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Diallel analysis for traits of economic importance in globe artichoke (*Cynara scolymus*)

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Abstract A breeding strategy for globe artichoke (*Cynara scolymus*) is suggested after General and Specific Combining Ability between several clones were estimated to determine the gene action for yield-related and morphological traits. Two sets of diallel crosses, without parents, using four selected clones in each were developed. A completely randomised design with three replications for each diallel cross was used. Significant differences between the mean values of several traits among both diallel sets were found. Most of the variables evaluated were primarily controlled by additive genetic effects. Therefore, simple recurrent selection would be effective for increasing the mean value of these variables.

Keywords *Cynara scolymus*; general combining ability; specific combining ability; additive gene action; non-additive gene action; diallel crosses; clones; breeding strategy; seed multiplication; vegetative propagation

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INTRODUCTION

Commercially, globe artichoke (*Cynara scolymus* L.) is mainly vegetatively propagated. Consequently, many diseases can be transmitted causing considerable losses of heads and even plants, thus lowering crop productivity. Furthermore, the general vigour of the culture is often reduced (Ryder et al. 1983). These problems could be avoided if seed-propagated cultivars were available to the growers.

Most of the globe artichoke cultivars are highly heterozygous *per se*. Those commercial varieties that are propagated by cloning of a single selected genotype can show in their yield either additive or the dominance-epistatic effects (Hayward & Bresse 1994). Therefore, when they had been propagated by seed, the yield of their progeny is frequently different from that of the parental generation. The market requires homogeneous heads of commercially acceptable uniformity from open-pollinated seed-propagated varieties as well as from inbreed lines and F_1 hybrids. At the present time, seed for varieties of good quality and uniformity is scarce in the globe artichoke market. Consequently, the production of seeds for high yielding varieties is an important objective of artichoke breeding programmes. In such programmes the selection of the best clones as parental genotypes and their subsequent cross-pollination could generate a large amount of genetic variability. Estimates of the genetic components of this variability can be used to determine its significance in a given cross and to estimate the relative importance of additive versus non-additive variation. The breeding procedure to be applied will depend on the prevalence of one or the other type of gene action.

The diallel analysis method of Griffing (1956), especially method IV, explores gene action involved in quantitative traits (Cruz & Vencovsky 1989; Ramalho et al. 1993). The diallel approach was originally used to analyse crosses between homozygous lines, but as shown by Griffing (1956) and Oakes (1967), they may be also applied to analyse the amount and the kind of genetic variability generated by crossing genetically heterogenous clones.

The aim of our study was to estimate the General and Specific Combining Ability between several clones of globe artichoke to determine the gene action for yield-related and morphological traits. A breeding strategy for this crop will then be recommended.

MATERIAL AND METHODS

We performed two sets of diallel crosses without parents (Griffing, Method 4, Model I, 1956) with four selected clones in each. The first set (Diallel I) was composed of clones that are frequently used in the local area (Ñato, Precoce Italiano, Camus de Bretagne, Francés) and the second set (Diallel II) was composed of clones that were obtained from a local breeding programme (named as 102, 107, 112, 116). The hybrid seed within each diallel was obtained by hand pollination. The experiments started in February 1999 at the Experimental Field J. F. Villarino of Rosario National University, Argentina (33º01′SL, 60º53′WL and 50 m a.s.l.).

A completely randomised design with three replications for each diallel cross was used. Each plot was made up of 15 plants. Plant spacing was 140 cm between rows and 80 cm within rows. In the spring of 2000 the following traits were evaluated: days to first harvest (FH) measured as the number of days from shoot plantation to harvest of the main head, number of heads per plant (NH) considering only a single shoot, weight of the main head (WH), total yield (TY), and marketable yield (MY) per plant (total yield multiplied by the quality of the heads that was evaluated by visual inspection using a scale ranging from 0.2 to 1 taking into account the spineless bracts, tightness, colour and general aspect of main head) (Asprelli et al. 2001). The following traits were also evaluated: length (LH) and diameter (DH) of the main head, length-diameter ratio (R), receptacle weight (WR), receptacle height (HR), and receptacle diameter (DR) of the first head and the length (LB) and width (WB) of the bract. These traits were measured on bracts of the third external line on the first head.

