Theor Appl Genet (2013) 126:889–899
DOI 10.1007/s00122-012-2023-3

ORIGINAL PAPER

Relative efficiency of the genotypic value and combining ability effects on reciprocal recurrent selection

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Received: 11 July 2012 / Accepted: 26 November 2012 / Published online: 9 December 2012

Abstract Reciprocal recurrent selection (RRS) has been successfully applied to maize breeding for more than 60 years. Our objective was to assess the relative efficiency of the genotypic value and the effects of general and specific combining abilities (GCA and SCA) on selection. The GCA effect reflects the number of favorable genes in the parent. The SCA effect primarily reflects the differences in the gene frequencies between the parents. We simulated three traits, three classes of populations, and 10 cycles of half- and full-sib RRS. The RRS is a highly efficient process for intra- and interpopulation breeding, regardless of the trait or the level of divergence among the populations. The RRS increases the heterosis of the interpopulation cross when there is dominance, and it decreases the inbreeding depression in the populations and the genetic variability in the populations and in the hybrid. When there is not dominance and the populations are not divergent, the RRS also determines population differentiation. The half-sib RRS, which is equivalent to selection based on the GCA effect, is more efficient than the full-sib RRS based on the genotypic value, regardless of the trait or the level of improvement of the populations. The full-sib RRS based on the SCA effect is not efficient for intra- and interpopulation breeding.

Introduction

The reciprocal recurrent selection (RRS) was idealized by Comstock et al. (1949) as a breeding process of the hybrid between two populations. They proposed experimental assessment of interpopulation paternal half-sib families and S_1 progeny recombination. Their goal was to improve both the general and specific combining abilities. The RRS has been shown to improve the hybrid and to increase the heterosis of the populations, relative to maize grain yield, disease and pest resistance, resistance to root and stalking lodging and other agronomic traits (Penny and Eberhart 1971; Eberhart et al. 1973; Souza 1987; Keeratinijakal and Lamkey 1993; Santos et al. 2007). The same can be said about modifications of the RRS method (Rodriguez and Hallauer 1991; Butruille et al. 2004). The most important modified procedures were proposed by Hallauer (1967), Lonnquist and Williams (1967), Hallauer and Eberhart (1970), and Russell and Eberhart (1975). Hallauer (1967) developed a method for continually assessing inbred interpopulation full-sib families to obtain hybrids. Lonnquist and Williams (1967) proposed evaluating interpopulation full-sib progeny to develop sister-line or modified hybrids. Hallauer and Eberhart (1970) proposed evaluating interpopulation full-sib families with S_1 progeny recombination. Russell and Eberhart (1975) proposed using inbred lines from each population as testers. This procedure offered an efficient way to simultaneously improve the breeding populations and develop elite single crosses.

Communicated by M. Sillanpaa.

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Regardless of the family or the tester, the RRS is efficient from the first cycle. Jenweerawat et al. (2009) verified that the modified procedure suggested by Russell and Eberhart (1975) improved the specific combining ability. They observed that the grain yield of the top ten cycle 1 maize interpopulation hybrids was greater than that of the top ten cycle 0 interpopulation hybrids. The same conclusion was established by Souza et al. (2010). This study compared between the grain yields of the maize hybrids from the S_3 lines of each population with commercial single crosses. They also observed an increase in the relative importance of the non-additive effects over the additive effects for grain yield. In addition to increasing the grain yield and the heterosis of the hybrid, Romay et al. (2011) observed an increment in the grain yield in one population, no change in the other population and a reduction in the inbreeding depression after three cycles of full-sib RRS in maize. Keeratinijakal et al. (1993) also observed an increase in the grain yield of the hybrid and one population without a relevant change in the other population after 11 cycles of half-sib RRS in maize. They also observed an increment in the heterosis. The inbreeding depression decreased in one population and increased in the population cross. Based on the testcross evaluation, they verified that the general combining ability was improved.

Comparisons among the RRS procedures were also made. However, these comparisons did not reveal consistent results. Ordas et al. (2012) compared two RRS methods using maize full-sib progeny. They modified the full-sib RRS by additionally using an S_2 progeny test in the selection. The modified method successfully improved the grain yield of the population cross under artificial Mediterranean corn borer infestation conditions. There was no change under the high infestation condition. The standard procedure, in contrast, failed to improve the yield of the population cross under optimum infestation condition and tended to decrease the yield under high infestation. Rademacher et al. (1999) compared half-sib RRS and a modified procedure using elite inbred lines as testers. After six cycles, the standard procedure resulted in a greater interpopulation gain in the grain yield. Peiris and Hallauer (2005) concluded based on the simulation results that half- and full-sib RRS were equally efficient, regardless of the recombination units. Based on the selection intensity, effective population size, time required to complete a selection cycle, and available financial and human resources, they concluded that full-sib RRS was the more efficient method. In the simulation study of Jones (1971), the relative efficiency of the two schemes depended on the selection intensity and the environmental variance.

Molecular markers have also been used to study the effects of RRS on the genetic diversity among the populations. From the analysis of simple sequence repeat (SSR), restriction fragment length polymorphism (RFLP) and amplified fragment length polymorphism (AFLP) loci in the populations derived from 6 to 12 cycles, Solomon et al. (2010), Hinze et al. (2005), Butruille et al. (2004) and Labate et al. (1997) observed a reduction in the number of alleles, a decrease in the genetic variability within the populations, and an increase in the genetic divergence among the populations as the RRS program progressed. The population differentiation was primarily a result of complementary alleles that were fixed in the populations (Solomon et al. 2010). Butruille et al. (2004) also reported that genetic drift did not appear to impede the selection response.

Thus, there is an extensive theoretical and applied knowledge on the reciprocal recurrent selection. We aimed to increase this broad knowledge by assessing the relative efficiency of the genotypic value and the effects of general and specific combining abilities on the selection.

Materials and methods

Reciprocal recurrent selection with half-sib families

Let the probabilities of the gene A_1 that increase the trait expression be p and r in populations A and B, respectively. Let q and s be the probabilities of the allelic form (A_2), which decreases the trait expression. Assuming that the populations are in Hardy–Weinberg equilibrium, the genotypic means of the interpopulation half-sib progenies of the plants from population A are

$$\bar{G}_{A_1A_1(A)} = m + ra + sd$$

$$\bar{G}_{A_1A_2(A)} = m + [(r - s)/2]a + (1/2)d$$

$$\bar{G}_{A_2A_2(A)} = m - sa + rd$$

where m is the mean of the genotypic values of the homozygotes, a is the deviation between the genotypic value of the homozygote with the greatest expression and m, and d is the deviation due to dominance (Hallauer et al. 2010).

