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Combining ability and correlations for yield components in early generations of potato breeding

J. I. Ruiz de Galarreta, B. Ezpeleta, J. Pascualena and E. Ritter

NEIKER – Basque Institut for Agricultural Research, P.O. Box. 46, E 01080-Vitoria, Spain, E-mail: jiruiz@neiker.net

With 4 tables

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Abstract

A partial diallel set of crosses was made between 14 potato cultivars chosen for their fertility, from those included in a potato breeding programme at the NEIKER – Basque Institute for Agricultural Research. The progeny were grown in completely randomized trials from 1997 to 1999. Performance for yield, tuber number and average tuber weight was analysed in seedling and two clonal generations. Variance estimates due to both general combining ability (GCA) and specific combining ability (SCA) were significant in all generations for all traits under study. However, SCA was more important than GCA in almost all cases. Correlation coefficients among characters, generations, GCA and SCA effects were examined. For tuber yield no relation was obtained between generations; however, average tuber weight and yield were positively associated in all generations. The results indicate that appropriate selection criteria depend strongly on the particular cross. The implication for a breeding strategy are discussed.

Key words: *Solanum tuberosum* — seedlings — general combining ability — specific combining ability

Several studies of combining abilities for yield components are available in potato. However, contradictory results have been obtained. Some authors found a preponderance of general combining abilities (GCA) to be more important than specific combining abilities (SCA; Plaisted et al. 1962, Tai 1976, Killick 1977, Gopal 1998), while other authors suggested that SCA was more important (Veilleux and Lauer 1981, Brown and Caligari 1986, Maris 1989, Neele et al. 1991, Bradshaw et al. 2000, Ortiz and Golmirzaie 2004). Most of these works analysed the first clonal generation (FCG) of a potato breeding programme. There is hardly any information about combining ability in the seedling generation (SG) and its variation in subsequent generations.

From a practical point of view it would be convenient if performance of particular genotypes could be predicted at the seedling stage in order to reduce the amount of plant material for selection from the beginning. For this purpose a close relationship between seedling performance and performance in subsequent field generations must exist. Again, different opinions can be found in the literature. Selection at the seedling stage does not seem to be efficient according to Tai and Young (1984) and Neele et al. (1991). However, according to Brown and Caligari (1986), Caligari et al. (1986), Maris (1988) and Gopal (1992), this is possible, but with some limitations.

The objective of this study was to assess tuber yield and its components, trait correlations and combining ability effects in an incomplete diallel cross of 14 potato cultivars over three successive generations. The results are used to illustrate the value and limitations of a diallel analysis for use in a potato breeding programme.

Materials and Methods

A set of 14 male-fertile parents (cv. 'Asterix', 'Leyla', 'Lido', 'Lyra', 'Nena', 'Karida', 'Sissi', 'Margit', 'Optima', 'Sandra', 'Berolina', 'Tomensa', 'Cinja' and 'Ute') from the local potato breeding programme *Solanum tuberosum* L. at NEIKER-Basque Institute of Agricultural Research (Vitoria, Spain) were crossed with each other resulting in an incomplete diallel of 34 progeny. Male parents were selected on the basis of their diversity and capacity to produce abundant fertile pollen. Each cultivar participated as parent in four to nine crosses. No selfs or reciprocal crosses were considered.

Crosses were performed during the summer of 1996 in Arkaute (northern Spain, 550 m above sea level). The 34 progeny obtained were grown and evaluated in the field in Iturrieta (northern Spain, 990 m above sea level) from 1997 to 1999, in three successive generations (SG and two clonal generations).

Seeds were sown in wooden trays containing a 1 : 1 (v/v) mixture of compost and sand. Twenty-five days after sowing, the seedlings were transplanted to polythene bags (5 × 10 cm) containing a 1 : 1 (v/v) mixture of compost and sand. After another 25 days, seedlings along with the soil balls were transplanted into the field at distances of 35 cm within and 75 cm between rows. At harvest of the SG 20, genotypes were selected randomly per progeny. Three homogeneous tubers were retained and stored in a darkened cold room at 4°C until the planting next year. On 21 May 1998, this FCG was planted in Iturrieta in a completely randomized design with three replications. The plots were planted in short rows of five tubers with intra- and inter-row distances of 35 and 75 cm, respectively. The same procedure was repeated to plant the second clonal generation (SCG) on 25 May 1999 in Iturrieta using the same design as in the previous year. The fertilizer applied and the use of herbicides, fungicides and aphicides were the standard for seed potatoes in Spain.