The normal distribution of the traits was tested according to Shapiro & Wilk (1965). The mean values of the traits among the two diallel sets were compared by ANOVA (Sokal & Rholf 1969). Griffing Method 4, Model 1 (1956) was used to partition the sum of squares for the crosses into General Combining Ability (GCA) and Specific Combining Ability (SCA). The analysis of variance was carried out by the Interactive Basic program (Magari & Kang 1994) following the model:

$$Y_{ijk} = m + a_i + b_{ij} + e_{ijk}$$

where Y_{ijk}, mean performance of the i^{th} parental line mated to the j^{th} parental line; m, the general mean; a_i, the general combining ability of the i^{th} (j^{th}) parental line; b_{ij}, the interaction of the i^{th} and j^{th} parents; and e_{ijk}, the random error.

The GCA:SCA ratios, with a theoretical maximum of unity for each trait, were computed according to Baker (1978) as follows: $GCA{:}SCA = 2\alpha^2 g_i/(2\alpha^2 g_i + \alpha^2 s_{ij})$ where g_I = the GCA effect of the *i* parent and s_{ij} = the SCA effect of the cross *i x j*.

RESULTS

We found significant differences between the mean values of the traits among both diallel except for WH and FH traits (Table 1). Diallel II had higher values for the yield-related variables than Diallel I such as NH, TY and MY, WR, LR, and DR. Diallel I had plants with more conic heads (R = 1.14) than Diallel II (R = 1.03) and these differences were because of the LB (6.23 cm versus 5.74 cm, respectively). Mean values for the different crosses in each diallel are shown in Table 2. The respective GCA and SCA values and the ratio GCA:SCA are shown in Table 3.

It was found that GCA was significant for most of the variables in Diallel I, except for DR. However, for SCA only the WH and WR variables were highly significant.

In Diallel II, the mean values of LH, LB, WB, and MY were not significant between crosses. For NH and LR, only the GCA was significant whereas both GCA and SCA were significant for DH, R, WR, FH, and TY. For DR, only the SCA was significant.

In Diallel I, the variety Camus de Bretagne produced, in any combination, offspring with the highest values for TY ($g_i = 96.5$) and MY ($g_i = 96.7$) (Table 4). Also, crosses involving this variety had the largest NH ($g_i = 0.5$) of globular forms. In Diallel II, clone 116 showed a tendency to generate offspring with the higher TY ($g_i = 95.9$) through an increment in NH ($g_i = 0.8$) (Table 4). The best performance for TY was obtained for cross 116 × 112 (x = 836.43 g) (Table 2).

The relative sizes of mean squares can be used to assess the relative importance of GCA and SCA. The

GCA:SCA ratio for WH in Diallel I; DH, R, FH, and TY for Diallel II and WR in both diallel sets were greater than 0.5 (0.62 to 0.69). Therefore, the predictability of performance may be based on GCA alone.

DISCUSSION

The differences observed between both diallels could be attributed to the different origins of the genotypes in each set. In Diallel I, the parents were traditional cultivars whereas in Diallel II, the parents were obtained from a local breeding programme where one of the objectives is head tightness.

Dellacecca & Marzi (1976) have demonstrated the existence of a tight relationship between the form of the head and its tightness and Macua (1996) has also pointed out that this last trait is very important for both the processing industry and the fresh market. In this way, the most compact buds would correspond to those with a globular form because the disposition and form of the bract inserts contribute to their tightness.