The mean of the interpopulation hybrid is

$$M_{A\times B} = m + (p + r - 1)a + (p + r - 2pr)d.$$

Thus, the general combining ability effects (GCA) of the plants from A are

$$\mathrm{GCA}_{A_1A_1(A)} = \bar{G}_{A_1A_1(A)} - M_{A\times B} = q[a + (s - r)d] = q\alpha_B$$

$$\mathrm{GCA}_{A_1A_2(A)} = \bar{G}_{A_1A_2(A)} - M_{A\times \mathrm{B}} = [(q - p)/2]\alpha_B$$

$$\mathrm{GCA}_{A_2A_2(A)} = \bar{G}_{A_2A_2(A)} - M_{A\times B} = -p\alpha_B$$

with $E(\mathrm{GCA}) = 0$. The parameter α_B is the average effect of a gene substitution in population B.

Thus, the genotypic variance among the progenies is the variance of the general combining ability effects of the plants from A. This measure is given by

$$\sigma^2_{GHSF(A\times B)} = (1/2)pq\alpha_B^2 = \sigma^2_{GCA(A)}$$

For population B,

$$\begin{aligned}\sigma^2_{GHSF(B\times A)} &= (1/2)rs\alpha_A^2 = (1/2)rs[a+(q-p)d]^2\\ &= \sigma^2_{GCA(B)}\end{aligned}$$

where α_A is the average effect of a gene substitution in population A.

The correlation between the genotypic mean of the half-sib progeny and the general combining ability effect of the common parent is 1. Thus, the selection among the families is equivalent to the selection for the general combining ability. The general combining ability effect expresses the superiority of the parent for the number of favorable genes. The correlation between the number of genes that increase the trait expression (*N*) and general combining ability effect is $\rho_{N,\mathrm{GCA}_A} = pq\alpha_B/\sqrt{(2pq)\sigma^2_{GCA(A)}} = 1$ or -1. The result from this equation depends on the degree of dominance and gene frequency. The effect of a gene substitution assumes a negative value only under overdominance condition.

Reciprocal recurrent selection with full-sib families

The genotypic means of the interpopulation full-sib families ($S_0 \times S_0$ hybrids) between the plants of the A and B populations are

$$\bar{G}_{A_1A_1\times A_1A_1} = m + a$$

$$\bar{G}_{A_1A_1\times A_1A_2} = m + (1/2)(a+d)$$

$$\bar{G}_{A_1A_1\times A_2A_2} = m + d$$

$$\bar{G}_{A_1A_2\times A_1A_2} = m + (1/2)d$$

$$\bar{G}_{A_1A_2\times A_2A_2} = m + (1/2)(-a+d)$$

$$\bar{G}_{A_2A_2\times A_2A_2} = m - a$$

Thus, $M_{A\times B} = m + (p+r-1)a + (p+r-2pr)d$ and

$$\begin{aligned}\sigma^2_{\mathrm{GFSF}} &= (1/2)pq\alpha_B^2 + (1/2)rs\alpha_A^2 + pqrsd^2\\ &= \sigma^2_{\mathrm{GCA}(A)} + \sigma^2_{\mathrm{GCA}(B)} + pqrsd^2\end{aligned}$$

The genotypic mean of a full-sib family can be expressed as

$$\bar{G}_{A_iA_j\times A_kA_l} = M_{A\times B} + \mathrm{GCA}_{A_iA_j} + \mathrm{GCA}_{A_kA_l} + \mathrm{SCA}_{A_iA_j\times A_kA_l}$$

where $\mathrm{SCA}_{A_iA_j\times A_kA_l}$ is the specific combining ability effect of the parents. For each gene,

$$\mathrm{SCA}_{A_1A_1(A)\times A_1A_1(B)} = -2qsd$$

$$\mathrm{SCA}_{A_1A_1(A)\times A_1A_2(B)} = q(r-s)d$$

$$\mathrm{SCA}_{A_1A_2(A)\times A_1A_1(B)} = s(p-q)d$$

$$\mathrm{SCA}_{A_1A_1(A)\times A_2A_2(B)} = 2qrd$$

$$\mathrm{SCA}_{A_2A_2(A)\times A_1A_1(B)} = 2psd$$

$$\mathrm{SCA}_{A_1A_2(A)\times A_1A_2(B)} = [(p-q)(s-r)/2]d$$

$$\mathrm{SCA}_{A_1A_2(A)\times A_2A_2(B)} = -r(p-q)d$$

$$\mathrm{SCA}_{A_2A_2(A)\times A_1A_2(B)} = -p(r-s)d$$

$$\mathrm{SCA}_{A_2A_2(A)\times A_2A_2(B)} = -2prd$$

and

$$\begin{aligned}E(\mathrm{SCA}) &= E\left(\mathrm{SCA}_{A_1A_1(A)}\right) = E\left(\mathrm{SCA}_{A_1A_2(A)}\right) = E\left(\mathrm{SCA}_{A_2A_2(A)}\right)\\ &= E\left(\mathrm{SCA}_{A_1A_1(B)}\right) = E\left(\mathrm{SCA}_{A_1A_2(B)}\right) = E\left(\mathrm{SCA}_{A_2A_2(B)}\right) = 0\end{aligned}$$

where $\mathrm{SCA}_{A_iA_j(A\text{ or }B)}$ is the average of the specific combining ability effects for all the full-sib families from parent A_iA_j of a population.

The specific combining ability primarily reflects the differences in the gene frequencies between the parents. The magnitude of this value also depends on the differences in the gene frequencies between the populations as well as the degree of dominance. Regardless of the degree of dominance or the gene frequencies in the populations, the greatest specific combining ability effects are associated with parents with the maximum gene frequency differences. Generally, the greater the differences in gene frequencies between parents and between populations, and the greater the degree of dominance, the greater is the absolute value of the specific combining ability effect.

