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EUROPEAN MAIZE LANDRACES: GENETIC DIVERSITY, CORE COLLECTION DEFINITION AND METHODOLOGY OF USE

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ABSTRACT - Since its introduction in Europe five centuries ago, maize spread in Europe and numerous landraces have been cultivated. During the second half of the XXth century, large collections have been established to preserve this genetic diversity. The objectives of this paper are (i) to review recent results on the genetic structuration and the origin of European maize, (ii) to present the constitution of the representative core-collection of European maize landraces built in RESGEN CT96-088 project, and (iii) to study the methodology of use of these landraces in present breeding programs. Based on molecular markers, five studies found a high allelic richness in landraces from Mediterranean regions such as Spain, and (for two of them) a strong similarity between several populations from Southern Spain and a group of Caribbean populations. These studies also attest the originality of Northern Eastern Europe landraces, for which a similarity is observed with American Northern Flint landraces. Historical investigations confirm the hypothesis of introductions of maize from this origin in the North of Europe, only a few decades after introduction of tropical maize in Southern Spain by Colombus. Starting from a total of 2899 European landraces, we established with the Mstrat software a representative core collection of 96 maize accessions that maximizes allelic richness at molecular markers and best represents variation at phenotypic traits. This collection is characterized for traits of agronomical interest such as silage quality and insect tolerance. Regarding the transfer of relevant traits to elite material, comparison of F_2 versus backcross foundation populations showed that this last strategy leads to a higher population mean while not leading to a decrease in variance, therefore backcross method appears superior. Preliminary selection of superior material within a landrace did not increase average expected genetic gain but increased stability in variable environments. Molecular markers should prove helpful to extend this back-cross approach to the targeted transfer of donor interesting genomic regions.

KEY WORDS: *Zea mays* L.; Corn; European landraces; Genetic diversity; Core collection; Backcross; Foundation population.

INTRODUCTION

Maize was first introduced into Europe by Colombus, who brought it back from the West Indies to Southern Spain in 1493. Other introductions are hypothesized to have occurred later from other regions of the world and to have contributed to the diffusion of maize in the Mediterranean region, as well as in Central and Northern Europe (Brandolini, 1970). Hybridizations probably occurred between different introductions. Associated with the selection pressures which have been exerted by the farmers and by climatic conditions, they likely contributed to develop specific European varieties. European maize traditional varieties display a large diversity, but also share some common characteristics, such as insensitivity to the photoperiod, mainly flint texture of the grain and low to medium yield (Gay, 1999).

Since the middle of the XXth century, this diversity has been used to derive inbred lines. These lines appeared highly complementary with inbred lines of US origin to produce hybrids cultivated in Europe areas. Progress brought by plant breeding and agronomical practices constitute a true revolution which made it possible to produce average grain yields of about 90 q/ha (Fao, 2004). Some time after the introduction of the first commercial hybrids, the necessity to preserve genetic resources appeared and led to the constitution of many national maize collections (Edwards and Leng, 1965). In order to properly use the populations in breeding programmes, breeders characterised extensively these collections of populations. Morphological de-

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scriptions and classifications have been carried out on Spanish (SANCHEZ-MONGE, 1962), Italian (BRANDOLINI and MARIANI, 1968), Yugoslavian and Romanian (PAVLICIC and TRIFUNOVIC, 1966), Portuguese (COSTA-RODRIGUES, 1971) and more recently French (GOUESNARD *et al.*, 1997) national collections. Comparison of populations from different countries was carried out on populations from Italy, Hungary, Yugoslavia and Romania (LENG *et al.*, 1962) and on populations from Italy, Yugoslavia and Romania (PAVLICIC, 1971). BRANDOLINI (1969, 1970, 1971) realised several syntheses on major European maize races.

The relevance of morphological characters for the classification of populations appears limited, mainly because the effect of environment on the expression of characters. Genetic markers not affected by environmental conditions therefore received considerable attention for the analysis of genetic diversity. Isoenzymatic markers were used first, and allowed to analyze associations among different samples of European populations (SALABOUNAT and PERNÈS, 1986; GERIC *et al.*, 1989; LEFORT-BUSON *et al.*, 1991; GARNIER, 1992; LLAURADO *et al.*, 1993, REVILLA *et al.*, 1998). DNA markers, particularly RFLP and then SSR, were used subsequently. Based on these DNA markers, maize inbred lines were classified into distinct heterotic groups (for review see MELCHINGER, 1999).

With the large number of accessions contained in most crop germplasm collections, the genebank managers are to face to the maintenance and utilization of these collections. The core collection concept was proposed as one approach to this problem. The design of the core collection should minimize repetitiveness within the collection and should represent the genetic diversity of crop species (and possibly its relatives) (FRANKEL, 1984). The theory was developed on the basis of neutral marker by BROWN (1989) who showed that 10% of the base collection, and a maximum of 3000 individuals, allow preservation of about 70% of alleles. Most researchers currently believe that the sampling should first be stratified, according to the organization of variability in groups and sub-groups (HINTUM, 1995). The criteria used could be taxonomic, geographical or ecological, or could be based on neutral or non-neutral characters (HAMON *et al.*, 1995). To choose inside the groups, BROWN (1989) proposed the R, P, L, H strategies for which the number of accessions inside a group is given by random, proportional, logarithmic, or diversity index, respectively. Two main methods proposed a determinist choice. The M strategy (SCHOEN and BROWN, 1993) supposes the availability of molecular or biochemical data for accessions. This method maximizes the allelic richness. The PCSS method (NOIROT *et al.*, 1996) requires quantitative or qualitative data for accessions. This method maximizes the generalized sum of squares of the selected accessions in a space of factorial axes. UPADHYAYA *et al.* (2003) gave examples of core collection constitution in many species. In maize, RADOVIC and JELOVAC (1994), ABADIE *et al.* (1999), MALOSETTI and ABADIE (2001) constituted a core collection of populations from Yugoslav maize gene bank, Brazilian maize germplasm and Uruguayan maize landraces, respectively.

