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Evaluation of agronomic traits and analysis of exotic germ plasm polymorphism in adapted × exotic maize crosses

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Abstract The utilization of exotic germ plasm is difficult due to its non-adaptability. This study investigates the possibility of exotic germ plasm loss during adaptation, and the effect of an additional cross with elite material on the breeding value of exotic × adapted material. The study was conducted on a temperate × highland tropical composite (or pool) developed in order to broaden the genetic variability of maize in north western Europe. The frequency of unique exotic alleles and the isoenzymatic polymorphism at four loci were analysed in the pool itself, in the pool after mild selection, and in the selected pool crossed with elite material. Based on these data, no significant deviation seemed to occur during the mild selection and the cross. The pool and the pool × elite germ plasm cross were evaluated in testcrosses with two complementary testers for both grain and forage production. The pool was later in maturity, more susceptible to lodging, and yielded less than the pool × elite germ plasm crosses for all evaluations. The highest estimates of genetic variance were obtained in the pool for earliness and height traits, and for yield. However, based on the predicted genotypic mean of the selected population, the pool had a lower breeding value than the pool × elite germ plasm cross. The pool × elite germ plasm cross is thus preferred to initiate selection.

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Introduction

A relationship between the lack of genetic diversity and the problems of genetic vulnerability and selection plateaus has been identified. Increasing genetic variability by crossing adapted germ plasm to populations has been suggested by many plant breeders. With the non-adaptability of exotic germ plasm, the utilization of such material for the development of lines is not really promising, at least on a short-term basis. In north western Europe, highland tropical maize germ plasm has been introduced so as to broaden the genetic variability of maize adapted to the cold spring (Stamp 1984; Kaan and Derieux 1985; Giauffret 1993). These races have undesirable features in temperate regions, such as weak roots and grain moisture at harvest (Eagles et al. 1989; Eagles and Lothrop 1994).

The use of exotic germ plasm in selection requires an adaptation phase before the onset of the selection. The most common procedure has been to cross exotic germ plasm with adapted germ plasm so as to raise the performance of the population more rapidly (Holley and Goodman 1988). A thorough mixing of adapted and exotic chromosome segments is needed so as to avoid the loss of useful linked factors. Several generations of random mating, with or without mild selection, are recommended before the application of more stringent selection (Wellhausen 1965; Lonnquist 1974; Hallauer 1978).

The optimum proportion of exotic and adapted material to form the foundation population is another question that needs to be resolved in the utilization of exotic material. Theoretical studies have taken into account the divergence between parents, the level of dominance of the considered trait, and the long-term or short-term goals, in order to determine the best foundation population (Dudley 1982; Bridges and Gardner 1987; Crossa 1989). For an adapted population with a higher mean than the exotic population, the backcross foundation population was found to be better that the F_2 population. The exception was for the long-term goal with the presence of favourable alleles at loci with large effects (Bridges and Gardner 1987). In experimental studies, the predicted response to selection and the genetic variance were used to compare foundation populations. Crossa and Gardner (1987) found some advantage in using the cross, rather than the backcross, for yield. Albrecht and Dudley (1987) reported the superiority of the backcross generation for yield, and the superiority of the F_2 generation for an index of five traits in which the weight of the yield is low.

The present study was conducted on a temperate maize synthetic × tropical highland maize pool. Its purposes were (1) to determine if a significant loss of tropical germ plasm occurred during random mating and mild selection, and (2) to analyze the effect of an additional cross with elite material on the breeding value of the exotic × adapted cross.

Materials and methods

Population development

A temperate × highland tropical pool (or composite) was initiated in 1983 by intermating an early temperate synthetic (the French Canadian synthetic or SYNFC) with highland tropical populations. Two generations of random mating followed the cross. The pool was called POOL14. Its constitution is expected to be 50% SYNFC: 50% highland tropical populations. In 1987 the pool was selected on *S*1 family values in three locations. The selected version of POOL14 was called POOL14SEL. The forty two best *S*1 families were crossed with an elite dent hybrid. POOL14A was developed by random mating of the testcross progenies. The constitution of POOL14A is expected to be 25% SYNFC: 25% highland tropical populations: 50% elite dent hybrid.

