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Evaluation of three grain maize composites developed from broad-base synthetics by divergent selection on three complementary testers

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Summary — Three composites, FC(TC)C0, FC(TD)C0 and FC(TI)C0, were developed from S1 families with good general combining ability, derived from broad-base maize synthetics. These synthetics were developed by the INRA (Institut national de la recherche agronomique) maize laboratory of Montpellier from inbred lines belonging to different heterotic groups. The idea was to develop new heterotic groups. Composite development is the initial phase of a recurrent selection program. The grain productivity of the composites (yield, grain moisture and lodging resistance) and their genetic divergence were evaluated in both diallel and topcross designs. In crosses with testers, the yields of composites were on average 11–14 q/ha less than that of commercial checks with a comparable grain moisture, and they were more susceptible to lodging. Heterosis for yield between composites was low. This low divergence is consistent with the constitution procedure of the composite, based mainly on the general combining ability.

***Zea mays* L = maize / synthetic / composite / recurrent selection**

Résumé — Évaluation de trois composites de maïs grain constitués à partir de synthétiques à base large par sélection divergente sur trois testeurs complémentaires. *Trois composites de maïs, FC(TC)C0, FC(TD)C0 et FC(TI)C0, ont été constitués à partir des familles S1 ayant une bonne aptitude à la combinaison sur trois testeurs complémentaires, et issues de synthétiques à base large. Ces synthétiques ont été constitués par le laboratoire maïs de l'Institut national de la recherche agronomique (Inra) de Montpellier (France) à partir de lignées appartenant à divers groupes hétérotiques. L'idée était de développer de nouveaux groupes hétérotiques. La constitution des composites est la phase initiale d'un programme de sélection récurrente réciproque. Le comportement agronomique des composites pour la production de grain (rendement, humidité à maturité, résistance à la verse) et leur divergence génétique ont été évalués dans un réseau multilocal dans un plan de croisement diallèle associé à un plan de croisement avec les testeurs utilisés pour la sélection des constituants des composites. En croisement avec les testeurs, les composites ont un rendement moyen de 11 à 14 q/ha moins élevé que les témoins commerciaux actuels à précocité égale et une plus grande sensibilité à la verse. L'hétérosis pour le rendement entre les composites est faible. Cette faible divergence est en accord avec la procédure de constitution des composites privilégiant l'aptitude générale à la combinaison.*

Zea mays *L = maïs / synthétique / composite / sélection récurrente*

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INTRODUCTION

The ultimate goal of maize (*Zea mays* L) breeding programs is the development of new hybrid cultivars which exploit the phenomenon of heterosis. Hybrids are issued from crossing inbred lines with both high general combining ability (AGC) and good complementary (specific combining ability; ASC) between them. In order to broaden the germplasm base, new heterotic groups can be looked for. Recurrent selection methods can be used to develop new heterotic groups and to enhance those identified previously. To initiate recurrent selection, populations may be chosen from two complementary heterotic groups and kept separated, or obtained by splitting into two parts the hybrid population resulting from a cross between two populations. The reasoning for such splitting is based on the hypothesis that heterozygosity itself is the cause of heterosis. Thus, when the best allelic combination already exists in one population, separated management of the two populations cannot achieve the best possible heterosis level. On theoretical data, Cress (1966) found that, at overdominant loci, the maximum hybrid combination could not be obtained by maintaining separate populations. Griffing (1963) found the same result in the cases of superdominance or partial dominance.

The INRA maize laboratory of Montpellier (France) developed broad-base synthetics from inbred lines belonging to various combining ability groups. The idea was to develop new heterotic groups. Synthetics were evaluated in crosses with three complementary testers. Selection was made for a high combining value for grain production. On the basis of topcross values, three composites were developed from the synthetics. The objective of this paper is to evaluate this material, and particularly the divergence between the three composites.

MATERIALS AND METHODS

Original synthetics and selection procedure

The three composites FC(TC)C0, FC(TD)C0, FC(TI)C0 were developed from selected S1 families derived from ten broad-base maize synthetics. These synthetics were constituted by intermating inbred lines belonging to different combining ability groups.

