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Abstract – The pyramidal recurrent selection system which is presented for breeding maize silage is designed to enhance variety development by preparing elite populations. From an early synthetic dent, two synthetics were developed: the 'base' synthetic with a low selection rate and the 'elite' synthetic with a high selection rate. Two cycles of recurrent selection with tester were achieved through this system, using multitrait selection with one-year evaluation of dry matter yield and dry matter content in three locations. The mean of 'elite' synthetic was 2.7 % better than 'base' synthetic for dry-matter yield in the second cycle. Genetic variance of 'elite' synthetic appeared to be about 50 % of that of 'base' population for dry matter yield in cycle 2 and for dry matter content in both cycles. Genotype × environment interaction variance was the same for both types of populations. Thus, strong differences in genetic variances were associated to relatively small differences in means. Results are discussed in terms of the effects of selection intensity, multitrait selection and genetic drift. (© Inra/Elsevier, Paris.)

recurrent selection / pyramidal recurrent selection / maize / genetic variances / variety development

Résumé – Premiers résultats d'un schéma de sélection pyramidal pour l'amélioration du maïs ensilage. Un schéma de sélection récurrente pyramidale est proposé pour le maïs ensilage afin de favoriser les sorties vers la création variétale. Partant d'une synthétique dentée précoce, deux synthétiques ont été développées : une synthétique de « base » conduite à une faible intensité de sélection et une synthétique « élite » conduite à forte intensité de sélection. Selon ce schéma, deux cycles de sélection récurrente avec testeur ont été réalisés avec, pour chaque cycle, une année d'évaluation dans trois lieux du rendement en matière sèche et de la teneur en matière sèche. Au second cycle, le rendement du niveau élite a été supérieur de 2,7 % à celui du niveau base. La variance génétique du niveau « élite » est apparue nettement plus faible (50 %) que pour le niveau « base » au deuxième cycle pour le rendement et dans les deux cycles pour

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la teneur en matière sèche. La variance d'interaction génotype × environnement a été la même pour les deux populations. Les résultats sont discutés en termes d'effets de l'intensité de la sélection, de la sélection multicaractère et de la dérive génétique. (© Inra/Elsevier, Paris.)

sélection récurrente / sélection récurrente pyramidale / maïs / variances génétiques / création variétale

1. INTRODUCTION

Recurrent selection has been proposed as a means of managing genetic variability at the population level in order to prepare for long-term genetic advance. It requires a low selection intensity to avoid an over-rapid decrease in genetic variability. For short-term efficiency, varietal development can be connected to any cycle of recurrent selection. However, it can be difficult and expensive to develop varieties or elite material directly from a population bred at a low selection rate. Indeed, material developed by such a low intensity recurrent selection can be, on average, excessively inferior to elite material. Then, even if the variability in the breeding material is large, the probability of extracting genitors as good as the elite material will be low, and it will be necessary to invest heavily. To solve this problem, and to improve the preparation for varietal development, Gallais [5] proposed inserting a high selection rate population between the low selection rate population and variety development.

Similarly, to ensure the valorisation of recurrent selection by preparing the development of new breeding material in corn, a pyramidal breeding system called Hope (hierarchical open-ended) has been proposed by Cramer and Kannenberg [3]. The aim of the Hope system is to increase genetic diversity and breeding potential by continually incorporating a wide range of new germplasms into breeding populations concurrently subjected to increasingly stringent recurrent selection, in order to prepare the development of useful inbreeds for hybrid production. The Hope system involves two heterotic sets of four open-ended populations based on a hierarchy of performances: elite, high, intermediate, or low. According to the breeding level of the material, different breeding methods are used: stratified mass selection at the low level, modified ear-to-row selection at the intermediate and high levels. The elite level is synthesised with the best entries of high level populations, and a recurrent reciprocal selection (RRS) is applied.

