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P. Dubreuil · A. Charcosset

Relationships among maize inbred lines and populations from European and North-American origins as estimated using RFLP markers

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Abstract RFLP markers have proven to be a reliable and highly informative tool for characterizing genetic diversity in maize. Joint analysis of inbred lines and populations should provide valuable information with respect to (1) a better understanding of the genetic basis of present elite germplasm and (2) the identification of populations that may prove to be useful sources of genetic diversity for breeding programs. Sixty-two inbred lines of known heterotic groups and ten maize populations, some of them significant contributors to the genetic basis of the heterotic groups, were assayed at 28 RFLP loci. Joint data analyses first underlined that the populations displayed a large number of alleles that were absent in the set of inbred lines. Associations among inbreds and populations further proved consistent with pedigree data of the inbreds and provided new information on the genetical basis of heterotic groups. In particular, European flint inbreds were revealed to be as close to the Northeastern U.S. flint population studied as to the typical European populations. These results advocate the analysis of larger sets of populations by means of molecular markers in order to (1) gain insight into the history of maize germplasm and (2) set up appropriate strategies for the use of genetic resources in breeding programs.

Key words RFLP · Maize · Lines · Populations

Introduction

Since the development of the first inbred lines in the late thirties, genetically narrow-based populations (e.g. single-cross and backcross derived populations) have become the main source of new inbred lines as parents in hybrid combinations (Jenkins 1978; Hallauer 1990). While the use of such populations was associated with a continuous progress in maize breeding (Duvick 1984; Derieux et al. 1987), traditional germplasm was progressively being removed from the breeding programs (Goodman 1978) and unfortunately lost for the main part (Smith 1986). Although such germplasm is expected to contain a high genetic diversity that could be useful for future progress (Plucknett et al. 1990), its low agronomical value in comparison with those of inbred lines derived from several selection cycles hinders its direct use in breeding programs: In the mid 1980s only 1.7% of the selection programs in the USA included traditional open-pollinated varieties (Darrah and Zuber 1986). Nonetheless, some authors have suggested that this germplasm could be used directly after crossing with elite lines to improve its breeding value (Gallais et al. 1992), or, following a reciprocal approach, as a donor of favorable alleles for line improvment (Dudley 1988).

Although much information on heterotic patterns among maize germplasm is available from extensive field trials, it generally concerns inbred lines only and does not include traditional germplasm. As a knowledge of divergent genetic backgrounds greatly helps breeders in designing crosses, the use of traditional populations could be made easier and more efficient if the joint genetic structure among populations and inbred lines was available. In maize, molecular markers have proven to be a reliable tool for identifying similar or divergent germplasms either among inbred lines (Smith et al. 1990; Melchinger et al. 1991; Messmer *et al.* 1991, 1992; Livini et al. 1992; Mumm and Dudley 1994; Dubreuil et al. 1996;), or among populations (Dubreuil and Charcosset 1998). Although this information is not solely sufficient to choose among combinations which particular ones will exhibit high heterotic responses, it does provide significant guidelines to select those crosses to be tested.

The aim of the investigation presented here was to examine the genetic relationships among inbred lines from known heterotic groups and traditional populations of

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P. Dubreuil · A. Charcosset (✉)
INRA-Station de Génétique Végétale, Ferme du Moulon,
F-91190 Gif-sur-Yvette, France
e-mail: charcos@moulon.inra.fr
Fax: +33169332340

Table 1 Frequencies of RFLP alleles specific to either lines or populations at loci analyzed. Each frequency (×100) is preceded by an arbitrary letter that identifies the corresponding allele