Two synthetics, FS12C1 and FS18C0, were developed from inbreds with tolerance to the European corn borer (*Ostrinia mubilalis* Hubner; ECB). FS12C1 was the first cycle of selection of FS12C0 developed from 38 ECB-tolerant inbred lines released from 1976 to 1979. FS18C0 was developed from 38 ECB-tolerant inbred lines released during 1981 and 1982.

Three synthetics were developed from inbred lines with good combining ability for grain yield or tolerance to ECB. FS12AC0 was developed by crossing FS12C0 with an eight-way hybrid with both high combining value for grain yield and ECB tolerance. FS22C0 was developed by crossing FS12C0 with 37 inbred lines with high combining value for grain productivity and ECB tolerance. FS32Bulk was obtained by internating progenies of FS22C0, FS18C0 and IWGO3 (a synthetic developed by the International Working Group of *Ostrinia nubilalis*, IWGO).

Five synthetics were developed from inbred lines with good combining ability for grain production. FS14C1 is the first cycle of selection of FS14C0 developed from 14 inbred lines. FS14^2.HS was developed by crossing FS14C0 with various inbred lines. FS24C0 was developed by crossing 32 elite inbred lines with FS14C0. SynC2DE was developed from 12 inbred lines. FS10^2.HS was developed by crossing 13 profilic north American lines with four inbred lines.

Selection was undertaken in the ten synthetics to improve yield, grain moisture, root lodging resistance, and ECB tolerance. The selection procedure included three steps: mass, S1 family and topcross progenies selection. The selection intensity was similar. The number of S0 plants analyzed was variable (800–3 000) according to the width of the genetic base of the synthetic. Mass selection (15–22% intensity) was made on S0 plants for ECB tolerance. Subsequently, S1 family selection (5–10% intensity) was undertaken in nurseries in three locations for flowering earliness, root lodging resistance, productivity in ears, and ear health. The selected S1 families were then crossed on three complementary testers. From 1989 to 1991, topcross progenies were evaluated each year in two or three locations with three replicates per location. Data were collected for grain yield, grain moisture at maturity and root lodging resistance. For each trial, analysis of variance was computed and an index was calculated for each location as follows:

index = 2.5 * (grain moisture of references – grain moisture of S1 family) + 0.75 * (root lodging susceptibility of references – root lodging susceptibility of S1 family) + (yield of S1 family * 100 / yield of references).

The complementary testers for FS18C0, FS22C0, FS32Bulk and FS12C1 were a flint early tester (F2 x F283), a dent early tester (F252 x F272) and an iodent tester (MBS847). For FS12AC0, FS14C1 and SynC2DE, the testers were MBS847, Mo17 (a Lancaster tester) and B73 (a Stiff Stalk tester). For FS24C0, the testers were F252 x F272, Mo17 and B73. For FS14^2.HS, the S1 family were tested on the five complementary testers.

For each topcross, selection was based on the mean index averaged across locations. We selected S1 families with an index value larger than the index mean for each topcross evaluation (around 50% selection intensity). Then, the selected S1 families were distributed among the different composites according to their specific combining ability on the complementary tester. The specific combining ability was estimated from the indices calculated over location for each tester.

The composite FC(TC)C0 was constituted from the 26 S1 family, with high combining ability with the early flint tester. The composite FC(TD)C0 was constituted from the 25 S1 family, with high combining ability with the early dent tester. The composite FC(T1)C0 was constituted from 60 S1 families, with high combining ability with the iodent tester. This higher number of the S1 family included with the FC(TI)C0 was due to the higher number of synthetics evaluated in crosses with the iodent tester.

We analyzed the genetic variation of three synthetics evaluated on the early testers (FS18C0, FS22C0 and FS32Bulk). This analysis was performed on data for which the three topcrosses were evaluated in the same location; otherwise, the tester effect would be confounded with the location effect. Analyses of variance were calculated on data obtained at Saint-Martin-de-Hinx. FS18C0 and FS22C0 were evaluated in the same trial (23 and 24 progenies respectively), and FS32Bulk (60 progenies) in another trial. Rank correlation coefficients were estimated among index means.