The core collection is a mean to manage a large collection by making possible the evaluation of a part of the collection which represents the total collection. Then it is an "entry key" to exploit all the collection by identifying of the best source(s) for the improvement of trait(s) of agronomical importance. Following this identification, the second step is the transfer of this quality to elite accessions.

The objectives of this study were to (i) review the genetic analysis of European collection of maize landraces in order to structure the variability, (ii) examine the methodology of constitution of the European core collection in order to manage and exploit the available genetic diversity for traits of interest, and (iii) compare several alternatives to use genetic resources for the improvement of elite breeding material.

GENETIC DIVERSITY OF EUROPEAN MAIZE LANDRACES

We review the results of five published studies on European and both European and American maize landraces (REBOURG *et al.* 2001, 2003; GAUTHIER *et al.*, 2002; REVILLA *et al.*, 2003, DUBREUIL *et al.*, 2005) (Table 1). The sampling consists of two bulks of 15 plants in all studies except for isozymes for which analyses were performed for individual plants. The use of RFLP and SSR for large scale molecular evaluations of genetic diversity within population is expensive and time-consuming effort. In contrast, the use of bulk analysis (MICHELMORE *et al.*, 1991) for maize diversity analysis with RFLP (DUBREUIL *et al.*, 1999) or with SSR (DUBREUIL *et al.*, 2003) allows an analysis of larger samples.

TABLE 1 - *Recent studies on genetic diversity among European maize populations: size of the analysed collection with reference to the programme, allelic richness in European and American landraces, used markers with type of sampling.*

	Number of European landraces	Mean number of alleles per locus in Europe	Number of American landraces	Mean number of alleles per locus in America	Markers	Sample
Rebourg *et al.* (2001)	131	9.59	–	–	29 RFLP	2 bulks of 15 plants
Gauthier *et al.* (2002)	488	11.48	–	–	23 RFLP	2 bulks of 15 plants
Rebourg *et al.* (2003)	131	9.55	88	12.34	29 RFLP	2 bulks of 15 plants
Revilla *et al.* (2003)	404	3.1	–	–	19 isozyme loci	20 plants
Dubreuil *et al.* (2005)	131	7.17	144	7.75	24 SSR	2 bulks of 15 plants

A higher degree of polymorphism was observed in American than in European maize populations (Table 1). Populations of Northern Eastern Europe exhibit a lower allelic richness than in Southern Europe ones, which suggests that (i) Southern Europe was the location of most of the introductions into Europe, (ii) northern introductions had a lower genetic diversity than southern ones (iii) that northern populations were submitted to a higher genetic drift, and/or (iv) that northern populations were stronger selected for adaptation. Revilla *et al.* (2003) observed the presence of several rare alleles in Spain that are absent in the other European countries, and suggested that Spain was the entry for most variability of European maize, or that there were several singular introductions of maize into Spain.

In all studies, a clear structuration identifies a cluster of Northern Europe landraces: one cluster of 39 populations in Revilla *et al.* (2003), two clusters for German Flint and North-Eastern European Flint in Rebourg *et al.* (2001, 2003), one cluster for North-Eastern populations in Gauthier *et al.* (2002). This suggests an origin of North-Eastern maize landraces different from the origin of the Southern European landraces. The structuration of other European landraces is variable among different studies. Revilla *et al.* (2003) and Rebourg *et al.* (2001, 2003) found a cluster for Mediterranean landraces, the other populations being in another large cluster, or separated in an Italian cluster and a Pyrenees-Galice cluster. Gauthier *et al.* (2002) found two main clusters: South-Eastern and South-Western clusters. These clusters are consistent with clusters found by Rebourg *et al.* (2001, 2003).

Results from studies investigating the population structure among European and American maize populations illustrated that Southern Spain populations were closely related to Caribbean populations. This can be explained by the historical data on the introduction of maize in the South of Spain by Colombus after his second trip in the Caribbean region. In addition, American Northern Flint populations were closely related to North-Eastern European populations considering molecular and morphological data. This suggests that the origin of Northern European germplasm was North America. Opposite to the Southern Spain and Northern European populations, materials from the Pyrenees and Galice in Spain do not display a close similarity with any American material. This suggests that Pyrenees and Galice populations are intermediate between the Caribbean and Northern American Flint populations. This can be explained as a result from hybridizations between these two types of landraces. Finally, it has to be noted that Italian populations constitute a homogenous independent group, which suggests an independent origin and/or local differentiation. Other introductions with lesser contribution may also have occurred, as suggested alleles Glu1-13, Acp1-3.5 and Mdh4-9 shared by maize from the Mediterranean countries (particularly Spain) and from Guatemala (Revilla *et al.*, 2003).

To complete the study on contribution of Northern Flints to European material, historical analyses were performed by M. Chastanet. They show that this North-American maize had probably been brought back at the time of the voyages of Giovanni Verazzano (1524) and possibly Jacques Cartier (1535), i.e. much earlier than one believed up to now (Rebourg *et al.*, 2003; Dubreuil *et al.*, 2005).