Locus		Presumed location	Total no. of alleles	Inbred lines				Populations									
Probe	Enzyme			European Flints	Northern USA			Europe					Northern USA				
					RYD	LSC	Min. 13	Lac	Gaz	MC	RC	Va84	CE	Min. 13	GG	BSL	BS13
BNL 5.59	*Hin*dIII	Chr. 1	9	–	–	–	–	H:13	I:4	I:9	–	I:5	–	–	G:19	–	–
BNL 5.62	*Eco*RI	Chr. 1	8	–	–	–	–	–	–	H:3	H:2	–	G:16	–	H:7	–	–
BNL 8.29	*Eco*RI	Chr. 1	5	–	–	–	–	–	–	–	–	–	E:9	E:27	–	–	–
UMC 107	*Eco*RI	Chr. 1	4	–	–	–	–	–	D:24	–	D:2	–	–	D:4	–	–	–
UMC 140	*Eco*RI	Chr. 1	8	–	–	–	–	–	B:13	B:8	B:16 F:2	–	A:3 B:2	F:2 G:3	H:15	G:13	–
UMC 84	*Eco*RI	Chr. 1	9	–	–	–	–	–	I:10	–	H:14 I:5	–	–	–	–	–	H:5
CSU 40	*Eco*RI	Chr. 2	7	–	–	–	–	–	–	–	–	–	–	G:37	G:31	G:18	F:4
UMC 10	*Eco*RI	Chr. 2	9	E:4	–	–	–	–	–	H:2	H:7 I:12	–	–	–	–	–	–
UMC 102	*Eco*RI	Chr. 2	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
UMC 4	*Hin*dIII	Chr. 2	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
UMC 60	*Eco*RI	Chr. 3	5	–	–	–	–	–	–	–	–	–	–	E:22	–	D:12	–
UMC 47	*Eco*RI	Chr. 4	4	–	–	–	–	–	C:10	C:5	–	–	C:4	C:2	C:2 D:10	–	C:6
UMC 66	*Eco*RI	Chr. 4	9	–	–	–	A:7	H:8	G:22 H:15	H:5	H:5	–	–	H:17	F:9 H:10 I:2	H:15	H:5 I:4
UMC 19	*Hin*dIII	Chr. 4	5	–	–	B:14	–	–	–	–	–	–	–	C:22	–	–	–
BNL 6.25	*Hin*dIII	Chr. 5	11	–	–	–	–	B:45 J:4	B:4 I:6 J:28 K:11	B:9 I:12 J:5	B:34 I:20 J:16	K:7	B:4 C:4 J:13	F:3	B:2	–	A:12 B:2 C:3
UMC 51	*Eco*RI	Chr. 5	11	–	–	–	K:7	–	–	–	–	–	–	–	–	–	–
UMC 54	*Eco*RI	Chr. 5	5	C:12	–	–	–	–	–	–	–	–	–	–	–	–	–
UMC 68	*Hin*dIII	Chr. 5	12	–	–	–	H:7	–	J:4 K:4	–	J:5	J:2	K:17	I:15 K:5	K:3 L:8	–	–
UMC 21	*Eco*RI	Chr. 6	7	–	–	–	–	G:30	G:2	–	–	–	–	–	–	–	G:11
UMC 62	*Eco*RI	Chr. 6	5	–	–	–	A:7	D:7	–	E:3	D:10	D:18	–	–	–	–	–
UMC 65	*Eco*RI	Chr. 6	9	–	–	–	A:23	–	G:17	–	G:4	–	–	–	–	H:38 I:8	–
UMC 85	*Hin*dIII	Chr. 6	7	–	–	–	–	–	–	D:10	–	D:30 G:4	–	–	–	–	–
CSU 81	*Hin*dIII	Chr. 7	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
UMC 35	*Hin*dIII	Chr. 7	8	–	A:57	A:12	–	–	H:15	H:3	H:16	–	–	G:5	H:20	–	–
BNL 9.11	*Hin*dIII	Chr. 8	6	–	–	–	–	–	–	F:10	–	–	–	–	F:12	–	–
UMC 103	*Eco*RI	Chr. 8	7	–	–	–	A:7 C:13	–	F:4	–	–	–	–	–	–	G:20	F:21 G:4
BNL 5.09	*Eco*RI	Chr. 9	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
BNL 5.09	*Hin*dIII	Chr. 9	7	–	–	–	–	–	–	–	F:10	–	F:28	–	F:8	F:65	–
BNL 5.10	*Eco*RI	Chr. 9	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Number of unique alleles within each heterotic group or population				2	1	2	7	6	17	13	17	6	10	13	15	8	11
Number of unique alleles within each type of germplasm				11				53									

great historical importance in the development of elite material. We especially focused on examining the consistency between the genetic diversity as revealed by restriction fragment length polymorphism (RFLP) markers and the genetic origin and history of lines and populations together.

Material and Methods

Lines and populations

The maize germplasm studied included ten traditional populations and 62 inbred lines of known heterotic groups. The lines have been fully described in Dubreuil *et al.* (1996). Briefly, they are classified into four different heterotic groups: the European flint group, and the Northern U.S. Reid Yellow Dent, Lancaster Sure Crop, and Minnesota 13 groups.