Evaluation of the three composites

The three composites were evaluated in a diallel design associated with a topcross design (crosses within and between composites and with the three testers used in the synthetic selection). The composite seeds for per se evaluation were produced in isolation fields in Mauguio in 1993 with 180 plants as female by composite. The composite topcrosses were realized with 90 plants as female by composite. Three early commercial hybrids were added in the evaluation (DEA, DK300 and FANION). A total of 21 entries were evaluated in 1994 in five locations with six replicates per location. Locations were Clermont-Ferrand (Puy-de-Dôme), Dijon (Côte-d'Or), Mazet (Maine-et-Loire), Lusignan (Vienne) and Saint-Martin-de-Hinx (Pyrénées-Atlantiques). The following traits were measured: grain yield adjusted to 15% moisture, grain moisture, and root lodging (percentage of plants lodged more than 45° from vertical).

Statistical methods

For each location, analysis of variance was performed for each trait. Homogeneity among residual variances was tested by a Kullback test. Analysis of variance was then computed across locations for each trait. The effects due to composites, testers and tester x composites were tested versus the effect by location interaction mean square.

RESULTS

Variability of three synthetics

The analysis of the sources of variation in FS18C0, FS22CO and FS32Bulk synthetics evaluated at Saint-Martin-de-Hinx are given in table I. For grain yield and grain moisture, the mean

Table I. Mean square estimates in FS18C0-FS22C0 and FS32Bulk synthetics evaluated in cross with three complementary testers in one location (Saint-Martin-de-Hinx).

Source of variation	*df*	*Grain yield (q/ha)*		*Grain moisture (%)*	
FS18C0-FS22C0					
Synthetic	1	168.19	**	0.1	
Tester	2	935.63	**	248.87	**
Rep (tester)	4	151.89	**	15.28	**
Genotype (synth)	40	87.54	**	6.74	**
Genotype x tester (synth)	81	36.78	**	1.69	**
Error	159	22.77		0.36	
FS32Bulk					
Tester	2	101.65	**	145.35	**
Rep (tester)	4	955.78	**	5.53	**
Genotype	59	95.73	**	8.02	**
Genotype x tester	118	27.05	**	1.41	**
Error	227	18.13		0.43	

*,** significant at 0.05 and 0.01 levels of probability respectively. df: degrees of freedom. rep: replicate.

Table II. Rank correlation coefficient estimates between indices calculated from the topcross values across locations on FS18C0 (23 genotypes), FS22C0 (24 genotypes) and on FS32Bulk (60 genotypes).

Synthetic	Index on flint tester	Index on dent tester	Index on iodent tester
FS18C0			
Index on flint tester	1	0.47*	0.67**
Index on dent tester		1	0.44*
Index on iodent tester			1
FS22C0			
Index on flint tester	1	0.56**	0.10
Index on dent tester		1	0.33
Index on iodent tester			1
FS32Bulk			
Index on flint tester	1	0.34**	0.22
Index on dent tester		1	0.22
Index on iodent tester			1

*,** significant at 0.05 and 0.01 levels of probability respectively.

squares due to genotype and genotype x tester interaction effects were significant at $P = 0.01$. Assessed with the percentage of the variation of the model, the magnitude of the genotype effect was much larger than the interaction effect for grain moisture, and was slightly larger than the interaction effect for grain yield. Thus additive effects seemed to be preponderant for genetic variation of these two traits. However, nonadditive effects seemed to coexist for grain yield variation.

For the three early synthetics, rank correlation coefficients between indexes were estimated and are reported in table II. Rank correlation coefficient estimates were positive among testers and significantly different from zero ($P = 0.01$) between the two early testers. With the iodent tester, rank correlation coefficients were positive and non significant at $P = 0.01$, except in the FS18C0 synthetic.

Evaluation of the composites

The analysis of variance calculated among locations is given in table III. For all traits, the mean squares due to entry and entry x location interaction were highly significant ($P = 0.01$). The magnitude of the entry x location interaction was less than the magnitude of the main effects. Also, the entries ranked similarly over locations. Consequently, the mean values of entries were estimated over locations.