In this paper, we give the first results from a pyramidal recurrent scheme, applied to corn, which is aimed at the development of new hybrids, according to the principles laid down by Gallais [5] and Cramer and Kannenberg [3]. Two connected populations, called 'base' and 'elite', are developed simultaneously from the same population: the 'base' population is improved with a low selection intensity, and the 'elite' population is improved with a high selection intensity, with gene fluxes from 'base' to 'elite'. Both types of populations are improved for their combining ability with a tester from another heterotic group. The selection rate for the 'elite' population is chosen such that the mean value of the best genotypes is close to that of the elite material. This 'elite' level should allow successful transition from recurrent selection to the pedigree scheme to generate new inbreds for hybrid production. The selection rate of the elite level of the Kannenberg system (10 %) is intermediate between the selection rate we used for the 'base' population (about 15 %) and that used for the 'elite' population (about 5 % or less). Our approach is aimed more at varietal development than at germplasm enhancement as is the Hope system and corresponds in fact to a subdivision of its 'elite' level. It could also be reciprocal by the use of two heterotic sets of two open-ended populations, 'base' and 'elite', with a tester for a set derived from the other heterotic set. We give here the results for a set of 'base' and 'elite' populations bred for their combining ability with a complementary tester during two cycles of selection, considering only the differences in means and variances between 'base' and 'elite' in each cycle. Indeed, we have not developed an experiment to evaluate genetic advance.

2. MATERIALS AND METHODS

2.1. Breeding scheme

The material used in this study is involved in a silage breeding programme initiated in 1983 by the three INRA breeding stations of Mons, Lusignan and Le-Moulon. The synthetic studied is called SMLF, which stands for 'synthetic from Mons and Lusignan, forage value'. SMLF results from an intercross between two early dent pools: one with a broad genetic base (population variety) and the other with a narrow genetic base (based upon 6 early dent lines). The SMLF population (C0) was developed in 1985 and followed a recurrent breeding scheme with a test-cross progeny evaluation for silage value. From the results of the trials of the SMLF–C0 population at two locations, progenies were selected according to a multitrait selection index combining silage yield and earliness value in both locations. The 15 % best entries were intercrossed to develop the 'base population' SMLFB–C1 and the top 5 % entries were intercrossed to develop the 'elite population' SMLFE–C1. The two levels of selection were maintained subsequently and at each cycle, multitrait selection indices were used to select: i) the 15 % best entries of the base population to be intercrossed to generate the next SMLFB cycle; and ii) the 5 % best entries of the base population to be intercrossed with the 5 % best entries of the elite population to produce the next cycle of SMLFE.

'Base' and 'elite' synthetics followed the same recurrent breeding scheme with a test-cross progeny evaluation with the single-cross tester (MBS847 × F271) representative of the American and Canadian dent groups which combine well with the synthetics. The cycle is 3 seasons long. In the first season, about 300 S_0 plants are selfed or crossed with three plants from the tester. As an alternative, S_0 plants could be selfed in a winter nursery and test-crosses developed the following season with S_1 progenies. At maturity, about one half of the S_0 plants are chosen according to their lodging resistance, stay green, tolerance to pests such as *Fusarium roseum* and *Ustilago maydis* and general aspect. The following season, test-crosses progenies are evaluated in replicated trials for silage value. As Sampoux et al. [14] showed that testing for both whole-plant yield and grain yield appeared necessary to keep a minimum grain content in forage, an evaluation of grain yield was introduced at the base level from the first cycle. The selection of the best genotypes is by two independent culling levels: progenies showing high stalk or root lodging, i.e. greater than the mean value of the trial, are first eliminated, then about 20 S_1 progenies for the 'base' level (22 among 140 in 1993 and 20 among 180 in 1996) and about 10 S_1 progenies for the 'elite' level (6 among 140 from the 'base' population and 11 among 130 from the 'elite' population in 1993 and 3 among 180 from the 'base' population and 7 among 180 from the 'elite' population in cycle 2) are selected according to their index values. The corresponding S_1 progenies are then intercrossed in the third season.