CONSTITUTION OF CORE COLLECTION OF EUROPEAN MAIZE LANDRACES

The European collections analyzed within the European RESGEN CT96-088 include a total of 2899 landraces (Table 2). The objective of the project was to build a core collection of around 100 landraces in order to evaluate them for several traits relevant to the European Common Agricultural Policy. The 2899 landraces were first described for passport data and some primary descriptors (such as flowering time, ear and kernel types, see http://www.montpellier.inra.fr/gap/resgen88/). The first step towards a core collection consisted in the definition of a representative national collection of maize landraces in each country. Size of these representative collections was decided in common by the different researchers (Table 2). The selection was based on passport data, primary descriptors, and secondary descriptors (such as plant height, ear length). The objective was to eliminate redundancy, to get accessions for each agro-ecological region of cultivating maize and a good representativity of the different categories of maize obtained after classification. On a second step, the different national representative collections were assembled and analysed for molecular markers. These 395 landraces were also evaluated for forage quality (MIEG *et al.*, 2001). The advantage of analysing together all representative national collections is to eliminate redundancy in frontier zones (Alsace and West Germany, French and Spanish Pyrenees, Galice and North of Portugal).

The method of constitution of the core collection is the M method proposed by SCHOEN and BROWN (1993) which maximizes the allelic richness. The software used is Mstrat (GOUESNARD *et al.*, 2001) for which richness is defined for alleles and classes of phenotypic values. To do so, distribution of quantitative traits is cut out in classes. The richness of a sample is defined as the number of classes for which there is at least one accession. In the case of two samples having the same richness scores, the software uses the inertia criterion, as defined in the principal score analysis method or PCSS (NOIROT *et al.*, 1996). The M method was found superior to random method and sampling methods proposed by BROWN (1989) (C, constant; P, proportional; L, logarithmic) on a simulated dataset (BATAILLON *et al.*, 1996). This method is used for the management of genetic resources collections (DAVID *et al.*, 2003; BARANGER *et al.*, 2004; MCKHANN *et al.*, 2004, and in other experimental works).

TABLE 2 - *Size of the total collection, representative collections and core collection for each country in Resgen088 programme.*

Country	Total collection	Representative collection	Core collection
France	272	80	16
Germany	15	15	8
Greece	201	50	12
Italy	562	90	19
Spain	948	90	24
Portugal	901	70	17
Total	2899	395	96

Reference maize landraces such as ones used for breeding, analysed in former studies, and/or of key historical importance are chosen. This first sample, inferior in size to the total size of the final sample, is called kernel core (22 landraces). In a second step, the genetic diversity (allelic or class richness) of the core collection sample is maximised using Mstrat by adding iteratively new accessions to the kernel core. Genetic diversity is defined for a whole of traits: passport data (country of origin), primary descriptors (growing degree units to female flowering, kernel type, ear shape, number of kernel rows, kernel and cob colour), isozyme analysis (14 loci and 47 alleles), RFLP analysis (21 loci with 127 alleles in frequency and 60 alleles in presence/absence). To choose the last accessions of the core collection, we have sampled among the accessions most frequently drawn by Mstrat (the most original accessions) those which were representative of the groups obtained by classification on the allelic frequencies with 19 loci RFLP.

The Mstrat strategy is mainly based on marker data (234 alleles versus 5 traits of primary descriptors and country of origin). The question is the effectiveness of the strategy mainly based on neutral diversity at other diversity levels such adaptation to ecogeographical conditions. It can be noted first that the classification obtained on 19 RFLP loci on the representative collections (GAUTHIER *et al.*, 2002) is in agreement with the geographical origin of accessions. Secondly in a previous study, GOUESNARD *et al.* (personal communication) analysed the diversity of 80 French Pyrenean maize landraces, both with 15 agromorphological traits and 16 RFLP loci. They compared the richness obtained at morphological traits by sampling either on morphological diversity (direct method), on molecular data (indirect method), or at random. Fig. 1 shows that the response of the indirect method is higher than the random sampling. The result was expected because the correlation coefficient estimated between morphological distances and molecular distances is significantly different from zero (0.18). Thus, strategy based on neutral diversity is effective to maximize the agronomical variability on this Pyrenean collection.

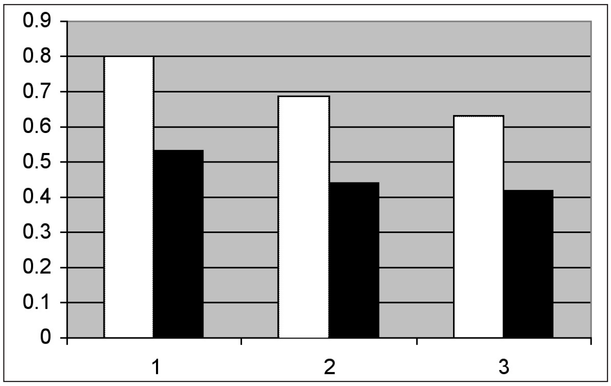

FIGURE 1 - Richness level measured on morphological variables in percentage of the total collection of 80 Pyrenean maize landraces (GOUESNARD *et al.*, personal communication). Measures for two sizes of the core collection (25% of the total in white, 12.5% of the total in black) and for three methods of constitution (1: direct method; 2: indirect method with molecular data, 3: random method).