The variance of the specific combining ability effects of the plants of populations A and B is

$$\sigma^2_{\mathrm{SCA}} = pqrsd^2$$

Thus,

$$\sigma^2_{GFSF} = \sigma^2_{\mathrm{GCA}(A)} + \sigma^2_{\mathrm{GCA}(B)} + \sigma^2_{\mathrm{SCA}}$$

The within progeny genotypic variance in the populations structured in half- and full-sib families are

$$\sigma^2_{\mathrm{GwHSF}(A\times B)} = \sigma^2_{\mathrm{GCA}(A)} + 2\sigma^2_{\mathrm{GCA}(B)} + 4\sigma^2_{\mathrm{SCA}}$$

$$\sigma^2_{\mathrm{GwHSF(B\times A)}} = \sigma^2_{\mathrm{GCA}(B)} + 2\sigma^2_{\mathrm{GCA}(A)} + 4\sigma^2_{\mathrm{SCA}}$$

$$\sigma^2_{\mathrm{GwFSF}} = \sigma^2_{\mathrm{GCA}(A)} + \sigma^2_{\mathrm{GCA}(B)} + 3\sigma^2_{\mathrm{SCA}}$$

The covariance between the genotypic mean of the full-sib family and the general combining ability effect of the parent of a population is $\mathrm{Cov}(\bar{G}_{A\times B}, \mathrm{GCA}) = \sigma^2_{\mathrm{GCA}}$. Further, $\mathrm{Cov}(\mathrm{GCA}_A, \mathrm{GCA}_B) = \mathrm{Cov}(\mathrm{GCA}_A, \mathrm{SCA}) = \mathrm{Cov}$

$(\mathrm{GCA}_B, \mathrm{SCA}) = 0$. Thus, $\rho_{\bar{G}_{A\times B},\,\mathrm{GCA}} = \sqrt{\sigma^2_{\mathrm{GCA}}/\sigma^2_{\mathrm{GFSF}}}$. The covariance between the genotypic mean of the full-sib family and the specific combining ability effect of the parents is $\mathrm{Cov}\left(\bar{G}_{A\times B,\,\mathrm{SCA}}\right) = \sigma^2_{\mathrm{SCA}}$. Thus, $\rho_{\bar{G}_{A\times B}}$, $\mathrm{SCA} = \sqrt{\sigma^2_{\mathrm{SCA}}/\sigma^2_{\mathrm{GFSF}}}$. Therefore, assuming genetic variability in the populations and dominance, selection among interpopulation full-sib families is equivalent to selection for general and specific combining ability.

For the inbred interpopulation full-sib families ($\mathrm{S_n} \times \mathrm{S_n}$ hybrids),

$$\sigma^2_{\mathrm{GFSF}} = (1+F)\sigma^2_{\mathrm{GCA(A)}} + (1+F)\sigma^2_{\mathrm{GCA(B)}} + (1+F)^2\sigma^2_{\mathrm{SCA}}$$

$$\sigma^2_{\mathrm{GwFSF}} = (1-F)\sigma^2_{\mathrm{GCA}(A)} + (1-F)\sigma^2_{\mathrm{GCA}(B)} + (3+F)(1-F)\sigma^2_{\mathrm{SCA}}$$

where F is the inbreeding coefficient.

Characterization of the gene systems, populations and selection methods

We simulated three popcorn traits, three classes of populations and two methods of reciprocal recurrent selection. The minimum and maximum genotypic values of the homozygotes for grain yield, expansion volume (EV) and days to maturity were 20 and 200 g plant^{-1}, 5 and 50 ml g^{-1}, and 100 and 160 days, respectively. Positive unidirectional dominance was assumed for the grain yield. In 80 % of the loci, the degree of dominance varied from 0.8 to 1.2. In the other genes, the dominance ranged from 1.3 to 1.6. The degree of dominance of the EV ranged between −1.2 and 1.2. Absence of dominance was assumed for days to maturity. Genetic control by 100 biallelic genes and the absence of epistasis were also assumed.

Because the gene frequencies in a cross-pollinated population vary between 0 and 1, we represented all breeding populations in three classes. The non-improved population was characterized by an assumed favorable gene frequency ranging between 0.2 and 0.4. The population with an intermediate degree of improvement was represented by an assumed favorable gene frequency between 0.4 and 0.6. The improved population was represented by an assumed favorable gene frequency between 0.6 and 0.8. Hardy–Weinberg equilibrium and linkage equilibrium were assumed for the populations.

We employed half- and full-sib reciprocal recurrent selection with $\mathrm{S_1}$ progeny recombination. To minimize the number of simulations, each method was carried out using contrasting populations (improved and non-improved), non-improved populations, populations with an intermediate degree of improvement and improved populations. Each RRS procedure was repeated for 10 cycles. There were 200 parents in the populations, and we selected the 40 best parents.

For the full-sib reciprocal recurrent selection, we considered three selection criteria. The selection was based on the average progeny genotypic value, the general combining ability effect and the specific combining ability effect. The half-sib RRS was based on the GCA effect (equivalent to the selection based on the progeny genotypic value). The intra- and interpopulation genetic gains were obtained by calculating the difference between the parametric means of the populations between cycles 10 and 0. Further, the heterosis of the hybrid was computed relative to the original populations. The change in the population mean as a result of one generation of selfing was computed as $-\sum pqd$.

The simulations were made in a program developed in REALbasic 5.5 (REAL Software 2004). Each combination of trait, populations, breeding method, selection criteria and cycles of selection was replicated 100 times. To estimate the population genetic parameters and perform an analysis of molecular variance (AMOVA), we employed the GenAlEx 6.4 software (Peakall and Smouse 2006).