2.2. Performance evaluation

In this study, we consider results from the replicated trials of first (C1) and second (C2) cycles of selection of SMLF 'base' and 'elite' synthetics (years 1993 and 1996). Test-crosses were evaluated: i) for silage value in three locations at both base and elite levels; and ii) for grain yield in a single location only at the base level (data not shown here). Three locations from the experimental INRA network were chosen for each year of evaluation (1993 and 1996): Le-Moulon (near Paris) for both silage and grain yields, Le-Pin (Normandie) and Mons (Picardie) for silage value. Plant density was 105 000 plants·ha^{-1} for silage evaluation. At Mons and Le-Pin, the two row plots were 5 m long and 1.6 m large. One row-plots for silage value at Le-Moulon were 5 m long and 0,8 m apart. Two main traits were observed: dry matter yield (DMY) (t·ha^{-1}) and dry matter content (DMC). In 1993 and 1996, 'base' and 'elite' levels were evaluated in the same locations but in separate trials. For each synthetic, S_0 plants chosen in the first season nursery (140 progenies in 1993 and 180 progenies in 1996) were randomly divided into two (1993) or three (1996) sets of equal size, four checks (reference varieties) were added to the sets and each set was arranged in a lattice design with two replicates (9 × 10 lattices in 1993 and 8 × 8 lattices in 1996). Due to differences in harvesting dates between trials within a site, the connection between 'base' and 'elite' synthetics was established through the check hybrids. Then, the synthetics were compared on the basis of the ratio of the observed value on the average value of the checks. Such a correction was also taken into consideration for the estimation of variances.

2.3. Statistical aspects and selection procedure

Analysis of variance was first performed for each location using incomplete block information of lattice design,

according to the model: $Y^t_{ijk} = \mu + G^t_i + r^t_j + b^t_k + \varepsilon^t_{ijk}$, where Y^t_{ijk}, G^t_i, r^t_j, b^t_k, ε^t_{ijk} are respectively the record for individual i in block k within replicate j for trait t, the random genetic effect of individual i, the fixed effect of replicate j, the random environmental effect of block k within replicate j and the random residual effect for plot ijk. The two or three trials by location were considered as one, the trial effect was included in the fixed replicate effect.

Within each location, variance-covariance components were estimated through restricted maximum likelihood (REML) procedure [11] using INRA Select Software [6, 10].

Heritabilities were defined on a progeny means basis as:

$$h^2 = \sigma^2_G / \left(\sigma^2_G + \frac{1}{b}\sigma^2_e \right),$$

where σ^2_G is the genetic variance, and σ^2_e is the residual variance. The 95 % confidence intervals were calculated according to Knapp et al. [9]. A multisite heritability was defined as:

$$h^2_m = \sigma^2_G / \left(\sigma^2_G + \frac{1}{l}\sigma^2_{GE} + \frac{1}{lb}\sigma^2_e \right),$$

where l is the number of locations, b is the number of replicates within each location, σ^2_G is the genetic variance, σ^2_{GE} is the genotype × environment variance and σ^2_e is the residual multisite variance. A multisite analysis of variance allowed the estimation of all the parameters of variance using the Varcomp procedure of SAS Inc. [12].

Following Falconer [4], performances of a given trait in two locations were considered as two different traits. Covariance between environmental effects of traits recorded in different locations equal zero. So, for two such traits evaluated in two locations m and n, we have: $cov\ (G^m, G^n) = cov\ (Y^m_i, Y^n_i)$.

The best linear unbiased predictors (BLUP) of genetic effects for all traits (calculation by INRA Select Software) were then used in linear combinations to obtain the desired gain selection index. Let $[\hat{G}]$ be the matrix of predicted genetic values (BLUP), with t columns (traits) and N rows (individuals). The index is defined as $[I] = [\hat{G}]\ [a]$, with $[a]$ being the vector of weights of dimension $(t,1)$. Under the assumption of multinormality, $[a]$ is estimated from equations of relative desired gains on traits concerned by selection: $[\Delta\hat{G}] = \lambda[k]$, where $[\Delta\hat{G}]$ is the vector of expected gains, $[k]$ is the vector of relative desired gains (or constraints) for chosen traits and λ is a positive scalar. $[a]$ is calculated by solving: $[\widehat{GG}]\ [PP]^{-1}[\widehat{GG}]\ [a] = [k]$, $[\widehat{GG}]$ is the variance-covariance matrix of BLUP $\hat{G}$ and $[PP]$ the variance-covariance matrix of phenotypic values P. For yield traits, the constraints, i.e. coefficients k, are such that the ratio of expected genetic advances for any two yield traits are equal to ratios of the maximum expected gains, that is the gains based upon selection on a unique trait. The value given to the constraints for earliness traits was equal to zero in the case of negative yield-earliness correlation. In the case of positive yield-earliness correlation, no constraint was given for the trait.

'Base' (FB) and 'elite' (FE) populations were compared within each cycle of selection at the level of means and genetic variances. Comparison between the two cycles are not justified because they were not studied simultaneously.