The Model I of Griffing's analysis gives useful information for the selection of parents that have good GCA in a series of crosses and good SCA for specific pairs of parents. By definition, the mean performance, when expressed as a deviation from the mean of all crosses, is the GCA of the clone. Any particular cross has an "expected" value, which is the sum of the GCA of its parental clones. The cross, however, might deviate from this expected value to a greater or lesser extent. This deviation is called the SCA of the two clones in combination (Falconer & Mackay 1996). The GCA is supported mainly by additive genetics effects. The SCA term was interpreted by Sprague & Tatum (1942) as associated to genes with dominant and epistatic effects. Falconer (1991) has shown that heterosis will be expressed under the following conditions: presence of some level of dominance and relative difference in gene frequency of the parents to determine the magnitude of the heterosis expressed in crosses.

This implies that the traits with a significant SCA could be improved through the production of hybrids whereas selection could be made when the additive component is the more important gene action. Pacucci et al. (1973) and De Pace et al. (1973) showed that the variability of globe artichoke populations is a result of additive gene effects, although for some traits, such as weight of the first head and some secondary characteristics, dominant or non-additive gene effects prevail.

Because the SCA mean square was not significant for most of the variables in Diallel I, it would be possible to accept the hypothesis that the performance of a single-cross progeny can be predicted by the GCA values. The best performing progeny may be produced by crossing the two parents having the highest GCA.

The evaluations were carried out during one year. López Anido et al. (1998) in a study of several clones during a 3-year period, and in the same experimental

Table 1 Mean value and standard error for number of heads (NH); weight (WH), length (LH), and diameter (DH) of main head; length-diameter ratio (R), length (LB), and width (WB) of the bract; weight (WR), length (LR), and diameter (DR) of the receptacle; days to first harvest (FH); total yield (TY) and marketable yield (MY) in both diallel sets. (NS, not significant.)

	N	Diallel I	Diallel II	*F*
NH	18	3.68 ± 1.71	4.56 ± 1.96	11.39 $P < 0.001$
WH (g)	18	219.42 ± 44.78	225.30 ± 33.72	NS
LH (cm)	18	9.08 ± 0.15	8.46 ± 0.08	13.66 $P < 0.001$
DH (cm)	18	7.99 ± 0.08	8.26 ± 0.09	5.06 $P < 0.05$
R	18	1.14 ± 0.03	1.03 ± 0.02	13.30 $P < 0.001$
LB (cm)	18	6.23 ± 0.59	5.74 ± 0.24	10.62 $P < 0.001$
WB (cm)	18	4.27 ± 0.25	4.06 ± 0.24	6.82 $P < 0.05$
WR (g)	18	61.10 ± 12.42	76.60 ± 19.01	8.39 $P < 0.001$
LR (cm)	18	2.06 ± 0.23	2.29 ± 0.35	5.26 $P < 0.01$
DR (cm)	18	6.00 ± 0.43	6.53 ± 0.49	11.96 $P < 0.001$
FH	18	170.28 ± 7.64	174.08 ± 5.76	NS
TY (g)	18	583.38 ± 101.35	705.01 ± 101.71	12.92 $P < 0.001$
MY (g)	18	196.03 ± 80.42	305.26 ± 74.80	17.80 $P < 0.001$

Table 2 Mean value for number of heads (NH); weight (WH), length (LH), and diameter (DH) of main head; length-diameter ratio (R), length (LB), and width (WB) of the bract; weight (WR), length (LR) and diameter (DR) of the receptacle; days to first harvest (FH); total yield (TY) and marketable yield (MY) for each cross in both diallels sets. (PI, Precoce Italiano; CB, Camus de Bretagne.)