Results

In the case of divergent populations, genetic gains were observed in both of the populations, regardless of the trait under selection (Table 1). In this case, the greatest responses were observed in the non-improved populations. The most efficient process was the selection based on the GCA effects. The selection based on the SCA effects failed to achieve an intrapopulation gain. Using the GCA-based selection, the maximum accumulated gains relative to grain yield, EV and days to maturity were 35.4, 90.4 and 23.0 %, respectively, in the non-improved population. In the improved population, the maximum accumulated gains relative to grain yield, EV and days to maturity were 6.8, 31.5 and 12.3 %, respectively. A greater decrease in the inbreeding depression in the cycle of the greater accumulated gain was observed using the selection based on the GCA effects. The grain yield inbreeding depression decreased from −17.5 to −12.0 % in the non-improved population and from −10.7 to −0.7 % in the improved population. The EV inbreeding depression did not change in the non-improved population and decreased from −1.6 to −0.1 % in the improved population. The simulation system did not consider deleterious genes that affect adaptive value (germination, survival and fertility). Thus, the superiority of the GCA-based selection only reflects the greater homozygosity of the improved populations. The SCA-based selection was also ineffective in reducing the

Table 1 Population means, intra- and interpopulation genetic variances and gains (%), heterosis (%), inbreeding depression (%), effective number of alleles (Ne), gene diversity (He), F_{ST}, Nei's genetic distance and percentage of molecular variation among populations, relative to grain yield, expansion volume and days to maturity, before and after up to ten simulated selection cycles of reciprocal recurrent selection with contrasting populations, based on genotypic value and general and specific combining abilities effects

Population	Parameters	Grain yield (g plant^{-1})						Expansion volume (ml g^{-1})				Days to maturity		
		Cycle	Cycle 7	Cycle 8	Cycle 10			Cycle	Cycle 10			Cycle	Cycle 10	
		0	GCA	G	G	GCA	SCA	0	G	GCA	SCA	0	G	GCA
A	Mean	116.03	157.12	130.03	129.20	147.70	112.92	20.29	34.04	38.64	20.64	118.45	140.72	145.72
	Additive var.	67.08	34.38	50.77	48.25	29.76	54.70	2.49	2.52	2.06	2.20	3.78	3.40	2.88
	Dominance var.	17.42	15.92	17.12	15.78	10.97	15.30	0.50	0.43	0.36	0.45	0.00	0.00	0.00
	Genetic gain[†]		35.41	12.06	11.35	27.29	−2.68		67.72	90.42	1.71		18.80	23.03
	Inbreed. depress.	−17.54	−11.99	−15.25	−14.61	−9.76	−16.14	−3.60	−2.91	−3.66	−3.22	0.00	0.00	0.00
	Ne	1.73			1.72	1.51	1.66	1.73	1.66	1.52	1.66	1.73	1.68	1.55
	He	0.42			0.40	0.30	0.38	0.42	0.38	0.31	0.37	0.42	0.39	0.33
B	Mean	186.35	199.01	199.04	199.52	199.06	180.73	37.83	46.74	49.76	37.35	142.15	155.3	159.64
	Additive var.	11.80	0.91	0.94	0.50	0.81	17.41	2.02	0.76	0.06	1.88	3.70	1.19	0.10
	Dominance var.	16.80	2.03	2.29	1.11	0.78	14.97	0.47	0.08	0.01	0.44	0.00	0.00	0.00
	Genetic gain[†]		6.79	6.81	7.06	6.82	−3.02		23.53	31.52	−1.26		9.26	12.30
	Inbreed. depress.	−10.71	−2.38	−2.70	−1.46	−0.68	−9.93	−1.62	−0.24	−0.09	−1.58	0.00	0.00	0.00
	Ne	1.71			1.28	1.08	1.67	1.71	1.18	1.04	1.66	1.71	1.20	1.06
	He	0.41			0.12	0.04	0.38	0.41	0.13	0.03	0.38	0.41	0.16	0.04
	F_{ST}	0.16			0.42	0.37	0.19	0.16	0.20	0.21	0.20	0.16	0.13	0.11
	Nei's distance	0.33			0.65	0.36	0.37	0.32	0.25	0.19	0.37	0.33	0.12	0.11
	Among pop. var	43.77			76.50	76.51	50.04	43.76	57.06	64.74	50.36	43.85	40.70	46.52
A × B	Mean	166.62	202.07	198.55	202.41	206.70	166.48	29.56	42.85	47.02	29.64	130.30	148.02	152.68
	GCA_A[‡] variance	2.87	0.35	0.48	0.36	0.19	3.75	0.51	0.46	0.29	0.49	0.94	0.85	0.72
	GCA_B[§] variance	16.77	1.00	2.89	1.16	0.03	15.36	0.61	0.22	0.02	0.56	0.93	0.30	0.03
	SCA variance	4.23	0.81	1.16	0.60	0.06	3.45	0.12	0.03	0.01	0.10	0.00	0.00	0.00
	Genetic gain[†]		21.28	19.16	21.48	24.05	−0.08		44.97	59.10	0.30		13.60	17.18
	Heterosis	10.20	13.49	20.69	23.16	19.23	13.39	1.70	6.10	6.39	2.24	0.00	0.00	0.00

[†] Relative to cycle 0

[‡] For population A

[§] For population B

inbreeding depression. The GCA-based selection reduced the intrapopulation genetic variability primarily in the improved population. After 10 cycles of the GCA-based selection, the decreases in the additive variance for grain yield, EV and days to maturity were 55.6, 17.3 and 23.8 %, respectively, in the non-improved population. The decreases in the dominance variance were 37.0 and 28.0 %, for grain yield and EV. The reductions were >93 % in the improved population. This result is a consequence of a greater decrease in the effective number of alleles and the expected heterozygosity. The effective number of alleles decreased from 1.7 to 1.5 and 1.0 in the non-improved and improved populations, respectively. The expected heterozygosity decreased from 0.4 to 0.3 and 0.4 to 0.03 or 0.04 in the non-improved and improved populations, respectively.

The improvement of the population cross was also more efficient with the GCA-based selection, regardless of the trait under selection (Table 1). The increase in the grain yield heterosis was greater using the selection based on the genotypic value. The SCA-based selection did not improve the population cross. The GCA-based selection yielded maximum accumulated gains in the hybrid of 24.0, 59.1 and 17.2 % for the grain yield, EV and days to maturity, respectively. The selection based on the genotypic value increased the grain yield heterosis from 10.2 to 23.2 % and the EV heterosis increased from 1.7 to 6.4 % after 10 cycles of GCA-based selection. The increase in the heterosis reflected population differentiation. The incremental differences in the gene frequencies between the populations are also shown by the increase in the F_{ST} values for the genes determining grain yield and EV. These differences are also evident in the Nei's distance and in the magnitude of the molecular variance among populations. These effects were the strongest under the GCA-based selection. After 10 cycles of the GCA-based selection, these population parameters increased from 0.16, 0.33 and 44.0 % to 0.37, 0.36 and 76.5 %, relative to grain yield.