3. RESULTS

3.1. Comparisons of means for 'base' and 'elite' population at each cycle

Ratios of observed dry matter yield to that of the checks (*table I*) were significantly larger for synthetic FE than for synthetic FB at Mons in 1993, at Mons and Le-Pin in 1996 and for the mean of the three locations in 1996. For dry matter content, ratios of synthetic FB were larger than those for synthetic FE at Le-Moulon and for the three locations mean in 1993. In 1996, all ratios were comparable except at Le-Moulon where synthetic FE appeared earlier (greater ratios) than synthetic FB.

At the end of the first cycle of recurrent selection, the two synthetics were not significantly different for forage yield (1.2 % difference) but the 'base' level was significantly earlier than the 'elite' level. Following the second cycle, the 'elite' level appeared significantly superior to the 'base' level (2.7 % difference) for forage yield but the two synthetics became comparable for earliness traits.

3.2. Variance comparisons for 'base' and 'elite' population at each cycle

Considering the ratio of genetic variance of 'elite' population to that of 'base' population for each location for a given cycle, the results were approximately the same with or without correction of the data by the average value of the checks

Table I. Corrected means (ratio to checks) for FB and FE synthetics and their ratio, in cycle 1 (1993) and cycle 2 (1996) in three locations: Le-Moulon (ML), Mons (MN) and Le-Pin (PIN).

		Cycle 1 – 1993			Cycle 2 – 1996		
		FB	FE	FE/FB	FB	FE	FE/FB
DMY	ML	1.037 ± *0.022*§	1.032 ± *0.014*	0.99	0.860 ± *0.01*	0.875 ± *0.009*	1.02
	MN	0.942 ± *0.011*	0.967 ± *0.01*	1.03*	0.914 ± *0.009*	0.941 ± *0.011*	1.03*
	PIN	0.974 ± *0.012*	0.99 ± *0.011*	1.02	0.866 ± *0.011*	0.907 ± *0.014*	1.05*
	Average	0.984 ± *0.009*	0.996 ± *0.007*	1.01	0.880 ± *0.006*	0.907 ± *0.007*	1.03*
DMC	ML	1 ± *0.017*	0.976 ± *0.011*	0.98*	1.009 ± *0.008*	1.031 ± *0.006*	1.02*
	MN	0.973 ± *0.012*	0.972 ± *0.006*	1.00	1.032 ± *0.007*	1.039 ± *0.005*	1.01
	PIN	0.999 ± *0.013*	0.986 ± *0.006*	0.99	1 ± *0.008*	0.987 ± *0.009*	0.99
	Average	0.991 ± *0.007*	0.978 ± *0.005*	0.99*	1.014 ± *0.004*	1.019 ± *0.004*	1.01

* Significant (FB-FE) difference at 5 %
§ Standard deviation of the corrected mean
DMY: dry matter yield, DMC: dry matter content

Table II. Estimates of genetic variances of FB and FE synthetics and their ratio for cycle 1 (1993) and cycle 2 (1996) in three locations: Le-Moulon (ML), Mons (MN) and Le-Pin (PIN).

		C1–1993				C2–1996			
		FB	FE	FE/FB* uncor	cor	FB	FE	FE/FB* uncor	cor
DMY	ML	0.73# (0.26)§	0.68 (0.27)	0.93	0.85	0.87 (0.19)	0.73 (0.17)	0.84	0.84
	MN	0.49 (0.14)	0.75 (0.16)	1.53	1.74	0.33 (0.07)	0.22 (0.06)	0.67	0.69
	PIN	0.46 (0.12)	0.28 (0.14)	0.61	0.63	1.15 (0.23)	0.44 (0.18)	0.38	0.45
	σ^2_G	0.30 (0.08)	0.33 (0.09)	1.10	1.09	0.52 (0.09)	0.24 (0.06)	0.46	0.50
	σ^2_{GE}	0.26 (0.09)	0.25 (0.10)	0.96	0.94	0.26 (0.09)	0.22 (0.07)	0.84	1.04
	$\sigma^2_G + \sigma^2_{GE}$	0.56 (0.09)	0.58 (0.11)	1.04	1.02	0.78 (0.09)	0.46 (0.08)	0.59	0.66
DMC	ML	1.77 (0.57)	1.42 (0.52)	0.80	0.84	1.40 (0.37)	0.51 (0.19)	0.36	0.38
	MN	6.67 (0.87)	3.33 (0.50)	0.50	0.51	1.49 (0.21)	0.73 (0.14)	0.49	0.51
	PIN	3.72 (0.66)	2.34 (0.49)	0.63	0.51	2.83 (0.68)	1.87 (0.49)	0.66	0.70
	σ^2_G	3.58 (0.52)	1.76 (0.31)	0.49	0.46	1.26 (0.22)	0.63 (0.13)	0.50	0.50
	σ^2_{GE}	0.51 (0.22)	0.61 (0.20)	1.19	1.41	0.65 (0.20)	0.41 (0.15)	0.63	0.60
	$\sigma^2_G + \sigma^2_{GE}$	4.09 (0.42)	2.37 (0.28)	0.58	0.56	1.91 (0.24)	1.04 (0.16)	0.54	0.53