Data were recorded for all 34 progeny in the three generations. Tuber yield per plant, number of tubers per plant and average tuber weight were recorded. Correlations were established between characters, between generations and between characters and generations, considering either the individual data of the seedlings, or the means of the three replicates in the clonal generations. Mean squares of GCA and SCA were calculated applying the method of Garretsen and Keuls (1977), based on progeny means. Correlation analyses were also performed for GCA and SCA effects between characters and between generations. All computations were performed using the SAS program (SAS 2000).

Results

Character correlations based on average family values as well as on all genotype values are shown in Table 1 for all three generations. Correlations between character pairs showed in many cases a closer relationship within than between generations.

Considering family performances within generations, a negative association between tuber number and average tuber weight can be observed in the FCG ($r = -0.67$) and (SCG) ($r = -0.70$), while these characters were not related in the SG. In contrast, no relationship was found between tuber number and yield in clonal generations, while in the SG these characters were highly correlated ($r = 0.76$). However, average tuber weight and yield were positively associated in all generations. Moderate but significant correlation coefficients were found for tuber numbers between all pairs of generations. For average tuber weight a significant correlation was observed only between the FCG and SCG ($r = 0.56$). For tuber yield no relation was obtained between generations. Apparently, average tuber weight of FCG had a negative effect on tuber number of the second generation ($r = -0.62$). It is of note also that average tuber weight of the SG showed a moderate but significant association with tuber yield of the FCG ($r = 0.34$).

Analyses of variance for combining abilities revealed that mean squares of GCA as well as SCA were highly significant for all characters under study and in all generations (Table 2). The estimates of variance components varied considerably between generations and particularly for GCA of yield. General combining ability was only slightly more important than SCA for average tuber weight in the FCG (ratio = 0.53), while for all other characters SCA was much more important than GCA in all generations.

Table 3 shows the GCA estimates of the crossing parents for all generations and analysed characters and their average ranking from 1 (highest) to 14 (lowest). For some cultivars, such as 'Asterix' and 'Optima', GCA effects of all characters were consistent between generations. However, most cultivars showed varying positive and negative GCA effects depending on the genotype and trait under study. In order to evaluate GCA effects over all generations and to balance the ranges of GCA values in different generations, ranks were calculated (R). For tuber number, negative GCA effects were associated with the parents 'Karida', 'Leyla', 'Nena' and 'Optima' in all three generations, which are also reflected in low ranking values. For average tuber weight the same parents, except for 'Nena', were superior and obtained high ranks of 2.7, 2.7 and 3.3, respectively. 'Optima' obtained the highest GCA rank for tuber yield. Ranking values based on GCA effects were in good agreement, showing highly significant correlation coefficients between $r = -0.90$ and $r = -0.72$, although slight variations in the respective orders can be observed.

Table 4 shows correlations of GCA and SCA effects among generations. Specific combining ability effects for tuber number were significantly correlated in all three generations as well as for tuber yield between seedling and the FCG. With respect to GCA effects significant correlations were found for tuber numbers between SCG and SG or FCG and for average tuber weight between the two clonal generations.

Discussion

When analysing family means, a significant influence of both tuber number and tuber weight on tuber yield was observed in the SG, while in clonal generations only tuber weight had a significant influence on yield in this study. However, all character pairs were significantly related when analysing individual performances. Neele et al. (1991) obtained similar results. Maris (1988) and Gopal et al. (1994) observed that both yield components were associated with tuber yield and that, in the SG, tuber number as well as average tuber weight had an equal positive effect on tuber yield, while in clonal generations tuber weight was the only component influencing tuber yield. Maris (1988) determined that tuber number and average tuber weight had equal effects on total yield in the seedling and in the SCG. However, Gopal et al. (1994) found that tuber numbers were more important than average tuber weight in the SG.

Blomquist and Lauer (1962) suggested that seed tuber size must be taken into account for evaluating the FCG. Maris

Table 1: Correlations between tuber numbers, average tuber weight and tuber yield in seedling and clonal generations, based on genotype values and average family performance