On allelic and class richness criterion, 93% of the richness of the European representative collections is included in the core collection. On qualitative morphological variables, the Chi2 tests show that the percentage of each class is not significantly different between the total collection and the core collection. On quantitative variables, the mean of the variables are not significantly different. The minimum and the maximum of quantitative variables are nearly all identical. The distribution by country are globally conserved between the whole collection and the core collection (8% Germany, 12.5% Greece, 16.5% France, 18% Portugal, 20% Italy, 25% Spain) except for Germany for which the higher proportion of selected landraces is due to the originality of these accessions. Considering the classification found on 19 RFLP (GAUTHIER *et al.*, 2002), the distribution is the following: East Group (mainly Germany) 3%, Central Group (mainly France and Italy) 15.5%, South-Eastern Group (mainly Greece) 15.5%, South-Eastern Group (mainly Italy) 22%, South-Western Group (mainly Portugal) 22%, South-Western Group (mainly Spain) 22%. The list of the core collection is available in the database (http://www.montpellier.inra.fr/gap/resgen88/). The European Maize Landraces Core Collection (EUML-CC) was evaluated for various traits according to the European Common Agricultural Policy (Forage traits - MIEG *et al.*, 2001; Insect tolerance - MALVAR *et al.*, 2004; quality of the grains - BERARDO *et al.*, 2003; drought tolerance - DALLARD *et al.*, 2003; tolerance to low nitrogen level - BRICHETTE *et al.*, 2003).

USE OF EUROPEAN GENETIC RESOURCES

According to BERTHAUD (1997), there are three main ways to use genetic resources: (i) the linear model relied on an *ex situ* conservation for which an interesting accession is directly extracted from the gene bank for agricultural use, (ii) the triangular model in which a broad initial genetic diversity is progressively restricted by selection towards elite material suitable for agricultural use, and (iii) the "circular" model based on *in situ* conservation, in which agricultural use, multiplication and selection are fully integrated. Numerous examples of the triangular approach exist in maize: the Latin American Maize Project (SALHUANA, 1989; SEVILLA *et al.*, 1994), the Germplasm Enhancement of Maize (GEM, http://www.public.iastate.edu/~usda-gem/homepage.html), the INRA/PROMAIS project (GROUPE MAÏS DGAP-INRA and PROMAIS, 1994; GALLAIS and MONOD, 1998), the HOPE (Hierarchical Open-ended Population Enrichment; KANNENBERG, 2001).

The triangular model seems to be the more appropriate one for the utilisation of European maize landraces, mostly because of their low yield relative to present elite material. Indeed, maize landraces often yield only approximately half of present commercial hybrids and their hybrid performance is lower than that of elite inbred lines, when evaluated with the same tester lines (GALLAIS and MONOD, 1998). Therefore the main strategy to use them efficiently is to cross them with elite materials to create new breeding populations. This raises however several questions such as the proportion of elite material to be considered (e.g. 50% elite or 75% elite) and that kind of the necessity of a preliminary selection of individuals within landrace prior to crossing with elite material.

A pilot experiment was conducted on 4 French maize landraces to address these points (CHARCOSSET

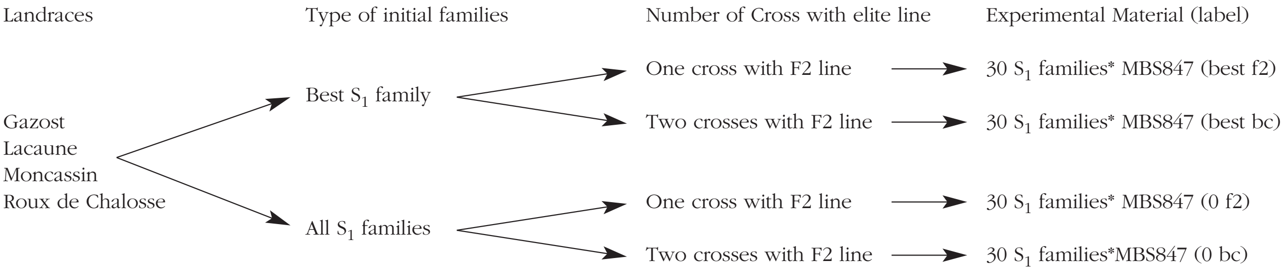

FIGURE 2 - Design of experiment on methodology of use of maize landraces (Charcosset *et al.*, personal communication). For each French landrace, initial families were an unselected pool of 30 S_1 families or the best S_1 family into this subset (Dubreuil, 1996). These materials were crossed once with the F2 line and then selfed (F_2 generation), or crossed twice with F2 line (Back-Cross generation). 30 S_1 families for each type were evaluated in crosses with the MBS847 tester.

et al., personal communication). The landraces were Lacaune (FRA0410015), Gazost (FRA0411041), Moncassin (FRA0410570), Roux de Chalosse (FRA0410622). The three last populations originated from south-western of France were studied by Dubreuil (1996) evaluating 30 S_1 progenies per population in crosses with two testers. For each population, four types of progenies (Fig. 2) were created by crossing to inbred line F2 (derived from the Lacaune population and widely used in commercial hybrids up to the early 1990s). They are combinations of: i) two types of initial donor material: unselected S_1 families or the best S_1 family derived from the landrace; ii) 50% or 75% of the elite material derived by one cross (F_2) and two crosses (BC) respectively. Thirty families for each such breeding population (16 in total) were evaluated in crosses with dent tester MBS847 in two locations (Gif sur Yvette, Clermont-Ferrand) with 2 replicates, in 1999 and 2000. Three traits were evaluated: grain yield, grain moisture and lodging. An economical index was estimated: I(CTPS) = yield – 2.5 * moisture. Three trials were considered in the study with an error variation coefficient lower than 7% for yield. Genetic variance and genetic x environment variance were estimated for each landrace and its 4 types of progenies. The interest of each type of progenies and landraces for breeding can be estimated by the utilisation criterion proposed by Schnell (1983). U= Mean + G(α) with G(α)= k(α) σ_g h, where k is the standardised selection differential for a given selected proportion (α), σ_g is the genotypic standard deviation, h is the square root of heritability.