* Ratio of variance estimate of FE to that of FB synthetic computed with uncorrected (uncor) or corrected (cor) values.
§ Standard deviation of the variance
# Variance of observed data (uncorrected)

(*table II*). Average genetic variance for the three locations, i.e. $\sigma^2_G + \sigma^2_{GE}$, showed a significant reduction (about 50 %) from 'base' to 'elite' population in C2 for dry matter yield and in both cycles for dry matter content. The same result was observed for the genetic variance across locations (σ^2_G). Note that, for both traits, unlike genetic variance, the genotype × environment variance (σ^2_{GE}) was approximately the same for 'base' as for 'elite' population. A tendency for a reduction in this variance is also observed for dry matter content in cycle 2.

Reduction in genetic variance across locations varied according to the location. However, there was clearly a tendency for reduction in all locations, except in C1 for dry matter yield. For dry matter yield in C2, the Le-Pin location showed the greatest reduction (about 60 %), but the reduction was also about 30 % at Mons, and only 15 % at Le-Moulon. Lack of accuracy is sufficient to explain such a variation. In comparison, multisite estimates of genetic variances were estimated with a higher accuracy and support the conclusion that for dry matter yield in C2, the tendency was toward a reduction in variance for the 'elite' as compared to the 'base' population.

It can be noticed that, for dry matter content as for dry matter yield, the decrease in average genetic variance across locations can be mainly attributed to a drop in the genetic variance but not in genotype × environment variance. This is quite consistent with what is expected. Indeed, a selection on an average over sites must induce a fall of genetic variance whereas the genetic × environment variance could remain unchanged because a given mean could be reached by different ways.

3.3. Heritabilities and genetic correlations

Values of one-site heritabilities for dry matter yield on a progeny mean basis (*table III*) showed small and non-significant differences between the two populations, FB and FE, in a given cycle. For dry matter content, significant differences in heritabilities appeared between 'base' and 'elite' levels, partly because of better accuracy in the evaluation of the trait that implied smaller confidence intervals. Heritabilities were higher for DMC than for DMY. Heritability of DMC at Mons was signifi-

Table III. Estimates of heritabilities for the first (1993) and second (1996) cycles of FB and FE synthetics for the three locations: Le-Moulon (ML), Mons (MN) and Le-Pin (PIN).

		Cycle 1 – 1993				Cycle 2 – 1996			
		FB		FE		FB		FE	
DMY	ML	0.58	(0.43–0.68)	0.42	(0.22–0.57)	0.59	(0.47–0.68)	0.63	(0.52–0.71)
	MN	0.52	(0.35–0.64)	0.61	(0.47–0.71)	0.62	(0.51–0.70)	0.53	(0.39–0.63)
	PIN	0.51	(0.34–0.63)	0.34	(0.11–0.51)	0.56	(0.43–0.66)	0.57	(0.44–0.66)
	multisite h^2	0.48	(0.32–0.61)	0.49	(0.32–0.60)	0.63	(0.54–0.71)	0.46	(0.33–0.57)
	mean of h^2	0.54		0.46		0.59		0.58	
DMC	ML	0.47	(0.28–0.60)	0.40	(0.19–0.55)	0.51	(0.36–0.62)	0.50	(0.35–0.61)
	MN	0.93	(0.91–0.95)	0.85	(0.80–0.89)	0.78	(0.71–0.83)	0.65	(0.55–0.73)
	PIN	0.71	(0.61–0.78)	0.62	(0.49–0.72)	0.47	(0.31–0.59)	0.65	(0.55–0.73)
	multisite h^2	0.83	(0.77–0.87)	0.73	(0.64–0.79)	0.62	(0.53–0.70)	0.53	(0.41–0.62)
	mean of h^2	0.7		0.62		0.59		0.60	