Table 2 Population means, intra- and interpopulation genetic variances and gains (%), heterosis (%), inbreeding depression (%), effective number of alleles (Ne), gene diversity (He), F_{ST}, Nei's genetic distance and percentage of molecular variation among populations, relative to grain yield, expansion volume and days to maturity, before and after up to ten simulated selection cycles of reciprocal recurrent selection with non improved populations, based on genotypic value and general and specific combining abilities effects

Population	Parameters	Grain yield (g plant^{-1})				Expansion volume (ml g^{-1})				Days to maturity		
		Cycle	Cycle 10			Cycle	Cycle 10			Cycle	Cycle 10	
		0	G	GCA	SCA	0	G	GCA	SCA	0	G	GCA
A	Mean	114.78	164.77	180.71	113.39	20.11	33.31	39.25	20.46	118.23	138.74	145.44
	Additive var.	67.57	28.55	16.53	54.88	2.51	1.99	1.64	2.21	3.74	3.53	2.91
	Dominance var.	16.78	16.41	11.76	15.19	0.49	0.47	0.34	0.45	0.00	0.00	0.00
	Genetic gain[†]		43.55	57.43	−1.21		65.67	95.19	1.74		17.34	23.02
	Inbreed. depress.	−17.47	−11.66	−8.34	−16.07	−3.57	−1.76	−1.26	−3.22	0.00	0.00	0.00
	Ne	1.72	1.73	1.52	1.58	1.73	1.71	1.53	1.67	1.72	1.73	1.54
	He	0.41	0.41	0.31	0.36	0.42	0.40	0.32	0.38	0.41	0.41	0.33
B	Mean	113.90	163.31	180.21	111.65	19.82	33.09	39.14	20.16	117.97	137.35	145.29
	Additive var.	67.73	29.38	16.52	54.76	2.51	2.04	1.68	2.21	3.72	3.61	2.93
	Dominance var.	16.82	16.54	11.68	15.03	0.49	0.48	0.36	0.44	0.00	0.00	0.00
	Genetic gain[†]		43.38	58.21	−1.97		66.90	97.45	1.71		16.44	23.16
	Inbreed. depress.	−17.56	−11.85	−8.37	−16.14	−3.41	−1.85	−1.39	−3.14	0.00	0.00	0.00
	Ne	1.71	1.72	1.54	1.55	1.71	1.72	1.53	1.68	1.71	1.74	1.56
	He	0.41	0.40	0.32	0.35	0.41	0.40	0.32	0.39	0.41	0.41	0.34
	F_{ST}	0.01	0.13	0.17	0.12	0.01	0.09	0.09	0.07	0.01	0.07	0.06
	Nei's distance	0.01	0.24	0.24	0.11	0.01	0.15	0.10	0.10	0.01	0.11	0.07
	Among pop. var.	3.33	38.59	48.75	25.20	3.14	28.59	29.82	22.72	3.31	22.84	21.17
A × B	Mean	115.02	177.38	195.74	118.53	20.00	34.11	40.13	20.62	118.10	138.04	145.36
	GCA$_{A}$[‡] variance	17.32	6.46	1.69	16.38	0.64	0.48	0.38	0.60	0.94	0.88	0.73
	GCA$_{B}$[§] variance	17.19	6.33	1.65	15.96	0.62	0.48	0.38	0.60	0.93	0.90	0.73
	SCA variance	4.15	3.85	2.01	3.38	0.12	0.11	0.07	0.10	0.00	0.00	0.00
	Genetic gain[†]		54.22	70.18	3.05		70.54	100.62	3.10		16.89	23.09
	Heterosis	0.59	8.14	8.48	5.35	0.18	2.75	2.38	1.54	0.00	0.00	0.00

[†] Relative to cycle 0

[‡] For population A

[§] For population B

The variance among populations of the EV increased from 44.0 to 64.7 %. The selection based on the GCA or genotypic value reduced the genetic variability in the population cross. The GCA-based selection reduced this parameter to a greater degree than did the genotypic value-based selection. After 10 cycles of the GCA-based selection, the decreases in the variances of the general and specific combining abilities were generally >91 %.

Applying reciprocal recurrent selection to non-divergent populations essentially produced the same results compared to the case of contrasting populations. However, there were differences in the magnitudes of the analyzed parameters (Tables 2, 3, 4). Although both the GCA- and genotypic value-based selections improved the two populations, the RRS was more effective with the GCA-based selection for the three traits. The maximum accumulated gains were inversely proportional to the level of improvement of the populations. The maximum accumulated gains for the grain yield, EV and days to maturity with GCA-based selection ranged from 5.3 to 58.2 %, 30.6 to 97.4 % and 12.2 to 23.2 %, respectively. The SCA-based selection also failed to determine intrapopulation improvement. The least inbreeding depression was observed with 10 cycles of the GCA-based selection. The inbreeding depression of the grain yield decreased from −17.5 to −8.3 % with the non-improved populations, from −15.3 to −5.1 % with the intermediate populations and from −11.0 to −3.2 % with the improved populations. Because of the bidirectional dominance of the EV, the inbreeding depression in the populations of cycles 0 and 10 were minimal. Generally, a decrease in the inbreeding depression resulted from an increase in the frequency of

Table 3 Population means, intra- and interpopulation genetic variances and gains (%), heterosis (%), inbreeding depression (%), effective number of alleles (Ne), gene diversity (He), F_{ST}, Nei's genetic distance and percentage of molecular variation among populations, relative to grain yield, expansion volume and days to maturity, before and after up to ten simulated selection cycles of reciprocal recurrent selection with intermediate populations, based on the genotypic value and general and specific combining abilities effects