	Tuber number			Average tuber weight			Tuber yield		
	SG	FCG	SCG	SG	FCG	SCG	SG	FCG	SCG
Tuber number									
SG		*0.51***	*0.64***	**0.11**	−0.51**	−0.64**	**0.76****	−0.09	−0.36*
FCG	*0.27***		*0.51***	0.26	**−0.67****	−0.47**	0.53**	**0.17**	−0.20
SCG	*0.23***	*0.33***		−0.22	−0.62**	**−0.70****	0.33	−0.22	**−0.03**
Average tuber weight									
SG	**0.10****	0.17**	−0.18**		*0.02*	*0.17*	**0.68****	0.34*	−0.02
FCG	−0.18**	**−0.52****	−0.33**	*0.14***		*0.56***	−0.38*	**0.58****	0.21
SCG	−0.27**	−0.29**	**−0.61****	*0.20***	*0.45***		−0.35*	0.25	**0.69****
Tuber yield									
SG	**0.77****	0.26**	0.05	**0.63****	−0.04	−0.07*		*0.11*	*−0.23*
FCG	0.07*	**0.34****	−0.05	0.36**	**0.56****	0.23**	*0.23***		*0.14*
SCG	−0.09*	0.01	**0.23****	0.05	0.18**	**0.55****	*−0.03*	*0.22***	

*, ** Significant at P = 0.05 and P = 0.01, respectively.
SG, seedling generation; FCG, first clonal generation; SCG, second clonal generation.
Correlations between performances based on all genotype values are given in the lower diagonal matrix. Correlations based on average family performance are given in the upper diagonal matrix.
Character correlations within generations are displayed in bold, while correlations for identical characters between generations are in italics.

Table 2: Mean squares for general (GCA) and specific combining ability (SCA) and estimates of variance components (σ^2_{GCA}, σ^2_{SCA}, σ^2_E) for yield components in three generations

		Tuber number			Average tuber weight			Tuber yield		
Source of variation	df	SG	FCG	SCG	SG	FCG	SCG	SG	FCG	SCG
GCA	13	5.43**	4.29**	2.78**	37.8**	877.1**	692.8**	4328**	39.2**	16.8**
SCA	20	3.35**	3.50**	1.25**	32.3**	164.9**	367.6**	4378**	21.9**	30.4**
Error	646	0.41	0.32	0.25	3.1	28.6	34.6	508	3112	2592
σ^2_{GCA}		0.44	0.15	0.34	0.9	159.6	70.6	0.01	3756	0.01
σ^2_{SCA}		2.98	3.22	1.01	29.6	138.2	337.6	3923	19,030	28.2
σ^2_E		0.41	0.32	0.25	3.1	28.6	34.6	508	3112	2592

*, ** Significant at P = 0.05 and P = 0.01, respectively.
SG, seedling generation; FCG, first clonal generation; SCG, second clonal generation.

Table 3: General combining ability (GCA) effects and ranking of parents from the partial diallel for yield components in three generations

	Tuber number				Average tuber weight				Tuber yield			
Parent	SG	FCG	SCG	R	SG	FCG	SCG	R	SG	FCG	SCG	R
Asterix	0.68	2.49	0.55	2.3	−3.18	−18.59	−3.47	10.3	2.20	28.58	31.00	5.7
Berolina	−1.02	1.15	−0.39	8.7	2.68	−9.79	−3.56	7.7	−0.06	−33.39	−125.95	11.3
Cinja	3.47	1.19	2.44	1.3	−3.49	−36.75	−29.81	13.3	50.38	−270.40	−42.74	9.0
Karida	−0.44	−0.57	−1.04	11.3	8.05	14.42	9.23	2.7	56.59	144.61	−37.01	4.3
Leyla	−0.06	−1.88	−1.26	11.7	−0.32	20.28	26.16	2.7	−24.15	17.65	79.12	5.7
Lido	−0.98	−0.16	0.09	8.3	−0.71	3.31	−5.00	8.7	−34.43	8.56	−19.30	9.0
Lyra	−0.25	−1.64	0.30	8.3	−3.50	14.06	0.51	7.7	−30.62	−0.86	58.20	7.3
Margit	−1.24	−0.45	0.15	9.3	−3.69	19.12	−7.09	9.3	−44.94	174.32	−14.35	7.3
Nena	−1.90	−0.47	−0.12	11.3	−0.72	−0.51	10.24	6.7	−45.35	−28.44	92.75	8.3
Optima	−0.03	−0.42	−1.12	9.3	5.41	8.25	19.66	3.3	35.93	37.77	53.53	4.0
Sandra	1.28	−0.10	0.02	5.3	0.84	−4.69	−4.76	8.0	39.10	5.83	−48.80	7.7
Sissi	−0.44	0.42	−0.15	8.0	2.36	8.80	2.45	4.7	18.97	107.06	26.83	4.7
Tomensa	−0.03	−0.11	0.08	6.3	−3.31	−11.49	−0.36	10.0	−34.58	−162.60	13.85	10.0
Ute	0.97	0.54	0.53	3.3	−0.42	−6.42	−14.20	10.0	10.97	−28.69	−67.13	10.0

SG, seedling generation; FCG, first clonal generation; SCG, second clonal generation; R, average rank from highest (1) to lowest (14).