Isoenzymatic analysis

Unique exotic alleles were searched for by comparing the isoenzymatic polymorphism of the temperature × exotic pool (POOL14) and the temperate synthetic (French Canadian synthetic). Eight enzymes were assayed including acid phosphatase (ACP), alcohol dehydrogenase (ADH), catalase (CAT), glutamate oxalocetate transaminase (GOT), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), 6-phosphogluconate dehydrogenase (PGD) and phosphoglucoisomerase (PGI). Populations were analysed for 13 isoenzyme loci spanning at least eight of the ten chromosomes of maize. The electrophoretic techniques and genetic analyses employed have been described by Stuber et al. (1988) and Grenèche and Giraud (1989). The number of seedlings assayed per population ranged from 51 to 150.

For each allele, the allelic frequency was calculated, and the statistical method (Z statistics) suggested by Snedecor and Cochran (1971) was used to determine significantly different allozyme frequencies for the comparison of the two populations.

In a second step, the proportion of exotic germ plasm in the pool after mild selection and in the cross with elite germ plasm was estimated. The isoenzymatic polymorphism of POOL14, POOL14SEL and POOL14A was analysed for the loci revealing exotic alleles and other associated loci revealed on the same buffer (ACP1, ADH1, GOT1, GOT2). We assayed 40 *S*1 families selected on a per se value (POOL14SEL) with four or five seedlings per family. We assayed 73 seedlings for the POOL14A population. Exotic allele frequencies of POOL14, POOL14SEL and POOL14A were compared using a chi-square test. The relationships between POOL14, POOL14SEL and POOL14A were also studied on the four analysed loci. A principal component analysis was performed using the correlation matrix of allelic frequencies of the four loci analysed.

Population evaluation experiment

Two populations POOL14 and POOL14A, were evaluated for both silage and grain production in crosses with two complementary testers. Forty two and 49 *S*1 families were selected on *S*1 value from POOL14 and POOL14A, respectively. Then, they were crossed to two testers. The two testers were an early flint tester (F2 × F283), and a medium late Stiff Stalk tester (F618 × CM174). Each testcross for a population was evaluated in a lattice design is one location with two or three replicates. Replicates of the testcrosses from the two populations were randomized to build a complete block design. Testcrosses were grown in 1992 in France at Mons en Chaussée (49.8° N) for the evaluation of the two pools crossed with the early tester in terms of both grain and forage production, at Dijon (47.5° N) for the evaluation of the two pools crossed with the medium-late tester for forage production, and at Mauguio (43.4° N) for grain production. Commercial checks and experimental hybrids (cross between testers, cross between the French Canadian synthetic and the tester) were included in the evaluation.

For grain production, the following traits were measured: grain yield adjusted to 15% moisture, grain moisture, root lodging (percentage of plants inclined more than 45° from the vertical). For silage production, each row was whole-plant harvested and weighed; dry matter content was determined by drying a whole-plant sample. Root lodging at the vegetative stage and at the harvest stage was recorded. In two locations, the number of days from the 1st of July to 50% silking was recorded. Plant height and ear height (to the node of the upper ear) were measured on five plants per plot in one location.

Statistical analysis

All experiments were analyzed using methods appropriate for both a randomized complete block design or a partially balanced complete block design. For each location, multitrait analyses of variance were performed. For testcross progenies, components of variance and their standard errors were estimated separately for each population using a restricted maximum-likelihood method.

From these estimates, with the assumption of no genotype × environment effect, expected selection responses for each testcross population were calculated by the following formula (Falconer 1981): $G(\alpha) = k(\alpha)\,\sigma_g\,h$, where k is the standardized selection differential for a given selected proportion (α), σ_g is the genotypic standard deviation, h is the square root of heritability (h^2). Responses were determined for $\alpha = 38\%$ ($k = 1$) and $\alpha = 10\%$ ($k = 1.75$).

To account for differences in means and in selection responses, the usefulness of each population was assessed by the parameter U as proposed by Schnell (1983): $U(\alpha) = \text{Mean} + G(\alpha)$, where Mean is the population mean of the selected population. Expected selection responses were calculated for a more productive, an earlier, a taller, and a more root lodging-resistant population.

Results

Estimation of the proportion of exotic material in the exotic × adapted crosses using isoenzymatic alleles

Allelic frequencies with standard errors are given in Table 1 for the French Canadian synthetic (SYNFC) and the SYNFC × highland tropical pool (POOL14).

