpected differences between them. These results suggest that these traits are not affected by maternal effect carried out in  $F_1$ . Crop geneticist and breeders have recognized reciprocal effects as one source of genetic variability (Mann and Pollmer, 1981). In many cases, the differences between reciprocal hybrids, attributed to cytoplasmic and/or cytonuclear interactions contributed to divergence (Etterson *et al.*, 2006). However, our results demonstrated that the nonequivalence of reciprocals regards with the quantitative traits evaluated was manifested in the second and not in the first filial generation.

The success in identifying an artichoke genotype with increased high quality yield depends on genetic

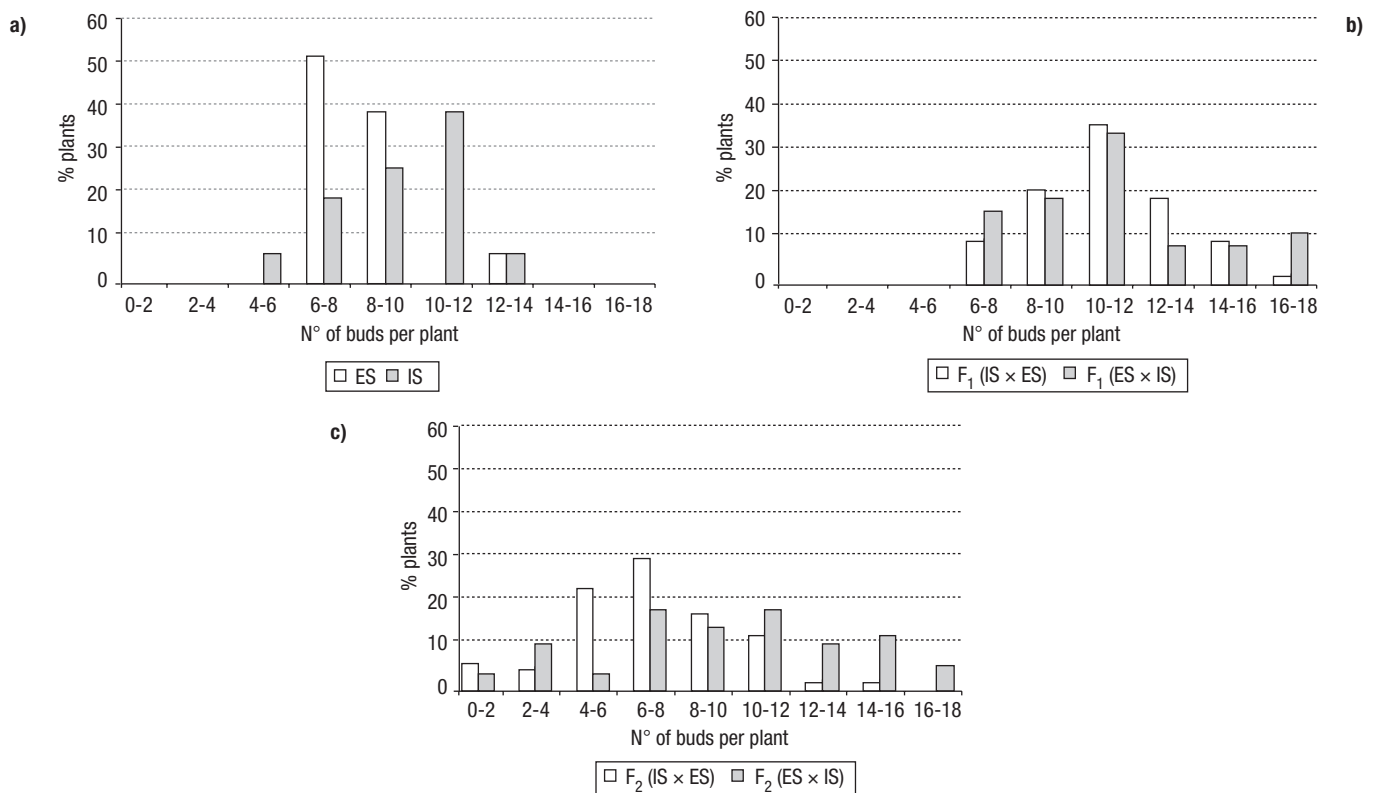
variation available. Thus, to know the genetic variation in those traits of interest is fundamental to achieve effective plant breeding.

The distribution of frequencies for each trait revealed an increase in the number of classes and variation range in  $F_2$  (ES  $\times$  IS) compared to  $F_2$  (IS  $\times$  ES) (Figs. 1 and 2). These results imply that different ranges of recombination are presents in the  $F_2$ s. The inflated segregational variance of the  $F_2$  (ES  $\times$  IS) (Table 2) could be attributed to recombination differentials of supergenes involved. This fact makes possible the arising of new genetic combinations, enlarging the genotypic classes and facilitating selection. In both  $F_2$  populations, some individuals exhibit phenotypes outlying the range of variations of both parental populations indicating transgressive segregation.