Only number of crosses with the elite material (BC or F_2) and landrace factors and their interaction had significant effects on the trait variation (data not shown). No difference between selected S_1 family and the landrace itself were observed. The criterions of utilisation for the different traits are presented in Table 3. For yield and I(CTPS), BC were better than one cross F_2 in all cases except in the case of Lacaune and Roux de Chalosse (yield only) where methods are equivalent. For grain moisture, the behaviour of progenies depends on the earliness of F2 compared with the landrace. For early landraces (Lacaune, Gazost), the criterion of utilisation is better for F_2 than BC. On the opposite, for Roux de Chalosse and Moncassin, the criterion of utilisation is better for BC than for F_2. Back-cross method has an advantage also for lodging when the level is high in the original landrace. Several instances exist where the criterion of utilisation exceeds the value of elite parent F2, confirming the usefulness of landraces for genetic improvement.

The main conclusions are: (i) BC is preferable than the method with one cross F_2 because it increases the average of the population without decreasing the variance; (ii) the cross with too closely related lines has to be avoided (here Lacaune with F2) because of the reduction of genetic variance (data not shown); (iii) preliminary selection within landraces has no effect on the cross performance but it tends to reduce the genotype x environment interaction.

The question of BC population in comparison with F_2 population is related with the choice of the optimum proportion of exotic and adapted material to create the foundation population. Theoretical studies have taken into account the divergence between the parents, the level of dominance of the considered trait, and long or short-term goals, in order to determine the best foundation population (Dudley, 1982; Bridges and Gardner, 1987; Mel-

TABLE 3 - *Mean, expected genetic progress for a selection of 10% (ΔG), criterion of utilisation (U), for yield, grain moisture, CTPS index, and lodging. gaz: Gazost, lac: Lacaune, mon: Moncassin, rdc: Roux de Chalosse; 0: unselected families, best: best S_1 family; bc and f2 indicate back-cross and F_2 populations, respectively, their absence indicate direct evaluation.*

type of progenies	**yield (q/ha)**			**grain moisture (%)**			**CTPS index**			**lodging (%)**		
	mean	**ΔG**	U	**mean**	**ΔG**	U	**mean**	**ΔG**	U	**mean**	**ΔG**	U
F2 (check)	96.51	0.00	96.51	27.88	0.00	27.88	26.85	0.00	26.85	1.73	0.00	1.73
Gaz 0	94.53	_	_	28.26	_	_	23.88	_	_	3.43	_	_
Gaz 0 f2	89.46	3.26	92.72	26.99	1.09	25.90	22.04	3.73	25.77	2.77	1.36	1.41
Gaz 0 bc	94.21	1.92	96.13	27.69	1.03	26.66	25.01	2.79	27.80	2.92	0.92	2.00
gaz best	81.19	_	_	26.12	_	_	15.21	_	_	5.19	_	_
gaz best f2	90.09	0.00	90.09	27.01	0.77	26.24	22.53	0.67	23.20	3.23	0.00	3.23
gaz best bc	93.25	5.63	98.88	27.67	1.27	26.40	24.12	4.08	28.20	2.83	0.67	2.16
lac 0	82.53	_	_	26.77	_	_	15.62	_	_	11.11	_	_
Lac 0 f2	92.59	2.71	95.30	27.14	1.09	26.05	24.74	2.74	27.48	5.79	0.16	5.63
Lac 0 bc	95.99	0.00	95.99	27.44	1.03	26.41	27.40	0.00	27.40	3.12	1.32	1.80
lac best	87.39	_	_	26.66	_	_	20.76	_	_	15.46	_	_
lac best f2	93.73	3.10	96.83	27.06	1.45	25.61	26.09	3.00	29.09	5.49	0.00	5.49
lac best bc	97.17	2.67	99.84	27.36	0.64	26.72	28.78	0.45	29.23	3.37	1.90	1.47
Mon 0	90.26	_	_	29.04	_	_	17.66	_	_	7.28	_	_
Mon 0 f2	92.98	2.38	95.36	28.21	0.50	27.71	22.35	2.61	24.96	5.39	0.92	4.47
Mon 0 bc	95.39	2.69	98.08	28.08	1.07	27.01	25.21	2.62	27.83	3.50	1.23	2.27
mon best	87.26	_	_	27.84	_	_	17.65	_	_	14.16	_	_
mon best f2	92.06	4.04	96.10	28.43	0.83	27.60	20.94	2.18	23.12	5.51	0.00	5.51
mon best bc	95.26	3.84	99.10	28.01	0.68	27.33	25.24	4.26	29.50	3.79	2.27	1.52
Rdc 0	87.56	_	_	28.92	_	_	15.26	_	_	5.83	_	_
Rdc 0 f2	95.19	3.20	98.39	28.00	1.45	26.55	24.95	3.09	28.04	4.56	1.06	3.50
Rdc 0 bc	93.85	5.08	98.93	27.88	1.82	26.06	24.06	6.13	30.19	3.81	1.55	2.26
rdc best	97.13	_	_	29.11	_	_	24.36	_	_	7.51	_	_
rdc best f2	93.95	1.70	95.65	28.21	0.93	27.28	23.45	2.41	25.86	4.09	1.00	3.09
rdc best bc	94.37	4.73	99.10	28.09	0.69	27.40	24.10	3.93	28.03	2.40	0.87	1.53

CHINGER, 1987; Crossa, 1989). In experimental studies, Crossa and Gardner (1987) found some advantage in using one cross with elite material (F_2 populations), rather than the backcross for yield. Albrecht and Dudley (1987), Melchinger *et al.* (1988), and Gouesnard *et al.* (1996), for a weak selection, reported the superiority of the backcross generation for yield. Results obtained here for European landraces comfort the conclusions of these last studies so that back-crossing should be recommended for their use in breeding.