Table 1 Allelic frequencies (Freq) with standard error (σ), and normal "Z" statistic of the French Canadian synthetic (SYNFC) and the "SYNFC × highland tropical population" pool (POOL14)

Locus	Allele	SYNFC Freq ± σ	POOL14 Freq ± σ	Z
ACP1	2	0.215 ± 0.024	0.302 ± 0.039	– 1.99
ACP1	3	0.148 ± 0.021	0.223 ± 0.035	– 1.95
ACP1	4	0.621 ± 0.028	0.468 ± 0.042	3.01
ACP1	6	0.017 ± 0.007	0.007 ± 0.007	0.80
IDH1	4	0.833 ± 0.028	0.885 ± 0.028	– 1.26
IDH1	6	0.167 ± 0.028	0.115 ± 0.028	1.26
IDH2	4	0.445 ± 0.031	0.629 ± 0.042	– 3.45
IDH2	6	0.555 ± 0.031	0.371 ± 0.042	3.45
PGD1	2	0.154 ± 0.058	0.580 ± 0.041	– 4.72
PGD1	3,8	0.846 ± 0.058	0.420 ± 0.041	4.72
PGI	3	0.000 ± 0.000	0.097 ± 0.025	– 3.26
PGI	4	0.689 ± 0.046	0.889 ± 0.026	– 3.91
PGI	5	0.311 ± 0.046	0.014 ± 0.010	6.67
MDH1	1	0.026 ± 0.010	0.089 ± 0.024	– 2.88
MDH1	6	0.974 ± 0.010	0.884 ± 0.027	3.79
MDH1	10,5	0.000 ± 0.000	0.027 ± 0.014	– 2.74
MDH2	3	0.401 ± 0.030	0.514 ± 0.041	– 2.21
MDH2	6	0.464 ± 0.031	0.432 ± 0.041	0.64
MDH2	4,5	0.135 ± 0.021	0.055 ± 0.019	2.52
MDH3	16	1.000 ± 0.000	1.000 ± 0.000	
MDH5	12	0.951 ± 0.012	0.949 ± 0.020	0.06
MDH5	15	0.049 ± 0.012	0.051 ± 0.020	– 0.06
GOT1	4	1.000 ± 0.000	0.851 ± 0.022	5.84
GOT1	6	0.000 ± 0.000	0.149 ± 0.022	– 5.84
GOT2	2	0.000 ± 0.000	0.024 ± 0.009	– 2.31
GOT2	4	1.000 ± 0.000	0.976 ± 0.009	2.31
ADH1	4	0.911 ± 0.022	0.947 ± 0.014	– 1.43
ADH1	6	0.089 ± 0.022	0.053 ± 0.014	1.43
CAT3	7	0.019 ± 0.013	0.382 ± 0.056	– 6.36
CAT3	9	0.837 ± 0.036	0.526 ± 0.057	4.51
CAT3	12	0.144 ± 0.034	0.092 ± 0.033	1.05

The allelic richness was greater in POOL14 than in SYNFC. Four alleles were present in POOL14 and absent in SYNFC : GOT1-6, GOT2-2, MDH1-10.5, PGI1-3. For all of the 12 polymorphic loci, except for IDH1, MDH5, ADH1, "Z" values were greater than 1.96 indicating that the allozyme frequencies were significantly different at $P = 0.05$ (Table 1). The SYNFC × highland tropical pool is more diverse than the SYNFC synthetic. As expected, the cross with the highland tropical population had broadened the genetic diversity.

The frequencies of the alleles specific to highland tropical populations were low. GOT-2 and MDH1-10.5 frequencies were close to zero. Only GOT1-6 frequency was sufficiently high to allow a study of the evolution of exotic allele frequency in the different SYNFC × highland tropical materials. For other exotic-specific alleles, the number of seedings needed to obtain accurate estimates of the expected frequency of POOL14A (i.e. half of the POOL14 frequency) would be too high. Also, the relationships between POOL14, POOL14SEL and POOL14A were studied in respect of GOT1-6 frequency. GOT1-6 frequencies for the unselected (POOL14) and the selected version of the pool (POOL14SEL) did not differ (Table 2). Moreover, the GOT1-6 frequency for POOL14A did not differ significantly from the expected frequency (i.e. one half of the frequency for POOL14SEL). During the selection on per se value and the cross with elite material, the exotic allele was not lost. The same conclusion was obtained from the principal component analysis performed on ACP1, ADH1, GOT1 and GOT2 frequencies (Fig.1). The unselected and selected versions of POOL14 were very close together. The first axis separated the SYNFC × highland tropical populations from the other materials with a high proportion of temperate germplasm, and the second axis separated the elite hybrid and derived elite material (POOL14A) from the other materials. As expected, the constitutions of POOL14SEL and POOL14A are 50% SYNFC: 50% highland tropical population, and 25% SYNFC: 25% highland tropical population: 50% elite dent hybrid, respectively.