95 % confidence intervals are indicated in parentheses.

antly higher for the 'base' synthetic than for the 'elite' synthetic in the 1993 and 1996 trials. A higher value of heritability for the 'elite' level than for the 'base' level was observed once in 1996 at Le-Pin. These values were comparable to those reported by Sampoux and Gallais [13] and Sampoux et al. [14] for dry matter yield as well as for dry matter content, for four populations with the same locations as ours during the period 1984–1990.

For both cycles and both traits, multisite heritabilities as well as the average of the three one-site heritabilities for 'base' population were equal or higher than those for the 'elite' population. This is consistent with the tendency to a decrease in genetic variance. From 'base' to 'elite' population, genetic variances for DMC in both cycles and DMY in cycle 2 decreased by 50 % whereas heritability fell by 10–30 %. This result could be explained by comparable values of genotype × environment and residual variances for the two levels (data not shown) and mostly by their small impact in the denominator of the formula of multisite heritability:

$$h_m^2 = \sigma_G^2 / \left(\sigma_G^2 + \frac{1}{l}\sigma_{GE}^2 + \frac{1}{lb}\sigma_e^2 \right).$$

Values of genetic correlations between locations for forage yield (*tables IV* and *V*) were high and sig-

Table IV. Genetic correlations for the first cycle (1993) of FB (below diagonal) and FE (upon diagonal) synthetics.

	DMY–ML	DMY–MN	DMY–PIN	DMC–ML	DMC–MN	DMC–PIN
DMY-ML		*0.66*	*0.47*	*–0.30ns*	*–0.73*	*–0.78*
DMY-MN	0.55		*0.45*	*–0.37*	*–0.54*	*–0.57*
DMY-PIN	0.43	0.5		*–0.44*	*–0.55*	*–0.51*
DMC-ML	–0.25ns	–0.71	–0.38		*0.65*	*0.66*
DMC-MN	–0.3	–0.62	–0.26	0.79		*0.92*
DMC-PIN	–0.42	–0.53	–0.24ns	0.8	0.91	

ns: Non significant correlation, the others being significant at 5 %, with an approximate confidence interval computed from ± twice the standard deviation computed with the Becker [1] formula.
ML: Le-Moulon, MN: Mons, PIN: Le-Pin. DMY: dry matter yield, DMC: dry matter content.

Table V. Genetic correlations for the second cycle (1996) of FB (below diagonal) and FE (upon diagonal) synthetic.

	DMY–ML	DMY–MN	DMY–PIN	DMC–ML	DMC–MN	DMC–PIN
DMY-ML		0.58	0.56	0.16ns	–0.44	–0.14ns
DMY-MN	0.79		0.24ns	–0.13ns	–0.30	–0.18ns
DMY-PIN	0.65	0.77		0.17ns	–0.03ns	0.44
DMC-ML	–0.20ns	–0.15ns	–0.31ns		0.64	0.48
DMC-MN	–0.29	–0.15ns	–0.24	0.74		0.67
DMC-PIN	–0.17ns	–0.26ns	–0.07ns	0.71	0.61	

ns: Non significant correlation, the others being significant at 5 %, with an approximate confidence interval computed from ± twice the standard deviation computed with the Becker [1] formula.
ML: Le-Moulon, MN: Mons, PIN: Le-Pin. DMY: dry matter yield, DMC: dry matter content.

nificant with few exceptions. Values for these correlations were almost invariant from FB to FE in 1993 but tend to decrease from FB to FE in 1996. This trend was also observed for genetic correlations between locations for dry matter content. In the absence of genotype × environment interactions, such correlations are also estimates of average heritability. So the decrease in genetic correlations from the 'base' to the 'elite' levels is consistent with the drop in heritability values. The small impact of genetic × environment interaction variance was also confirmed.

The correlations between DMY and DMC for 'base' and 'elite' levels were comparable in the first cycle (about –0.40) but they tend toward zero in the second cycle where the mean value of yield-earliness correlations was –0.20 for FB and –0.05 for FE. For comparable dent material in the first cycles of recurrent selection, Sampoux and Gallais [13] also reported significant negative or zero correlations between forage yield and dry matter content, ranging from –0.4 to 0.02.