PERSPECTIVES

The genetic diversity of European maize landraces is very broad and represented by thousands of populations. The morphological descriptors and now the molecular markers allowed to structure the genetic variability and to understand the great lines of the phenomena that shaped it: foundation and hybridization events in particular. To manage such a collection, the core collection concept is useful. Maximisation of allelic or class richness is effective and makes it possible to represent the diversity in a small sample size that facilitates further evaluation and use.

It can be noted that results presented here mostly address all or representative samples of the 2899 landraces maintained in Western European collections and less European Eastern landraces (30 landraces among 131 European ones in Rebourg *et al.*, 2001). These may therefore contain further original sources, which should deserve investigations in a global survey of molecular diversity and agronomical evaluation of Eastern European maize landraces, in order to constitute a core collection really representative for all Europe.

Our result show that use of landraces in (back-)-cross with elite material can yield promising breeding populations. Use of molecular markers is expected to increase the efficiency of this approach by means of targeted utilisation of some genomic regions. Recent investigation on polymorphism within candidate genes and its association with phenotypic variation appear promising to identify favourable alleles and closely associated markers (THORNSBERRY *et al.*, 2001), which offers promising avenues for the transfer of alleles from genetic resources to elite material by marked-assisted selection.

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REFERENCES

ABADIE T., J.R. MAGALHAES, S.N. PARENTONI, C. CORDEIRO, R.V.D. ANDRADE, 1999 The core collection of maize germplasm of Brazil. Plant Gen. Res. Newsletter **117:** 55-56.

ALBRECHT B., J.W. DUDLEY, 1987 Evaluation of four maize populations containing different proportions of exotic germplasm. Crop Sci. **27:** 480-486.

BARANGER A., G. AUBERT, G. ARNAU, A.L. LAINE, G. DENIOT, J. POTIER, C. WEINACHTER, I. LEJEUNE-HENAUT, J. LALLEMAND, J. BURSTIN, 2004 Genetic diversity within *Pisum sativum* using protein- and PCR-based markers. Theor. Appl. Genet. **108:** 1309-1321.

BATAILLON T.M., J.L. DAVID, D.J. SCHOEN, 1996 Neutral genetic markers and conservation genetics: Simulated germplasm collections. Genetics **144:** 409-417.

BERARDO N., R. REDAELLI, M. MOTTO, 2003 Qualitative evaluation of the European maize core collection. pp. 32-33. *In:* Rencontre Européenne sur la Diversité des Populations de Maïs. Montpellier 12 - 13 juin 2003.

BERTHAUD J., 1997 Strategies for conservation of genetic resources in relation with their utilisation. J.C. Glaszmann, B. Clerget, J. Schwendiman (Eds.), Special issue. EUCARPIA Meeting on Tropical Crop Breeding, Montpellier, France, 11-15 March 1996. Euphytica **96:** 1-12.

BRANDOLINI A.G., 1969 European races of maize. pp 36-48. Proceeding of the 24th Annual Corn and Sorghum Research Conference.

BRANDOLINI A.G., 1970 Razze Europee di mais. Maydica **15:** 5-27.

BRANDOLINI A.G., 1971 Preliminary report on south European and Mediterranean maize germplasm. pp. 108-116. *In:* I. Kovacs (Ed.), Proc. Fifth meeting of the maize and sorghum section of Eucarpia, September 2-5 1969, Martonvasar.

BRANDOLINI A.G., G. MARIANI, 1968 Il germosplama italiano nella fase attuale del miglioramento genetico del mais. Genetica Agraria **22:** 189-206.

BRICHETTE I., J. MORENO-GONZÁLEZ, R.C. ALONSO FERRO, L. CAMPO RAMÍREZ, 2003 Evaluation of European maize core collection: tolerance to low nitrogen level. pp. 36-38. *In:* Rencontre Européenne sur la Diversité des Populations de Maïs. Montpellier 12-13 juin 2003.

BRIDGES W.C., C.O. GARDNER, 1987 Foundation populations for adapted by exotic crosses. Crop Sci. **27:** 501-506.

BROWN A.H.D., 1989 Core collections: a practical approach to genetic resources management. Genome **31:** 818-824.

COSTA-RODRIGUES L., 1971 Races of maize in Portugal. Agronomia Lusit **31:** 239-284.

CROSSA J., 1989 Theoretical considerations for the introgression of exotic germplasm into adapted maize populations. Maydica **34:** 53-62.

CROSSA J., C.O. GARDNER, 1987 Introgression of an exotic germplasm for improving an adapted maize population. Crop Sci. **27:** 187-190.

DALLARD J., G. EVGENIDIS, A. ALVAREZ, 2003 Evaluation de la core collection européenne de maïs: valorisation de l'eau. pp. 39-42. *In:* Rencontre Européenne sur la Diversité des Populations de Maïs. Montpellier 12 - 13 juin 2003.