Table 4: Correlations of GCA and SCA effects between characters and generations

	Tuber number			Average tuber weight			Tuber yield		
	SG	FCG	SCG	SG	FCG	SCG	SG	FCG	SCG
SG		**0.37**	**0.65****		**0.33**	**0.47**		**−0.06**	**−0.39**
FCG	*0.62***		**0.52***	*−0.29*		**0.58****	*0.47***		**0.27**
SCG	*0.55***	*0.49***		*0.01*	*0.32*		*−0.10*	*0.02*	

*, ** Significant at P = 0.05 and P = 0.01, respectively.
SG, seedling generation; FCG, first clonal generation; SCG, second clonal generation.
Correlations between GCA effects are displayed in bold while those between SCA effects are in italics.

(1986) indicated that differences in seed tuber weight had large effects on many important agronomic characters, particularly in the FCG. Brown (1988) also demonstrated the importance of tuber size of seedlings and their clonal performance when planted. He showed that this importance decreased with consecutive clonal generations. In the present trial the three most homogeneous seed tubers were chosen for planting the FCG, but of course from the available sizes. Moreover, tuber yield of the FCG was significantly correlated with average tuber weight of the seedlings generation, which was not the case between clonal generations. Therefore, one cannot exclude the influence of seed tuber weight on the yield of the FCG.

Most of the phenotypic correlations for identical characters between generations obtained in our study varied from low to moderate (Table 1). Correlations between tuber numbers were higher in our study than those reported by Brown and Caligari (1986), Neele et al. (1991) and Gopal (1997). For average tuber weight, only a relation between FCG and SCG was found, whereas Brown and Caligari (1986), Maris (1988) and Gopal (1992) determined also correlations between clonal generations. These authors also detected correlations for tuber yield, which were absent in the study presented here.

In general, a closer relationship between clonal generations than between clonal generations and SGs was observed. Despite the particular magnitudes of these correlations, Gopal et al. (1994) obtained similar results. These findings may be due to the different origins of the plant material, that is, tubers reproduced both clonal generations while the SG was raised from true seeds. Based on their results, Tai and Young (1984) and Neele et al. (1991) suggested that a selection at the seedling stage would not be efficient. However, Haynes and Wilson

(1991) and also Gopal (1997) indicated that a selection in tuberling populations could be possible. Brown and Caligari (1986) indicated that selection for yield in seedlings could be effective but could be overestimated because of the known influence of seed tuber weight.

Genetic variation is due to both general and specific combining ability. However, SCA seems to be more important than GCA in almost all cases. Plaisted et al. (1962) also found higher estimates of SCA than GCA for the same agronomic characters. They concluded that larger estimates of SCA might be due to previous selection that narrowed the genetic base of the lines tested. Killick and Malcolmson (1973) suggested that traits subjected to directional selection would be expected to show little additive genetic variation but a great degree of dominance and epistasis, whereas the reverse is true for traits subjected to stabilizing selection. In this sense, Tai (1976) determined large SCA for tuber number and tuber yield, but significant GCA for average tuber weight. He concluded that tuber numbers were subjected to directional selection while average tuber weight was subject to stabilizing selection. Gopal (1998) found as in this study a superior SCA for all characters and suggested that the characters were subjected to directional selection. High SCA estimates can also be found if closely related parents are used. In related material the number of different alleles is likely to be limited, so non-additive action, such as epistasis, can gain importance (Neele et al. 1991). Consequently, Maris (1989) observed significant GCA effects in his diallel of ssp. *tuberosum* varieties and ssp. *andigena* clones, as also Rowell et al. (1986), using hybrids between Tuberosum and Neo-Tuberosum, and Ortiz and Golmirzaie (2004) with true potato seed. The parents used in the current study are commercially grown cultivars. Therefore, they could be related and could descend from a directional selection in the past, explaining the observed preponderance of SCA.

Because both combining ability components were significant, it is not possible to predict accurately the best parents or even the best crosses. Moreover, the large variation of GCA and SCA effects between generations and the low correlation coefficients makes prediction even more difficult. Gopal (1998) studied the combining ability over generations and he also observed variation in GCA. He indicated that this variation could be attributed to genotype by environment interactions. On the basis of the results given here, a negative selection in the seedling stage is recommended.

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