		Diallel I		
		Ñato	PI	CB
NH	Francés	3.57	2.90	3.83
	Ñato	–	3.60	4.03
	PI	–	–	4.27
WH (g)	Francés	185.80	226.23	213.63
	Ñato	–	237.57	231.10
	PI	–	–	222.20
LH (cm)	Francés	9.61	9.16	8.75
	Ñato	–	9.89	8.68
	PI	–	–	8.37
DH (cm)	Francés	7.55	7.89	8.22
	Ñato	–	7.95	8.28
	PI	–	–	8.11
R	Francés	1.27	1.20	1.06
	Ñato	–	1.25	1.07
	PI	–	–	1.03
LB (cm)	Francés	6.54	6.85	5.72
	Ñato	–	6.83	5.63
	PI	–	–	5.79
WB (cm)	Francés	3.99	4.25	4.17
	Ñato	–	4.51	4.19
	PI	–	–	4.52
WR (g)	Francés	74.91	53.76	67.98
	Ñato	–	45.11	50.81
	PI	–	–	74.01
LR (cm)	Francés	2.28	1.79	2.18
	Ñato	–	1.74	2.08
	PI	–	–	2.03
DR (cm)	Francés	6.06	5.77	6.16
	Ñato	–	5.73	5.80
	PI	–	–	6.50
FH	Francés	172.13	165.57	171.37
	Ñato	–	169.77	180.03
	PI	–	–	162.83
TY (g)	Francés	508.73	471.05	607.98
	Ñato	–	577.30	669.52
	PI	–	–	665.63
MY (g)	Francés	141.01	122.51	257.45
	Ñato	–	131.17	267.34
	PI	–	–	256.69

		Diallel II		
		112	107	102
NH	116	5.20	5.00	5.17
	112	–	3.30	4.13
	107	–	–	4.57
WH (g)	116	239.93	209.20	231.23
	112	–	208.40	234.40
	107	–	–	228.73
LH (cm)	116	8.13	8.41	8.61
	112	–	8.45	8.55
	107	–	–	8.63
DH (cm)	116	8.63	7.66	8.03
	112	–	8.46	8.52
	107	–	–	8.26
LB (cm)	116	5.49	5.63	5.83
	112	–	5.85	5.70
	107	–	–	5.94
WB (cm)	116	3.99	3.99	3.88
	112	–	4.43	3.99
	107	–	–	4.05
WR (g)	116	73.37	75.98	100.17
	112	–	65.84	61.35
	107	–	–	79.55
LR (cm)	116	2.26	2.23	2.83
	112	–	1.93	2.32
	107	–	–	1.88
DR (cm)	116	6.37	6.52	7.04
	112	–	6.70	6.07
	107	–	–	6.83
FH	116	164.67	173.07	172.37
	112	–	179.83	174.53
	107	–	–	180.00
TY (g)	116	836.43	721.77	748.73
	112	–	536.92	709.32
	107	–	–	676.92
MY (g)	116	379.82	296.72	296.03
	112	–	258.17	291.65
	107	–	–	309.18

Table 3 *F* values of the analysis of variance for number of heads (NH); weight (WH), length (LH), and diameter (DH) of main head; length-diameter ratio (R), length (LB), and width (WB) of the bract; weight (WR), length (LR), and diameter (DR) of the receptacle; days to first harvest (FH); total yield (TY) and marketable yield (MY); and the GCA:SCA ratio in both diallel sets.