DAVID J.L., T. BATAILLON, S. POIRIER, P. ROUMET, S. SANTONI, A.C. THUILLET, 2003 Impact of demographic and selective events on the current genetic diversity of the *Triticum turgidum* complex, pp. 7-10. *In:* Tenth international wheat genetics symposium, Paestum, Italy.

DUBREUIL P., 1996 Etude de l'apport des marqueurs RFLP pour l'analyse de la diversité génétique et sa structuration chez le maïs (*Zea mays* L.). Relations avec les caractéristiques agronomiques de populations traditionnelles. Thèse de doctorat de l'Université Paris XI Orsay.

DUBREUIL P., C. REBOURG, M. MERLINO, A. CHARCOSSET, 1999 The DNA-pooled sampling strategy for estimating the RFLP diversity of maize populations. Plant Mol. Biol. Rep. **17:** 123-138.

DUBREUIL P., C. REBOURG, M. WARBURTON, M. CHASTANET, B. GOUESNARD, D. HOISINGTON, A. CHARCOSSET, 2003 Use of DNA pooling to assess diversity within and among maize populations. Application to the investigation of maize introduction into Europe. Maize Gen. Conf. Abstracts **45:** 129.

DUBREUIL P., M. WARBURTON, M. CHASTANET, D. HOISINGTON, A. CHARCOSSET, 2005 More on the introduction of temperate maize into Europe: large scale bulk SSR genotyping and new historical elements. Maydica (accepted).

Dudley J.W., 1982 Theory for transfer of alleles. Crop Sci. **22:** 631-637.

Edwards R.J., E.R. Leng, 1965 Classification of some indigenous maize collections from Southern and South eastern Europe. Euphytica **12:** 161-169.

Fao, 2004 Agricultural data, Faostat database: http://faostat.fao.org/faostat/

Frankel O.H., 1984 Genetic perspectives of germplasm conservation. pp. 161-170. *In:* W.K. Arber, K. Llimensee, W.J. Peacock, P. Starlinger (Eds.), Genetic manipulation: impact on man and society. Cambridge University Press, Cambridge.

Gallais A., J.P. Monod, 1998 La gestion des ressources génétiques du maïs en France: de leur caractérisation jusqu'aux premiers stades de leur valorisation. Comptes Rendus de l'Académie d'Agriculture de France **84:** 173-181.

Garnier P., 1992 Contribution à l'étude de la variabilité génétique inter et intra population chez le maïs (*Zea mays* L.): valorisation d'informations agromorphologiques et enzymatiques. Thèse de doctorat, INAPG.

Gauthier P., B. Gouesnard, J. Dallard, R. Redaelli, C. Rebourg, A. Charcosset, A. Boyat, 2002 RFLP diversity and relationships among traditional European maize populations. Theor. Appl. Genet. **105:** 91-99.

Gay J.P., 1999 Maïs, mythe et réalité. Ed Altantica. 619 pp.

Geric I., C. Zlokolica, C. Geric, C. Stuber, 1989 Races and populations of maize in Yugoslavia. Isozyme variation and genetic diversity. IBPGR, Rome.

Gouesnard B., J. Sanou, A. Panouillé, V. Bourion, A. Boyat, 1996 Evaluation of agronomic traits and analysis of exotic germplasm polymorphism in adapted x exotic maize crosses. Theor. Appl. Genet. **92:** 368-374.

Gouesnard B., J. Dallard, A. Panouillé, A. Boyat, 1997 Classification of French maize populations based on morphological traits. Agronomie **17:** 491-498

Gouesnard B., T.M. Bataillon, J.L. David, G. Decoux, C. Rozale, D.J. Schoen, 2001 MSTRAT, An algorithm for building germplasm core collections by maximizing allelic or phenotypic richness. J. Heredity **92:** 93-94.

Groupe Maïs Dgap-Inra & Promais, 1994 Cooperative program for management and utilisation of maize genetic resources. Proc. Genetic resources section of Eucarpia. 15-18 March 1994, Clermont Ferrand, France.

Hamon S., S. Dussert, M. Noirot, F. Anthony, T. Hodgkin, 1995 Core collections - accomplishments and challenges. Plant Breed. Abstr. **65:** 1125-1133.

Hintum van T.J.L., 1995 The general methodogoly for creating a core collection. pp. 10-17. *In:* R.C. Johnson, T. Hodgkin (Eds.), Core collection for today and tomorrow. IPGRI, Rome, Italy.

Kannenberg L.W., 2001 HOPE, a Hierarchical, Open-ended System for broadening the breeding base of maize. pp. 311-318. *In:* H.D. Cooper, C. Spillane, T. Hodgkin (Eds.), Broadening the Genetic Base of Crop Production. CABI Publishing, Oxon, UK.

Lefort-Buson M., V. Lavergne, J.J. Daudin, A. Charcosset, J.P. Sampoux, A. Gallais, 1991 Genetic variability among populations of maize germplam. 2. Enzymatic polymorphism and its relationship to quantitative trait diversity. Maydica **36:** 237-246.

Leng E.R., A. Tavcar, V. Trifunovic, 1962 Maize of Southeastern Europe and its potential value in breeding programs elsewhere. Euphytica **11:** 263-272.

Llaurado M., J. Moreno-Gonzales, P. Arus, 1993 Classification of Northern Spanish populations of maize by methods of numerical taxonomy: II isozyme variation. Maydica **38:** 249-258.

Malosetti M., T. Abadie, 2001 Sampling strategy to develop a core collection of Uruguayan maize landraces based on morphological traits. Gen. Res. Crop Evol. **48:** 381-390.