Population	Parameters	Grain yield (g plant^{-1})					Expansion volume (ml g^{-1})				Days to maturity		
		Cycle	Cycle 8	Cycle 10			Cycle	Cycle 10			Cycle	Cycle 10	
		0	GCA	G	GCA	SCA	0	G	GCA	SCA	0	G	GCA
A	Mean	156.20	190.47	183.46	188.55	151.36	28.71	41.99	46.88	28.54	129.50	148.67	154.41
	Additive var.	41.98	8.93	14.83	9.91	40.34	2.63	1.57	0.67	2.42	4.44	2.47	1.41
	Dominance var.	23.53	9.11	12.57	7.13	19.20	0.69	0.32	0.19	0.56	0.00	0.00	0.00
	Genetic gain[†]		21.94	17.46	20.72	−3.10		46.24	63.27	−0.60		14.80	19.23
	Inbreed. depress.	−15.27	−6.51	−8.66	−5.09	−14.01	−2.76	−2.32	−2.24	−2.48	0.00	0.00	0.00
	Ne	1.97		1.56	1.31	1.81	1.97	1.48	1.25	1.81	1.97	1.45	1.24
	He	0.49		0.33	0.19	0.44	0.49	0.30	0.17	0.44	0.49	0.28	0.17
B	Mean	159.06	191.85	185.65	190.35	153.20	29.41	42.50	47.22	29.25	130.42	149.19	154.92
	Additive var.	39.41	7.59	12.93	8.42	38.83	2.55	1.47	0.60	2.35	4.45	2.39	1.30
	Dominance var.	23.61	8.41	11.71	6.58	19.06	0.69	0.29	0.16	0.56	0.00	0.00	0.00
	Genetic gain[†]		20.62	16.72	19.67	−3.68		44.52	60.54	−0.55		14.39	18.78
	Inbreed. depress.	−15.02	−6.16	−8.17	−4.74	−13.77	−2.71	−1.98	−2.00	−2.45	0.00	0.00	0.00
	Ne	1.97		1.52	1.32	1.80	1.97	1.45	1.25	1.80	1.97	1.45	1.25
	He	0.49		0.31	0.20	0.44	0.49	0.29	0.17	0.44	0.49	0.29	0.18
	F_{ST}	0.02		0.13	0.17	0.07	0.02	0.07	0.05	0.07	0.01	0.05	0.03
	Nei's distance	0.01		0.17	0.18	0.13	0.01	0.07	0.05	0.12	0.02	0.04	0.02
	Among pop. var.	2.75		39.09	56.47	23.86	2.60	26.84	26.37	22.22	2.57	16.94	13.83
A × B	Mean	158.26	200.33	195.00	203.58	159.10	29.09	42.92	47.70	29.22	129.96	148.93	154.66
	GCA$_A$[‡] variance	9.82	0.48	1.60	0.22	9.99	0.64	0.36	0.13	0.60	1.11	0.62	0.35
	GCA$_B$[§] variance	10.53	0.51	1.73	0.19	10.35	0.66	0.36	0.13	0.62	1.11	0.60	0.32
	SCA variance	5.89	1.07	2.22	0.35	4.63	0.17	0.06	0.03	0.14	0.00	0.00	0.00
	Genetic gain[†]		26.58	23.21	28.64	0.53		47.55	63.98	0.45		14.60	19.00
	Heterosis	0.40	4.80	5.66	7.46	4.48	0.10	1.60	1.39	1.14	0.00	0.00	0.00

[†] Relative to cycle 0

[‡] For population A

[§] For population B

homozygotes. The GCA-based selection yielded the greatest reductions in the additive and dominance variances. The reductions in the additive and dominance variances of the grain yield after 10 cycles ranged from 28.1 to 78.6 % and from 29.9 to 75.3 %, respectively. The reductions relative to EV were proportional to the level of improvement of the populations. The additive variance was reduced by 33.1 to 97.1 %, and the dominance variance was reduced by 26.5 to 87.5 %. The reduction in the additive variance of the days to maturity was also proportional to the level of improvement of the populations. This reduction ranged from 21.2 to 97.3 %. Regardless of the level of improvement of the populations, the GCA-based selection decreased the effective number of alleles from 1.71–1.97 to 1.5–1.2 and the expected heterozygosity decreased from 0.41–0.49 to 0.30–<0.10.

The GCA-based selection was also the most efficient process of interpopulation breeding, with gains inversely proportional to the level of improvement of the populations (Tables 2, 3, 4). The SCA-based selection was not efficient, having promoted a small increase in the mean of the hybrid only for non-improved populations. The GCA-based selection yielded maximum accumulated gains of 10.8 to 70.2 % for the grain yield, 32.7 to 100.6 % for the EV and 12.5 to 23.1 % for the days to maturity. The greatest increase in grain yield heterosis was also observed with the GCA-based selection. The greatest increase in EV heterosis was observed with the genotypic value-based selection. After 10 cycles, the grain yield heterosis increased from 0.6 to 8.5 % in the non-improved populations, from 0.4 to 7.5 % in the intermediate populations and from 0.3 to 11.8 % in the improved populations. The EV heterosis

Table 4 Population means, intra- and interpopulation genetic variances and gains (%), heterosis (%), inbreeding depression (%), effective number of alleles (Ne), gene diversity (He), F_{ST}, Nei's genetic distance and percentage of molecular variation among populations, relative to grain yield, expansion volume and days to maturity, before and after up to ten simulated selection cycles of reciprocal recurrent selection with improved populations, based on genotypic value and general and specific combining abilities effects