Table III. Analysis of variance for grain yield (q/ha), grain moisture (%) and root lodging on the composite trial over locations.

Source of variation	Grain yield	Grain moisture		Root lodging	
	CM	CM	df	CM	df
Location	10 973**	1 519.4**	4	6 211**	2
Replicate in location	100**	1.7**	25	324**	15
Entry	1 508**	98.9**	20	862**	20
Entry x location	110**	4.9**	80	165**	40
Error	37	0.4	458	94	300

df: degrees of freedom. CM: mean-square estimates. ** significant at 0.01 level of probability.

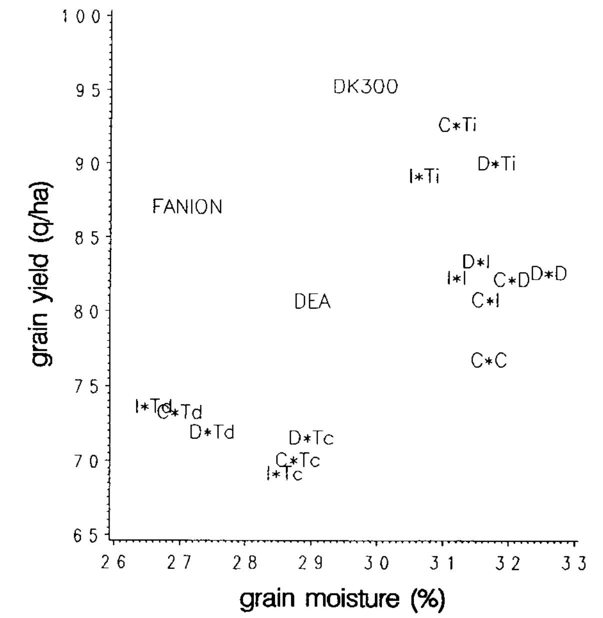

Fig 1. Relationship between grain yield (q/ha) and grain moisture (%) for the composites in crosses and for the three hybrid checks (DEA, FANION, DK300). The first letter represents the composite (C: FC(TC)CO, D: FC(TD)CO, I: FC(TI)CO), the second expression represents the tester (Tc: early flint tester, Td: early dent tester, Ti: iodent tester).

In figure 1, the grain yield of entries is plotted against grain moisture. Comparison of grain yield between composites and commercial checks must be made at a similar level of grain moisture. In crosses with the flint tester, the composites exhibited a yield 11 q/ha less than the DEA check. In crosses with the dent tester, the composite yields were on average 14 q/ha less than the check FANION. For lodging resistance, comparison was made between the value of the composite crossed with the most resistant tester (MBS847) and DEA (2.5% of lodging plants). The estimates of percentage of lodging plants were 11.6, 9 and 6.8% for FC(TC)CO, FC(TD)CO and FC(TI)CO respectively.

Table IV. Heterosis level between the three composites (expressed as percentage of the midparent) for grain yield, estimated over locations with the minima and maxima values in brackets.

	FC(TD)CO	*FC(TI)CO*
FC(TC)CO	3.07 (0.4–5.6)	1.57 (–7.0–7.3)
FC(TD)CO		0.36 (–4.7–5.7)

In per se value, the three composites were significantly different ($P = 0.01$) for grain moisture; their means exhibited a ranking of FC(TI)CO < FC(TC)CO < FC(TD)CO. The yields of FC(TD)CO and FC(TI)CO were not significantly different ($P = 0.05$), whereas FC(TC)CO exhibited a low yield value. The mid-parent heterosis estimates for yield between components are given in table IV with the minimum and maximum estimates over locations. Mid-parent heterosis estimates were low; the highest heterosis value was for the cross FC(TC)CO x FC(TD)CO.