Malvar R.A., A. Butron, A. Alvarez, B. Ordas, P. Soengas, P. Revilla, A. Ordas, 2004 Evaluation of the European Union Maize Landrace Core Collection for resistance to *Sesamia nonagrioides* (Lepidoptera: Noctuidae) and *Ostrinia nubilalis* (Lepidoptera: Crambidae). J. Econ. Entomol. **97:** 628-634.

McKhann H.I., C. Camilleri, A. Berard, T. Bataillon, J.L. David, X. Reboud, V. Le Corre, C. Caloustian, I.G. Gut, D. Brunel, 2004 Nested core collections maximizing genetic diversity in *Arabidopsis thaliana*. Plant J. **38:** 193-202.

Melchinger A.E., 1987 Expectation of means and variances of testcrosses produced from F2 and backcross individuals and their selfed progenies. Heredity **59:** 105-115.

Melchinger A.E., 1999 Genetic diversity and heterosis. Chapter 10. *In:* J.G. Coors, S. Pandey (Eds.), The genetics and exploitation of heterosis in crops. CSSA, Madison, Wisconsin

Melchinger A.E., W. Schmidt, H.H. Geiger, 1988 Comparison of testcrosses produced from F2 and first backcross populations in maize. Crop Sci. **28:** 743-749.

Michelmore R.W., A.E. Paran, R.V. Kesseli, 1991 Identification of markers linked to disease resistance genes by bulked segregant analysis: a rapid method to detect markers in specific genomic regions by using segregating populations. Proc. Natl. Acad. Sci. USA **88:** 9828-9832

Mieg I.B., J. Moreno-Gonzalez, A. Lopez, 2001 Variability of European maize landraces for forage digestibility using near infrared reflectance spectroscopy (NIRS). Maydica **46:** 245-252.

Noirot M., S. Hamon, F. Anthony, 1996 The principal component scoring: a new method of constituting a core collection using quantitative data. Gen. Res. Crop Evol. **43:** 1-6.

Pavlicic J., 1971 Contribution to a preliminary classification of European open pollinated maize varietes. pp 93-107. *In:* I. Kovacs (Ed.), Proc. 5th Meeting Maize Sorghum Sect. Eucarpia, Martonvasar, Hungary.

Pavlicic J., V. Trifunovic, 1966 A study of some important ecologic corn types grown in Yugoslavia and their classification. J. Sci. Agr. Res. **19:** 44-62.

Radovic G., D. Jelovac, 1994 The possible approach in maize 'core collection' development. Evaluation and exploitation of genetic resources: pre-breeding. pp. 109-115. *In:* Proc. of the Genetic Resources Section Meeting of Eucarpia. 15-18 March 1994, Clermont-Ferrand, France.

Rebourg C., B. Gouesnard, A. Charcosset, 2001 Large scale molecular analysis of traditional European maize populations.

Relationships with morphological variation. Heredity **86:** 574-587.

Rebourg C., B. Gouesnard, C. Welcker, P. Dubreuil, M. Chastanet, A. Charcosset, 2003 Maize introduction into Europe: The history reviewed in the light of molecular data. Theor. Appl. Genet. **106:** 895-903.

Revilla P., P. Soengas, R.A. Malvar, M.E. Cartea, A. Ordas, 1998 Isozyme variation and historical relationships among the maize races of Spain. Maydica **43:** 175-182

Revilla P., P. Soengas, M.E. Cartea, R.A. Malvar, A. Ordas, 2003 Isozyme variability among European maize populations and the introduction of maize in Europe. Maydica **48:** 141-152.

Salanoubat M., J. Pernès, 1986 Enzyme polymorphims within and between European maize populations. Maydica **31:** 269-278.

Salhuana W., 1988 Seed increase and germplasm evaluation. pp. 29-38. *In:* Recent advances in the conservation and utilisation of genetic resources. Proc. of the global maize germplasm workshop, CIMMYT, Mexico.

Sanchez-Monge E., 1962 Razas de maiz en Espana. Ministerio de Agricultura, Madrid.

Schnell F., 1983 Probleme der Elterwahl-Ein Uberblick. In Arbeistagung der Arbeitsgemeinschaft der Saatzuchtleiter in Gumpenstein. Gumpenstein, Austria: Verlag und Druck der Bundesanstalt fur alpendische Landwirtschaft.

Schoen D.J., A.H.D. Brown, 1993 Conservation of allelic richness in wild crop relatives is aided by assessment of genetic markers. Proc. Natl. Acad. Sci. USA **90:** 10623-10627.

Sevilla R., W. Salhuana, J. Rubio, G. Avila, O. Paratori, F. Cardenas, L.H. Zhu, L. Pollak, A. Bejarano, M.X. Santos, C. Diaz, M. Fuentes, H. Sanchez, M. Ferrier, G. Vivo, 1994 Latin America maize project: a cooperative genetic resources evaluation project. pp. 289-290. *In:* F. Balfourier, M.R. Perretant (Eds.), Evaluation and exploitation of genetic resources, prebreeding. Proc. of the Genetic resources section meeting of Eucarpia: 15-18 March 1994, Clermont Ferrand, France.

Thornsberry J.M., M.M. Goodman, J. Doebley, S. Kresovich, D. Nielsen, E.S. Buckler, 2001 Dwarf8 polymorphisms associate with variation in flowering time. Nature Genetics **28:** 286-289.

Upadhyaya H.D., R. Ortiz, P.J. Bramel, S. Singh, 2003 Development of a groundnut core collection using taxonomical, geographical and morphological descriptors. Gen. Res. Crop Evol. **50:** 139-148.