	Diallel I				Diallel II			
	F				*F*			
	Cross	GCA	SCA	GCA:SCA	Cross	GCA	SCA	GCA:SCA
NH	3.45	4.71	NS		4.77	6.36	NS	
	$P < 0.05$	$P < 0.05$			$P < 0.05$	$P < 0.05$		
WH	9.54	9.07	10.24	0.69	9.12	NS	22.02	
	$P < 0.01$	$P < 0.01$	$P < 0.01$		$P < 0.01$		$P < 0.01$	
LH	12.31	18.32	NS		NS	NS	NS	
	$P < 0.01$	$P < 0.01$						
DH	3.93	3.99	NS		13.02	11.65	15.07	
	$P < 0.05$	$P < 0.05$			$P < 0.01$	$P < 0.01$	$P < 0.01$	0.62
R	9.84	16.30	NS		6.14	4.20	9.05	
	$P < 0.01$	$P < 0.01$			$P < 0.01$	$P < 0.05$	$P < 0.01$	0.69
LB	12.86	21.26	NS		NS	NS	NS	
	$P < 0.01$	$P < 0.01$						
WB	4.30	6.65	NS		NS	NS	NS	
	$P < 0.05$	$P < 0.01$						
WR	27.18	14.70	45.89	0.69	29.81	18.12	47.34	
	$P < 0.01$	$P < 0.01$	$P < 0.01$		$P < 0.01$	$P < 0.01$	$P < 0.01$	0.69
LR	5.56	6.86	NS		8.78	12.59	NS	
	$P < 0.05$	$P < 0.01$			$P < 0.01$	$P < 0.01$		
DR	NS	NS	NS		2.91	NS	4.73	
					$P < 0.05$		$P < 0.05$	
FH	5.67	7.93	NS		13.48	14.05	12.64	
	$P < 0.01$	$P < 0.01$			$P < 0.01$	$P < 0.01$	$P < 0.01$	0.69
TY	5.28	8.66	NS		10.68	10.18	11.44	
	$P < 0.05$	$P < 0.01$			$P < 0.01$	$P < 0.01$	$P < 0.01$	0.67
MY	4.63	7.71	NS		NS	NS	NS	
	$P < 0.05$	$P < 0.01$						

Table 4 General Combining Ability effects for each parent (PI, Precoce Italiano; CB, Camus de Bretagne).

Diallel I					Diallel II				
	g_i					g_i			
Variable	Francés	Ñato	PI	CB	Variable	116	102	107	112
NH	–0.4	0.05	–0.2	0.5	NH	0.8	–0.5	0.08	–0.3
WH	–16.3	–1.9	13.9	4.3	DH	–0.2	0.1	–0.2	0.3
LH	0.1	0.5	0.1	–0.7	R	0.02	0.03	0.004	–0.05
DH	–0.2	–0.1	–0.03	0.3	WR	10.7	–0.4	–5.6	–4.7
R	0.04	0.08	0.02	–0.1	LR	0.3	0.2	–0.1	–0.3
LB	0.2	0.2	0.4	–0.8	FH	–6.1	2.2	2.7	1.1
WB	–0.2	–0.06	0.2	0.03	TY	95.9	–60.0	–3.5	–32.4
WR	6.7	–6.2	–5.2	4.8					
LR	0.1	0.02	–0.2	0.1					
FH	–0.9	5.5	–6.3	1.7					
TY	–81.2	2.7	–18.1	96.5					
MY	–33.6	–24.3	–38.9	96.7					

field as this current work, did not find significant clones-year interactions for yield, bud weight, diameter and height of the heads. However, the plants following the first year of evaluation were asexually propagated. This propagation modality allows a change in development as demonstrated by Cosentino & Mauromicale (1990) and Esteva (1999). Plants that originate from seeds use water and nutrients more efficiently because of the development of a pivotal radicular system that penetrates more deeply into the soil than the adventitious root system of the vegetatively propagated shoot. Thus, propagation system has the potential to impact on yield. Tesi (1976) found that material derived from seed is generally more vigorous and has higher shoot production than material of asexual origin.

The present trend for artichoke multiplication is by botanical seed. Thus, it is important that the selection of parental lines to be used for hybrid production should be made under the same propagation conditions. Although for the parents used in this study the SCA effect was relatively small for most traits, using sexually produced seed means a heterotic effect is possible. The additional benefit of the development of a pivotal root system is an added factor to explain increased vigour and productivity of the plant.

CONCLUSIONS

Most of the variables evaluated are primarily controlled by additive genetic effects. However the inferences must be limited to the four-parent diallel experiments, because the parents were not selected at random. The large magnitude of GCA effects compared to the SCA effects strongly indicates that additive gene action is the primary determinant in this sample of parents.

Breeding schemes such as simple recurrent selection, which make use of additive genetic variance, would be effective for increasing the mean value of those variables that show significant GCA in a population derived from the material examined. Where dominant effects are important, hybrid varieties will show the highest performance.

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