4. DISCUSSION

At the level of means, the observed differences in C2 between 'base' and 'elite' populations are in agreement with what is expected, a significant difference in dry matter yield and a low difference in dry matter content. The small difference in dry matter content is the result of the constraint imposed on this trait. For dry matter yield, the difference between elite and base is 2.7 % in C2. This is quite consistent with what is expected with a single trait selection, with the observed parameters. However, we may wonder about the sizeable reduction in variances between the 'base' and the 'elite' populations in the second cycle for dry matter yield and in both cycles for dry matter content in comparison to the small changes in means.

For dry matter content, the differences in genetic variances between 'base' and 'elite' population, observed at both cycles, could be due to differences induced by the initial choice of individuals to develop 'base' and 'elite' populations. Since no important selection pressure was made on this trait in the following cycles, the difference between the two synthetics could remain stable. Our results, showing a high heritability and a low variance of genotype × environment effects for this trait, confirmed that the choice of individuals with close values for dry matter content would have irremediably decreased the variation of the trait in the 'elite' population.

Unlike the changes in variances for dry matter content, the 50 % fall in variance for dry matter yield in the second cycle for the 'elite' level as compared to the 'base' level may have been induced by the choice of the plants, i.e. selection or genetic drift, in cycle 1 to develop C2 populations. Consider first the effect of selection intensity. The estimation of genetic variance in an infinite population after a truncation selection is, according to Bulmer [2], $\sigma_G^2{}^* = \sigma_G^2 [1 - i (i - x) h^2/2]$ where σ_G^2 and $\sigma_G^2{}^*$ are the genetic variances before and after selection, h^2 the heritability value, i the selection intensity and x the abscissa of truncation under normal distribution hypothesis. According to this formula, the expected ratio between 'elite' and 'base' variances after the first cycle was of 0.97. A second cycle of selection does not greatly change the result. So, the sole effect of differential selection intensity could not explain the large difference between the two variances.

Random genetic drift could have occurred in the second cycle at the 'elite' population, because fewer than twenty individuals were selected at each cycle for recombination. According to Hallauer and Miranda [7], more than twenty families should be recombined in each cycle of selection if the long-term goals of the selection programme are expected to be achieved. Without any selection, the expected additive variance in the presence of genetic drift in a finite population could be predicted with the formula $E(V_t) = (1 - {}^1/_{2N})^t V_0$, where V_0 is the initial genetic variance of the population, N is the size of the population and t the generation number [2]. At cycle 0, the two populations were confounded with initial variance V_0. After two separate cycles: $E(V_2) = 0.95\ V_0$ for the 'base' level and $E(V_2) = 0.90\ V_0$ for the 'elite' level. Then, a difference of only about 5 % between the two levels in the second

cycle could be attributed to random genetic drift. This is low in comparison to the observed reduction in variance. It should be noted that, for a specific 'elite' population, due to sampling effect, i.e. foundation effect, the reduction in variance could be greater than expected. However, we reported that, unlike genetic variances, genetic × environment interaction variances remained stable from 'base' to 'elite' levels for both cycles. This is consistent with a low effect of random genetic drift on the components of the genetic variance.

The combined effect of genetic drift and selection remains to be considered. It is well known that in such a situation, genetic variance decreases more quickly than with either selection alone in an infinite population or than with genetic drift alone [8]. With the observed heritabilities, selection intensities and number of intercrossed plants, a simulation study for a polygenic additive trait, according to the Hospital and Chevalet [8] model, with 10 to 50 independent loci, shows a reduction in variance from 'base' to 'elite' population of about 20 % in C2. This is still less than 50 %. However, for a specific population, the reduction could be greater than this expected value, and furthermore, we have to consider the accuracy of the estimates. Sampling effects, which are expected to be of sizeable effect with only about 10 selected plants, could also explain the absence of observed reduction in C1. Such results are quite consistent with the constancy of genotype × environment interaction variance between 'base' and 'elite' populations. Indeed, as already mentioned, selection has a low effect on such a variance, and so, at this level, it remains a possible effect of genetic drift, which is expected to be low in the first two cycles. Then, the whole results appear to be well explained by the selection process.

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