Table 2 GOT1–6 frequency (Freq) with standard error (σ) of the "temperate × highland tropical" pool (POOL14), the "selected temperate × highland tropical" pool (POOL14SEL), and the "elite material × POOL14SEL" pool (POOL14A)

Population	Freq ± σ
POOL14	0.149 ± 0.022
POOL14SEL	0.163 ± 0.041
POOL14A	0.048 ± 0.018

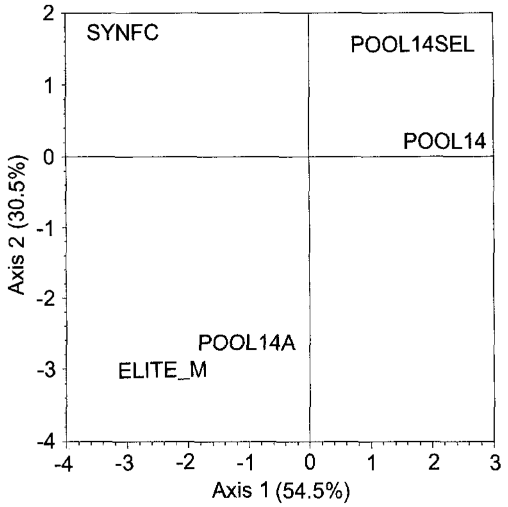

Fig. 1 Principal component analysis of allelic frequencies at four loci (ACP1, ADH1, GOT1, GOT2) for the French Canadian synthetic (SYNFC), the "SYNFC × highland tropical populations" pool (POOL14), the selected version of POOL14 (POOL14SEL), the "POOL14SEL × elite germ plasm" pool (POOL14A), and the elite germ plasm (ELITE_M)

Effect of an additional cross with elite material on the exotic × adapted cross in respect of its breeding value

Means of populations

For most traits, the means of POOL14 and POOL14A were significantly different at $P = 0.05$ (Table 3). The mean yield, the dry matter content and the root-lodging resistance increased, whereas the days of silking, the grain moisture and the plant and ear heights decreased, with an increasing proportion of elite germplasm. A significant non-linear response among population means due to the proportion of elite germ plasm was noted for the earliness traits (dry matter content, grain moisture, days to silking), and for root-lodging susceptibility. Comparing the earliness of POOL14A with POOL14 and elite material, the cross with exotic material was always later than the value expected from the additivity of the two parents. The exotic material seems to contain dominant alleles or major genes for tardiness. For root-lodging resistance, the elite material seems to contain favourable alleles. For plant and ear heights, the measures of POOL14A were similar to one half of the parental measures. For yield, the test of linear regression was variable; the regression was linear for the forage yield evaluated in the cross with a Stiff Stalk tester and for the grain yield evaluated in the cross with a flint tester, but was non-linear for other situations.

Differences between the productivity means of POOL14 and POOL14A were greater for grain production than for forage production.

Genetic variability and expected selection response

Estimates of $\sigma^2 g$ for the traits measured were significantly different from 0 in the two populations (Table 4). For yield, plant and ear heights, and for the earliness traits except for grain moisture evaluated in the cross to the

Table 3 Means with standard errors (σ) for traits measured on POOL14, POOL14A, elite material, and French Canadian synthetic (SYNFC) in crosses to different testers, and a statistical test for the difference between POOL14 and POOL14A