Positive transgressive segregation for total yield was found only in  $F_2$  (ES  $\times$  IS) (3.7%) whereas negative



**Figure 1.** Frequency distribution for total yield (TY) in a) parental generation, b) reciprocal  $F_1$  generation, c) reciprocal  $F_2$  populations. ES: Estrella del Sur FCA. IS: Imperial Star.



**Figure 2.** Distribution of frequency for number of heads (NH) in a) parental generation, b) reciprocal F<sub>1</sub> generation, c) reciprocal F<sub>2</sub> populations. ES: Estrella del Sur FCA. IS: Imperial Star.

transgressive segregation was found in both F<sub>2</sub> populations (22.5% in F<sub>2</sub> IS × ES and 17.0% in F<sub>2</sub> ES × IS).

The results of PCA are shown in Table 3. The two first principal components (PC) explained 80.0% (60% PC<sub>1</sub> and 20% PC<sub>2</sub>) and 81.0% (65% PC<sub>1</sub> and 16% PC<sub>2</sub>) of the total variation observed for both F<sub>2</sub> populations. The compositions of PCs are different in both F<sub>2</sub> mainly by WH. These results were not clearly interpretable; however some possible explanations are stressed. The

genetic recombination in a given organism can vary considerably due to many factors. It is known that the amount of recombination between marker loci can be increased or decreased by environmental factors such as temperature during gametogenesis. In many organisms, recombination during male and female gametogenesis occurs at different rates (Reeves *et al.*, 1990; Burt *et al.*, 1991). In plants, very little is known about different rates of recombination in male and female gameto-

**Table 2.** Variance values and heritability (He) for days to first harvest (FH), weight of the main head (WH), number of heads (NH), total yield (TY), marketable yield (MY) and length-diameter ratio of head (R) in Imperial Star (IS) and Estrella del Sur (ES) cultivars and F<sub>1</sub> and F<sub>2</sub> generations

	FH	WH	NH	TY	MY	R
IS (P <sub>1</sub> )	24.01	2,735.3	6.25	169,332.3	17,8675.3	0.0025
ES (P <sub>2</sub> )	21.16	2,106.8	3.24	95,976.1	74,747.6	0.0016
F <sub>1</sub> IS × ES	31.36	1,197.2	6.25	103,555.2	106,732.9	0.0049
F <sub>1</sub> ES × IS	46.24	823.7	8.41	181,902.3	163,296.8	0.0064
F <sub>2</sub> IS × ES	72.25	2,227.8	9.61	142,808.4	157,767.8	0.0144
F <sub>2</sub> ES × IS	68.89	4,057.7	19.36	373,932.3	328,443.6	0.0484
He <sub>IS × ES</sub>	0.57	0.23	0.38	0.05	0.19	0.74
He <sub>ES × IS</sub>	0.55	0.58	0.69	0.64	0.61	0.92

**Table 3.** Eigenvalues for PC<sub>1</sub> and PC<sub>2</sub> in F<sub>2</sub> reciprocal crosses between Imperial Star (IS) and Estrella del Sur (ES) cultivars

Variables	F <sub>2</sub> IS × ES		F <sub>2</sub> ES × IS	
	e <sub>1</sub>	e <sub>2</sub>	e <sub>1</sub>	e <sub>2</sub>
FH	-0.39	0.22	-0.41	0.14
WH	0.45	0.04	0.39	-0.41
NH	0.41	-0.29	0.43	0.30
TY	0.50	-0.10	0.48	0.33
MY	0.45	0.20	0.47	0.18
R	-0.16	-0.90	-0.20	0.77

genesis. In tomato, some experiments showed a higher rate of recombination during female gametogenesis (De Vincente and Tanksley, 1993; Van Oijen *et al.*, 1994). In some organisms, the most of meiotic recombinant events fall in recombinational hotspots whose presence can be influenced by the genetic makeup (haplotype) as well as the sex of the parental heterozygote involved in the recombination event (Lafuse and David, 1986; Steinmetz *et al.*, 1986; Shiroishi *et al.*, 1990).

Independently of the cause, the greater genetic variance developed in F<sub>2</sub> (ES × IS) allowed the selection. In clonally reproduced plants such as artichoke, the entire genome is inherited intact, acting as a single linkage group. On the other hand, in sexual reproduction systems the transmission of genes at different loci are independent events and the crossing-over is the responsible. An increase in genetic variance may enhance selection response. Thus, this strategy in artichoke breeding has strong implications since quickly can be obtained a rapid selection response and phenotypic uniformity.

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