Population	Parameters	Grain yield (g plant^{-1})						Expansion volume (ml g^{-1})				Days to maturity		
		Cycle	Cycle 5	Cycle 8	Cycle 10			Cycle	Cycle 10			Cycle	Cycle 10	
		0	GCA	G	G	GCA	SCA	0	G	GCA	SCA	0	G	GCA
A	Mean	184.73	195.99	192.66	192.02	185.31	178.93	37.38	47.87	49.38	36.88	141.31	156.62	159.47
	Additive var.	13.40	3.90	6.87	7.56	7.46	18.94	2.08	0.46	0.13	1.95	3.80	0.89	0.15
	Dominance var.	17.40	6.76	8.72	7.85	4.29	15.51	0.52	0.17	0.11	0.47	0.00	0.00	0.00
	Genetic gain†		6.10	4.30	3.95	0.32	−3.14		28.04	32.10	−1.34		10.83	12.85
	Inbreed. depress.	−11.04	−5.35	−6.39	−5.68	−3.23	−10.31	−1.87	−2.10	−1.37	−1.75	0.00	0.00	0.00
	Ne	1.74			1.36	1.18	1.65	1.74	1.21	1.09	1.67	1.74	1.15	1.03
	He	0.42			0.23	0.12	0.37	0.42	0.14	0.06	0.38	0.42	0.12	0.03
B	Mean	186.76	196.71	193.84	193.05	184.28	181.12	38.03	48.05	49.67	37.53	142.30	156.86	159.66
	Additive var.	11.50	3.53	6.11	6.93	8.27	17.23	2.05	0.41	0.06	1.90	3.69	0.83	0.10
	Dominance var.	16.79	6.60	8.24	7.37	4.27	14.94	0.48	0.13	0.06	0.44	0.00	0.00	0.00
	Genetic gain†		5.32	3.79	3.37	−1.33	−3.02		26.36	30.63	−1.31		10.23	12.20
	Inbreed. depress.	−10.67	−5.08	−5.96	−5.23	−3.15	−9.90	−1.71	−1.82	−0.88	−1.61	0.00	0.00	0.00
	Ne	1.71			1.33	1.21	1.66	1.71	1.18	1.06	1.68	1.70	1.13	1.03
	He	0.41			0.21	0.13	0.38	0.41	0.13	0.04	0.38	0.41	0.11	0.03
	F_{ST}	0.01			0.12	0.23	0.07	0.01	0.05	0.08	0.06	0.01	0.03	0.01
	Nei's distance	0.01			0.11	0.22	0.10	0.01	0.03	0.02	0.09	0.01	0.01	0.00
	Among pop. var.	2.79			43.09	74.08	23.49	3.01	26.94	42.21	21.29	2.90	12.54	6.49
A × B	Mean	186.33	200.86	199.84	201.66	206.53	185.88	37.69	48.43	50.03	37.46	141.81	156.74	159.57
	$\mathrm{GCA}_{A}^{\ddagger}$ variance	2.88	0.26	0.50	0.33	0.08	3.58	0.53	0.08	0.00	0.49	0.95	0.22	0.04
	$\mathrm{GCA}_{B}^{\S}$ variance	3.11	0.28	0.53	0.35	0.10	3.78	0.51	0.09	0.00	0.48	0.92	0.21	0.02
	SCA variance	4.23	0.84	1.17	0.73	0.06	3.42	0.12	0.02	0.00	0.10	0.00	0.00	0.00
	Genetic gain†		7.80	7.25	8.23	10.84	−0.24		28.49	32.73	−0.61		10.53	12.52
	Heterosis	0.32	2.30	3.41	4.74	11.77	3.25	−0.02	0.99	1.02	0.70	0.00	0.00	0.00

† Relative to cycle 0

‡ For population A

§ For population B

increased minimally from <0.2 to 1.0–2.7 %. The SCA-based selection increased the grain yield heterosis from <1.0 to 3.0–5.0 %. The increase in heterosis reflects population differentiation and an increase in the genetic differences between non-divergent populations. This interpretation is supported by the increased F_{ST}, Nei's distance and molecular variance among the populations. These observations were primarily gleaned from the results of the GCA-based selection. With the GCA-based selection, the molecular variance among populations increased from approximately 3.0 to 48.7–74.1 % for grain yield and from 26.4 to 42.2 % for EV. The genotypic value-based selection yielded an increase in the molecular variance among populations for the days to maturity from 3.0 to 12.5–22.8 %. Although the GCA- and genotypic value-based selection procedures reduced the genetic variability in the hybrid, the GCA-based selection did so to a greater magnitude than the genotypic value-based selection. Regardless of the analyzed trait, the reductions in the GCA and SCA variances were proportional to the level of improvement of the populations. The reductions in the GCA variance for the grain yield were >90 %. The decreases in the GCA variance for the EV and days to maturity ranged from 38.7 to 99.9 %, and from 21.5 to 97.8 %. The SCA variance was reduced by 51.6–98.6 % for the grain yield and by 41.7–99.9 % for the EV.

Discussion

The results of the simulation are consistent with the experimental evidence and theoretical results gleaned from over 60 years of reciprocal recurrent selection research. The reciprocal recurrent selection is a highly efficient process for improving the interpopulation cross. This observation remains true even for traits with bidirectional dominance or without dominance and even if the populations are not genetically divergent. The half-sib RRS provided estimated gains in the grain yield of 22.0 % after three cycles (Santos et al. 2007), 28.8 % after four cycles (Penny and Eberhart 1971), 23.0 % after five cycles (Eberhart et al. 1973), 26.0 % after six cycles (Rademacher et al. 1999) and 77.0 % after 11 cycles (Keeratinijakal et al. 1993). Romay et al. (2011) estimated a gain of 12.3 % after three cycles of full-sib RRS. We applied a GCA-based selection procedure, which corresponds to half-sib selection, in contrasting populations. Following 3–10 cycles of this procedure, the results showed gains for the grain yield of 12.2–24.0 %. For the cases of non-improved and intermediate populations, we observed gains of 28.1–70.2 and 14.2–28.6 %, respectively. We also applied a genotypic value-based selection method that corresponds to full-sib RRS. In the case of contrasting populations, this procedure yielded a gain of 9.1 % after three cycles. We observed gains of 3.6–19.2 % after three cycles in the case of non-divergent populations. In this case, the gains were inversely proportional to the level of improvement of the populations.

In addition to promoting improvement in the population cross, reciprocal recurrent selection increases heterosis between the populations when dominance is present. Even in the absence of dominance or when the populations exhibit the same level of improvement, population differentiation or an increase in the gene frequency differences between the populations occurs. Penny and Eberhart (1971) observed an increase of 24.5 % in the heterosis of grain yield after three cycles. Eberhart et al. (1973) estimated a grain yield heterosis of 15.0 and 37.0 % in the populations of cycles 0 and 5, respectively. Keeratinijakal et al. (1993) estimated a grain yield heterosis of 25.4 and 76.0 % for the populations of cycles 0 and 11, respectively. Ten cycles of GCA-based selection, applied to contrasting populations yielded an increase in the grain yield heterosis from 10.2 to 19.2 %. The increase until the fifth cycle was 10.8 %. When this procedure was applied to non-divergent populations, the heterosis for grain yield was reduced. The results showed changes from <1.0 to 11.8 % after 10 cycles. Three cycles of genotypic value-based selection in divergent populations increased the grain yield heterosis. The results showed an increase of 38.6 %. This result was less than the increase of 100 % that was estimated by Romay et al. (2011). Differentiation between the populations relative to molecular markers was verified by Labate et al. (1997), Hinze et al. (2005) and Solomon et al. (2010). After 12 cycles, Labate et al. (1997) observed that the Nei's distance for 82 RFLP loci increased from 0.07 to 0.66. Hinze et al. (2005) and Solomon et al. (2010) analyzed 86 and 15 SSR markers in their experiments, respectively. The molecular variance among populations following 15 cycles increased from 4.0 to 58.0 %. The molecular variance following 11 cycles increased from 4.9 to 23.5 %.