Variables	POOL14	POOL14A	Test	Elite material	SYNFC
	Mean ± σ	Mean ± σ		Mean ± σ	Mean ± σ
Forage production with Flint tester					
Dry matter content (%)	28.98 ± 0.95	29.86 ± 0.52	**	32.94 ± 1.75	32.80 ± 1.75
Dry whole-plant yield (t/ha)	16.12 ± 0.53	17.13 ± 0.40	**	19.64 ± 1.85	15.62 ± 1.85
Harvest-stage root lodging (%)	62.51 ± 6.16	37.98 ± 5.85	**	39.73 ± 15.99	55.70 ± 18.47
Vegetative-stage root lodging (%)	56.76 ± 7.02	35.68 ± 5.98	**	39.73 ± 16.63	54.23 ± 19.20
Grain production with Flint tester					
Grain moisture (%)	34.48 ± 0.63	33.91 ± 0.35	**	32.76 ± 0.50	31.91 ± 0.50
Grain yield (q/ha)	85.73 ± 2.74	93.12 ± 2.15	**	102.98 ± 7.44	84.77 ± 7.44
Harvest-stage root lodging (%)	72.68 ± 5.24	59.09 ± 5.58	**	63.75 ± 16.61	67.50 ± 16.61
Vegetative-stage root lodging (%)	70.26 ± 5.71	57.03 ± 5.66	**	62.08 ± 17.56	65.00 ± 17.56
Forage production with Stiff Stalk tester					
Days to silking	23.82 ± 0.58	23.40 ± 0.43	**	21.50 ± 0.71	20.17 ± 0.71
Dry matter content (%)	31.70 ± 0.61	33.05 ± 0.49	**	36.57 ± 1.24	35.19 ± 1.24
Dry whole-plant yield (t/ha)	17.32 ± 0.37	17.53 ± 0.28	NS	17.75 ± 1.17	15.29 ± 1.17
Grain production with Stiff Stalk tester					
Days to silking	19.53 ± 0.32	19.31 ± 0.21	**	17.83 ± 0.86	16.83 ± 0.86
Ear height	137.11 ± 2.91	130.10 ± 2.20	**	119.67 ± 5.32	119.33 ± 5.32
Plant height	265.76 ± 3.17	260.80 ± 2.21	**	253.03 ± 5.85	253.37 ± 5.85
Grain moisture (%)	22.59 ± 0.37	22.93 ± 0.45	NS	20.03 ± 1.35	21.73 ± 1.35
Grain yield (q/ha)	70.69 ± 2.36	78.14 ± 1.92	**	77.75 ± 6.28	65.28 ± 6.88
Harvest-stage root lodging (%)	20.95 ± 2.49	13.61 ± 1.80	**	12.59 ± 7.60	19.99 ± 7.60

Table 4 Genetic variances ($\sigma^2 g$) with standard errors (σ), heritability (h^2) and predicted "usefulnesses" with weak ($\alpha = 38\%$, U1) and strong ($\alpha = 10\%$, $U1.75$) selection of testcross progenies of POOL14 and POOL14A. Expected selection responses were calculated for a more productive, an earlier, a taller and a more root lodging-resistant population

Variables	POOL14					POOL14A				
	$\sigma^2 g$	σ	h^2	$U1$	$U1.75$	$\sigma^2 g$	σ	h^2	$U1$	$U1.75$
Forage production with Flint tester										
Dry matter content (%)	8.62	±2.13	0.92	31.80	33.91	2.24	±0.71	0.79	31.19	32.19
Dry whole-plant yield (t/ha)	1.93	±0.66	0.70	17.29	18.16	1.51	±0.46	0.75	18.19	18.99
Harvest-stage root lodging (%)	373.42	±115.15	0.75	40.03	27.49	258.05	±96.61	0.59	23.35	14.10
Vegetative-stage root lodging (%)	296.56	±89.55	0.77	47.42	36.11	256.50	±91.94	0.61	25.46	16.07
Grain production with Flint tester										
Grain moisture (%)	3.98	±0.91	0.96	32.52	31.52	1.32	±0.30	0.90	32.82	32.00
Grain yield (q/ha)	65.11	±17.95	0.83	93.08	98.59	35.88	±12.25	0.64	97.89	101.48
Harvest-stage root lodging (%)	261.89	±77.70	0.76	56.10	45.49	286.53	±83.00	0.73	42.57	31.72
Vegetative-stage root lodging (%)	216.30	±65.75	0.75	59.95	50.40	289.21	±80.18	0.76	44.29	33.18
Forage production with Stiff Stalk tester										
Days to silking	3.63	±0.95	0.88	22.02	20.68	2.33	±0.55	0.90	21.96	20.87
Dry matter content (%)	4.23	±1.10	0.89	33.65	35.11	2.33	±0.71	0.73	34.36	35.34
Dry whole-plant yield (t/ha)	1.34	±0.41	0.80	18.35	19.13	0.63	±0.24	0.62	18.16	18.63
Grain production with Stiff Stalk tester										
Days to silking	1.04	±0.26	0.89	18.57	17.84	0.40	±0.14	0.69	18.78	18.39
Ear height	76.79	±22.87	0.80	144.93	150.80	38.48	±12.21	0.70	135.28	139.16
Plant height	97.86	±26.83	0.85	274.89	281.74	54.73	±15.19	0.79	267.39	272.34
Grain moisture (%)	0.73	±0.42	0.51	21.98	21.52	1.69	±0.70	0.64	21.89	21.10
Grain yield (q/ha)	49.71	±16.02	0.79	76.95	81.64	32.00	±13.08	0.67	82.77	86.25
Harvest-stage root lodging (%)	38.50	±19.61	0.56	16.29	12.79	28.25	±9.95	0.65	9.33	6.12