Analysis of variance computed on the topcross values of the composites is given in table V. The tester effect was the most important for all traits. The most productive tester in crosses with composites MBS847 was also the latest. The ranking of the testers was F252 x F272 < F2 x F283 < MBS847 for grain moisture, and F2 x F283 < F252 x F272 < MBS847 for yield. The composite effect was significant for grain moisture. FC(TI)CO was the earliest composite to reach maturity and FC(TD)CO was the latest. No significant difference was found between composites for yield. The tester x composite interaction was only significant at the 0.05 level for grain moisture. However, the composites had the same ranking in cross with the testers (fig 1).

DISCUSSION

The yield of composites in crosses with testers was lower than that of commercial checks (from 11–14 q/ha for comparable grain moistures). This result is not disappointing. First, the testers contribute to the topcross value of the composites and the tester effect was highly significant (table V). Second, considering the broad genetic base of the composites, the inbred lines which can be derived by a selection procedure should be more productive than the mean of the composite. The composites showed lower lodging resistance than commercial checks. Particular attention will need to be given to this trait in future selection procedures.

The results showed significant differences between composites for grain moisture. The earliest composite (FC(TI)CO) was selected on the latest tester (MBS847). This result could be explained by the weight of grain moisture in the selection index and the high heritability of this trait. Efficient selection occurred on grain moisture. For yield, low estimates of heterosis between composites and the nonsignificant com-

Table V. Analysis of variance for grain yield (q/ha) and grain moisture (%) on composites in cross with three complementary testers.

Source de variation	*CM*	*CM*	*df*
	Yield	*Grain moisture*	
Composite	9.4	14.4**	2
Tester	9629.9**	352.1**	2
Location	4262.0**	638.8**	4
Location x composite	11.3	1.3**	8
Location x tester	72.1	19.2**	8
Composite x tester	51.2	1.4*	4
Location x compt x tester	53.4	1.0*	16
Error	38.2	0.5	205

df: degree of freedom. CM: mean square estimates. *,** significant at 0.05 and 0.01 levels of probability, respectively.

posite x tester interaction indicate a low divergence between composites. This low divergence could be explained, in part, by the preponderance of additive effects in the genetic variation of synthetics. In the evaluation of three synthetics in one location, additive effects were found to be preponderant even though nonadditive effects seemed to coexist for grain yield variation. This result was consistent with other experimental results (Hallauer and Miranda (1981) for grain synthetics; Gouesnard et al (1989) for forage synthetics). The type of selection procedure could also have contributed to the low divergence between the composites. The selection for composite constitution was made in two steps: first on the mean effect over the topcross values and second on the value in crosses with the complementary tester. Therefore the general combining ability of progenies was taken into account in the selection more than the specific combining ability. The three testers chosen were complementary and representative of known combining-ability groups. Due to this complementarity, an increase in composite divergence was expected. To improve the divergence between composites, further selection cycles should be performed.

What selection procedure should be chosen? Comstock et al (1949) proposed the reciprocal recurrent selection procedure to improve the complementarity of two populations; this method is expected to be successful regardless of the type of gene action. Experimental results on full-sib reciprocal recurrent selection show an increase in mid-parent heterosis (Eyherabide and Hallauer, 1991; Keenratinijakal and Lamkey, 1993). For those composites which are not prolific, such a full-sib reciprocal recurrent selection procedure is difficult to apply. Only a modified reciprocal recurrent method, using inbred lines or narrow base hybrids as testers, would be easy to use. We propose a selection procedure based on S1 family selection followed by selection on progenies from a topcross on the complementary tester. Testers could be those used in the constitution of the composites or could belong to the same combining ability group. In comparison with reciprocal recurrent selection methods, these methods are not convenient for developing new heterotic groups. Composites will be complementary to the heterotic group of the tester. The modified reciprocal recurrent methods emphasize nonadditive genetic effects. Some experimental results reported are disappointing. For BS21 and BS22, Russel et al (1992) explained the results by the choice of testers or by a drift effect caused by small effective population size. Alternative procedures would be the possibility of changing the tester inside the same combining ability group and the possibility of introducing new material at each cycle in order to increase the effective population size. The S1 family selection would permit improvement of the inbred value of the composites, and indirectly their general combining abilities.

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