Our results confirm the assertions made by Hallauer and Eberhart (1970) and Russell and Eberhart (1975). Reciprocal recurrent selection is indeed a breeding procedure for concurrent population improvement and hybrid development. Regardless of the trait or the level of improvement of the populations, our results showed that both of the populations improved. Experiments with maize, however, revealed no significant changes in the parents for the grain yield (Eberhart et al. 1973). Other studies have shown grain yield improvement in only one of the populations (Penny and Eberhart 1971). Romay et al. (2011) and Keeratinijakal et al. (1993) estimated a grain yield gains of 20.1 and 20.9 % after 3 and 11 cycles, respectively. Three cycles of genotypic value-based selection (full-sib RRS) and 10 cycles of GCA-based selection (half-sib RRS) in contrasting populations yielded a grain yield gains of 7.2 and 27.3 % in the non-improved population (maximum value). These procedures in non-improved populations yielded maximum gains of 17.2 and 58.2 % for both populations.

The reciprocal recurrent selection procedure decreases the inbreeding depression in the populations and the genetic variability in the populations and in the hybrid. Keeratinijakal et al. (1993) observed a decrease in the grain yield inbreeding depression in only one population. In the studies of Labate et al. (1997), Hinze et al. (2005) and Solomon et al. (2010), gene diversity decreased from 0.60 to 0.30, 0.56 to 0.24 and 0.62 to 0.37, respectively. Labate et al. (1997) also observed that the mean number of alleles per locus decreased from approximately 4 to <3.

We found that the half-sib RRS (GCA-based selection) is more efficient than the full-sib RRS based on the progeny genotypic value. This result was independent of the trait analyzed and the level of improvement of the populations. Theoretically, the two RRS methods are equivalent when the selection is based on the GCA effect since there is no difference between the parametric values of the GCA effects of parents of half- or full-sib progeny. In the case of contrasting populations, the intra- and interpopulation genetic gains achieved with the GCA-based selection were 12.0–193.6 % greater than those achieved with the genotypic value-based selection. The superiority of the GCA-based selection in the cases of non-improved, intermediate and improved populations ranged from 29.4 to 45.7, 16.4 to 36.8 and 14.5 to 41.9 %, respectively. Jones et al. (1971) and Peiris and Hallauer (2005) compared half- and full-sib RRS using simulations. Jones et al. (1971) showed that the relative efficiency of the two procedures depended on the selection intensity and the environmental variance. The response rate was greater for the full-sib RRS when selection was less intense and when the environmental variance was large relative to the total genetic variation. Moreover, Peiris and Hallauer (2005) examined 40 independent loci, 11 genetic models, 110 parents, a selection intensity of 10 % and 20 selection cycles. These authors concluded that the two procedures had similar efficiencies in intra- and interpopulation breeding. The efficiencies were similar regardless of the recombination unit (S_1 or S_2) and the allele frequencies in the initial populations (equal or unequal). They also observed that both populations were improved. Furthermore, the heterosis increased and the intra- and interpopulation genetic variances decreased as a result of the fixation of favorable genes. It should be emphasized that half-sib RRS needs more crosses and experimental plots than full-sib RRS for similar intensities of selection.

In contrast, the SCA-based selection is inefficient for intra- and interpopulation improvement. We analyzed the changes in the frequencies of favorable genes to understand the reason of this inefficiency. Regardless of the degree of dominance and level of improvement of the populations, with SCA-based selection approximately 50.0 % of the favorable genes decreased in frequency, and approximately 50.0 % of the favorable genes increased in frequency. Depending on the degree of dominance, the GCA-based selection procedure increased the frequency of the favorable genes by 76.0–100.0 %. In the absence of dominance, the GCA-based selection increased the frequency of the favorable genes by at least 99.5 %. Under condition of bidirectional dominance, only 1.0–9.0 % of the favorable genes were reduced in frequency. Under condition of positive dominance, between 1.0 and 24.0 % of the favorable genes were reduced in frequency. In both of these cases, the greatest reduction was observed in the non-improved population, for the condition of contrasting populations. With non-divergent populations, 1.0–4.0 % of the favorable EV genes were reduced in frequency and 2.0–18.0 % of the favorable grain yield genes were reduced in frequency. This reduction was proportional to the level of improvement of the populations.

Unfortunately, it is not possible to make the full-sib RRS with S_1 progeny recombination as efficient as the half-sib RRS. With half-sib RRS is always possible to estimate (best linear unbiased estimation, BLUE) or predict (best linear unbiased prediction, BLUP) the GCA effects. With full-sib RRS only the genotypic value of each progeny ($S_0 \times S_0$) can be estimated or predicted. For the estimation or prediction of the GCA effects, it would be necessary to combine full- and half-sib families in each cycle. However, this is unjustifiable since it is efficient to only use half-sib progeny. Based on the results presented by Viana et al. (2011), which fitted the additive-dominant model from the analysis of second cycle's intrapopulation full-sib families, the GCA effects can be predicted by analyzing the $S_n \times S_n$ ($n \geq 1$) progeny, using BLUP with pedigree information. However, the purpose of the process described by Hallauer (1967) is to develop hybrids. Thus, performing selection based on the genotypic value should be more efficient since the hybrid performance is also affected by the SCA effect (dominance). Then, the best $S_n \times S_n$ hybrids should be selected based on their genotypic values and not on the GCA effects of its parents. Selection of $S_n \times S_n$ progeny based on the GCA effects should be considered for identification of the superior parents, aiming S_n progeny recombination.

Acknowledgments We thank the Foundation for Research Support of Minas Gerais State (Fapemig), the Brazilian Federal Agency for Support and Evaluation of Graduate Education (Capes), and the National Council for Scientific and Technological Development (CNPq) for financial support.

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