Stiff Stalk tester, the $\sigma^2 g$ estimates of POOL14 were higher than the estimates of POOL14A. For root-lodging traits, the $\sigma^2 g$ estimates for the two populations were not significantly different from each other. For these traits, $\sigma^2 g$ estimates were associated with relatively large standard errors. Thus, for all traits measured, the $\sigma^2 g$ estimates for POOL14 and POOL14A were never significantly lower than the estimates of POOL14A.

Predicted mean of the selected population

The "usefulness" criterion denotes the predicted genotypic mean of the upper α percentage function. For the comparison of POOL14 and POOL14A, the "usefulness" criterion estimated with low or high selection intensity gives a similar result (Table 4). For earliness traits on the flint tester and height traits on the Stiff Stalk tester, POOL14 had a higher expected breeding value than POOL14A. This is due to the higher genetic variance estimate in for POOL14 than in POOL14A. For other traits, the "usefulness" criterion was higher for POOL14A than for POOL14 (Table 4). In POOL14A, greater mean performances have compensated for the lower genetic variance estimates in the expression of the "usefulness" criterion.

The "usefulness" criterion could be compared to the mean performance of elite material. In the cross with the flint tester, POOL14A would have a lower productivity than, but a similar maturity to, the elite material. In the cross with the Stiff Stalk tester, POOL14A would have a higher productivity and would be later than the elite material (Table 3 and 4). In both cases, POOL14A would have a lower breeding value than the elite material.

Genetic correlations

Genetic correlations between yield and earliness traits showed differences between the two populations. In crosses with both testers, the correlation coefficient between yield and late maturity was positive in POOL14A, and was lower than in POOL14 (Table 5). In POOL14, the existence of late and low productive genotypes decreased the correlation coficient between yield and late maturity.

Table 5 Genotypic correlation coefficient estimations between productivity (grain yield, dry whole-plant yield) and earliness (grain moisture, dry matter content) in POOL14 and POOL14A

Variables	POOL14	POOL14A
Grain yield / grain moisture		
Flint tester	−0.28	0.42
Stiff Stalk tester	0.14	0.66
Dry whole-plant yield / dry matter content		
Flint tester	0.28	−0.20
Stiff Stalk tester	0.48	−0.01

Discussion

Estimation of the proportion of exotic material in the exotic × adapted crosses using isoenzymatic alleles

Isoenzymatic data showed that the allelic richness was greater in POOL14 (2.38) than in SYNFC (2.07). This indicates a greater genetic diversity of the introduced highland tropical germ plasm. The wide diversity of maize races in Mexico, Central America, and the Caribbean Islands is well known (Hallauer 1978). Goodman and Stuber (1983) found a high allelic richness in a collection of 31 races from Bolivia (5.67). Compared with other temperate materials, the allelic richness of SYNFC was also relatively high. Lefort-Buson et al. (1991) noted an average number of alleles per locus and per population lower than two among maize European populations in several studies (Salanoubat and Pernes 1986; Lavergne 1988; Geric et al. 1989). This result could be explained by the broad genetic base of the French Canadian synthetic. To rapidly raise the performance of a population, the choice of a narrow-based germ plasm is often discounted because of the difficulty in finding germ plasm without undesirable features, and because of the specific combining ability of the material in respect of its future breeding utility.

The non-significant difference between the frequencies of unique exotic alleles in POOL14SEL and POOL14, and the proximity of POOL14 and POOL14SEL on the first plane of the principal component analysis performed on allelic frequencies, indicated no significant deviation between the polymorphism of POOL14SEL and POOL14. Thus, no significant deviation occurred during mild selection in POOL14. The effects of random mating on an exotic × adapted cross have hardly been studied in maize. Rubino and Davis (1991) examined the maintenance of tropical isozyme alleles in a sweet corn × tropical maize composite during the four initial cycles of random mating conducted in a temperate location. They found that directional natural selection did not have a large impact. Eagles et al. (1989) compared the means of the testcrosses of two generations of two highland tropical × temperate populations in order to determine the effect of one generation of random mating on the breeding value. They observed that changes occured during recombination, and they supported the idea of the usefulness of random mating.

With the analysis of the frequencies of unique exotic alleles, the effect of the adaption phase on the loss of exotic germ plasm could be studied. Among the reasons given to explain the low success of exotic germ plasm, the loss of useful exotic factors due to the difficulty in breaking linkage blocks is often cited (Wellhausen 1965; Lonnquist 1974; Hallauer 1978; Bosch et al. 1994). In genetically diverse crosses, the breakup of linkage blocks could be restricted by barriers to recombination such as inviable meiotic products (Lonnquist 1974) or incomplete homology between chromosome pairs (Hanson 1959). Thus, several generations of random mating were practiced on exotic × adapted crosses before applying more stringent selection (Hallauer 1978; Sauvaire and Sanou 1989).

Incidence of an additional cross with elite material on the exotic × adapted cross

Compared with POOL14A and the elite hybrid, POOL14 had undesirable features: low productivity, tall plants, late maturity, root-lodging susceptibility. These undesirable features have been already mentioned by several authors (Goodman 1985; Eagles and Lothrop 1994). The late maturity and tall plants are probably due to the photoperiod susceptibility of POOL14. After the first cross with the early synthetic, the pool is not completely adapted to a photoperiod involving long days. The productivity of the adapted × exotic cross in temperate regions has been often found to be lower than, or else the same as, the productivity of the adapted × adapted cross, but never higher (Gerrish 1983; Crossa et al. 1987; Mungoma and Pollak 1988). The absence of numerous selection cycles on introduced germ plasm could partly explain this low productivity. Highland maize from central Mexico is known to have weak roots (Eagles and Lothrop 1994). Populations developed with highland tropical germ plasm have been noted for their root lodging susceptibility in both New Zealand (Eagles and Hardrace 1989, 1993) and France (Giauffret 1993; Montalant, personal communication).

The greater difference observed in forage production as compared to grain production between the productivity means of POOL14 and POOL14A could not be attributed to a greater potential of tropical germ plasm for forage production. The effects of elite hybrid and exotic germ plasm are confounded. However, Thompson (1968) found that a group of exotic and semi-exotic populations yielded 13–41% more digestible dry matter than the adapted checks. Recently, Bosch et al. (1994) reported that more than half of the studied exotic populations yielded more total dry matter than did the check.

For all measured traits, the $\sigma^2 g$ estimate for POOL14 was never significantly lower than the POOL14A estimate. Based on theoretical aspects, this results was expected in the absence of linkage disequilibrium, particularly repulsion-phase linkage. The same results were obtained from experimental data. Goodman (1965) found a higher estimate of genetic variance for grain yield for the West Indian Composite (consisting of approximately 50% exotic and 50% adapted germ plasm) than for the Corn Belt Composite. For grain yield and days to anthesis, Crossa and Gardner (1987) found that estimates of genetic variance were higher for the F_2 than for the backcross generation. Albrecht and Dudley (1987) reported the same result for days to pollen shed and rind puncture resistance. For grain yield, they found that estimates of genetic variances for the F_2 were lower than for the backcross generation. They formulated the hypothesis of linkage disequilibrium in the F_2, which could have hindered the release of useful genetic variation.

Based on the "usefulness" criterion, POOL14A was found to be better than POOL14 for most evaluated traits. POOL14 had only a slight advantage for earliness traits in crosses with flint tester and for height traits. POOL14A had a better adaptation than POOL14. As analysis of correlation coefficients showed in POOL14 there are no late and low productive genotypes. Moreover, POOL14A was more resistant to vegetative and harvest-stage root lodging. For these reasons, POOL14A would be preferred to begin a selection programme. However, following the advice of Crossa (1989) and Bridges and Gardner (1987), the number of progeny among POOL14A would need to be large so as to avoid the loss of useful exotic factors.

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