The populations have also been described in detail elsewhere (Dubreuil and Charcosset 1998). Half of them originated from northern U.S. germplasm, the others tracing back to the European flint germplasm. The U.S. populations consisted of three OP varieties ('Compton's Early', 'Minnesota 13', and its relative, 'Golden Glow') and two synthetics ('BS13-S-C4' and 'BSL-S-C4'). The populations 'BS13-S-C4', 'BSL-S-C4', and 'Minnesota 13' are representative of the initial maize varieties from which most U.S. lines included in this study were developed, either directly (i.e. first-cycle lines) or indirectly (i.e. recycled lines). The European flint populations were OP varieties from south-western France ('Gazost', 'Lacaune', 'Moncassin', and 'Roux-de-Chalosse') and northern Italy ('Va84 Cinquantino-Rosso'). Even though none of these except for 'Lacaune' are known to have contributed to the European flint heterotic group, all display morphological traits typical of European flint germplasm, indicating a reliable genetic origin, i.e. no evidence of past hybridizations with modern varieties (Gouesnard, personal communication).

RFLP genotyping

RFLP genotyping was conducted as reported by Dubreuil et al. (1996) and Dubreuil and Charcosset (1998). In total, 300 individuals randomly sampled within the populations (approximately 30 individuals per population) and 62 inbred lines were characterized for 28 common loci (29 different probe-enzyme combinations) mapping on the first nine chromosomes (Causse et al. 1996) (Table 1). Although the lines and populations were analyzed in two distinct experiments, the use of common genomic standards (balanced DNA pools of divergent inbred lines), and molecular-weight markers enabled us to match both scoring procedures.

Statistical analyses

The genetic similarity between a line I and a population P was investigated by computing the average gene identity over loci (Nei 1972):

$$S(P,I) = \frac{1}{L}\sum_{l=1}^{L}\sum_{a_l=1}^{A_l} f_{a_l}^{P}\,\theta_{a_l}^{I},$$

where $f_{a_l}^{P}$ is the frequency of allele a at locus l (among a total of L loci) within the population P, and $\theta_{a_l}^{I}$ a binary variable taking values 1 or 0 depending on whether the allele a_l is carried or not by the line I. Genetic similarity between the populations and heterotic groups was estimated by averaging similarities over lines from a given heterotic group. Differences between means were tested using the Student-Newman-Keuls test (SAS 1989).

To study the overall structure of genetic diversity, we extracted the first two principal components from the correlation matrix between allele frequencies among lines and individuals sampled within populations. Population barycenters were estimated by averaging principal coordinates of individuals and plotted with lines on a scatter diagram.

Results

Comparison between lines and populations for diversity parameters

The heterotic groups and populations displayed very comparable levels of internal genetic diversity as measured by Nei's diversity indice (1973). Estimates ranged from 0.39 to 0.57 among heterotic groups (Dubreuil et al. 1996) and from 0.36 to 0.57 among populations (Dubreuil and Charcosset 1998), providing no evidence that selection has significantly decreased the genetic diversity available among traditional germplasm. Nonetheless, this parameter of diversity is rather unsensitive to alleles present in low frequency and thus is not fully relevant to measure the effect of selection on allelic richness. On the other hand, the mean number of alleles per locus is highly dependent on the sample size. Therefore, we chose to investigate both (1) the alleles specific to either lines or populations, and (2) their frequencies among heterotic groups and populations.

The number of alleles specific to the populations was more than fourfold those of alleles specific to the heterotic groups (Table 1). This discrepancy suggested a significant effect of selection on the loss of diversity, even if it is likely that the difference between the numbers of alleles specific to each germplasm was probably biased upward due to the unbalanced sizes of the samples (62 lines versus 300 individuals from the populations). By considering an additional set of 54 lines from miscellaneous origins (see Dubreuil et al. 1996), the net deficit of alleles within lines as computed by the difference between the numbers of alleles specific to the populations and those specific to the lines was significantly decreased from 42 to 25. However, it is likely that it was underestimated in that case insofar as the additional unclassified lines traced back to a broader genetical basis than those covered by the ten populations considered in this study.

The distribution of the unique alleles (i.e. alleles specific to either lines or populations) was not uniform, either among heterotic groups or populations (Table 1). Among lines, the Reid Yellow Dent group displayed only 1 allele that was never detected among the populations, whereas the Minnesota 13 group was characterized by 7 unique alleles. Among the populations, the OP varieties 'Gazost' and 'Roux de Chalosse' had the highest number of unique alleles (17), while 'Lacaune' and 'Va84' had the least (6). As expected, the frequency of the unique alleles among the heterotic groups and the populations was rather low on average (0.12) but encompassed a large variation (0.002–0.65). The unique alleles that are present at a high frequency indicate past occurrences of significant genetic drift either in the process of

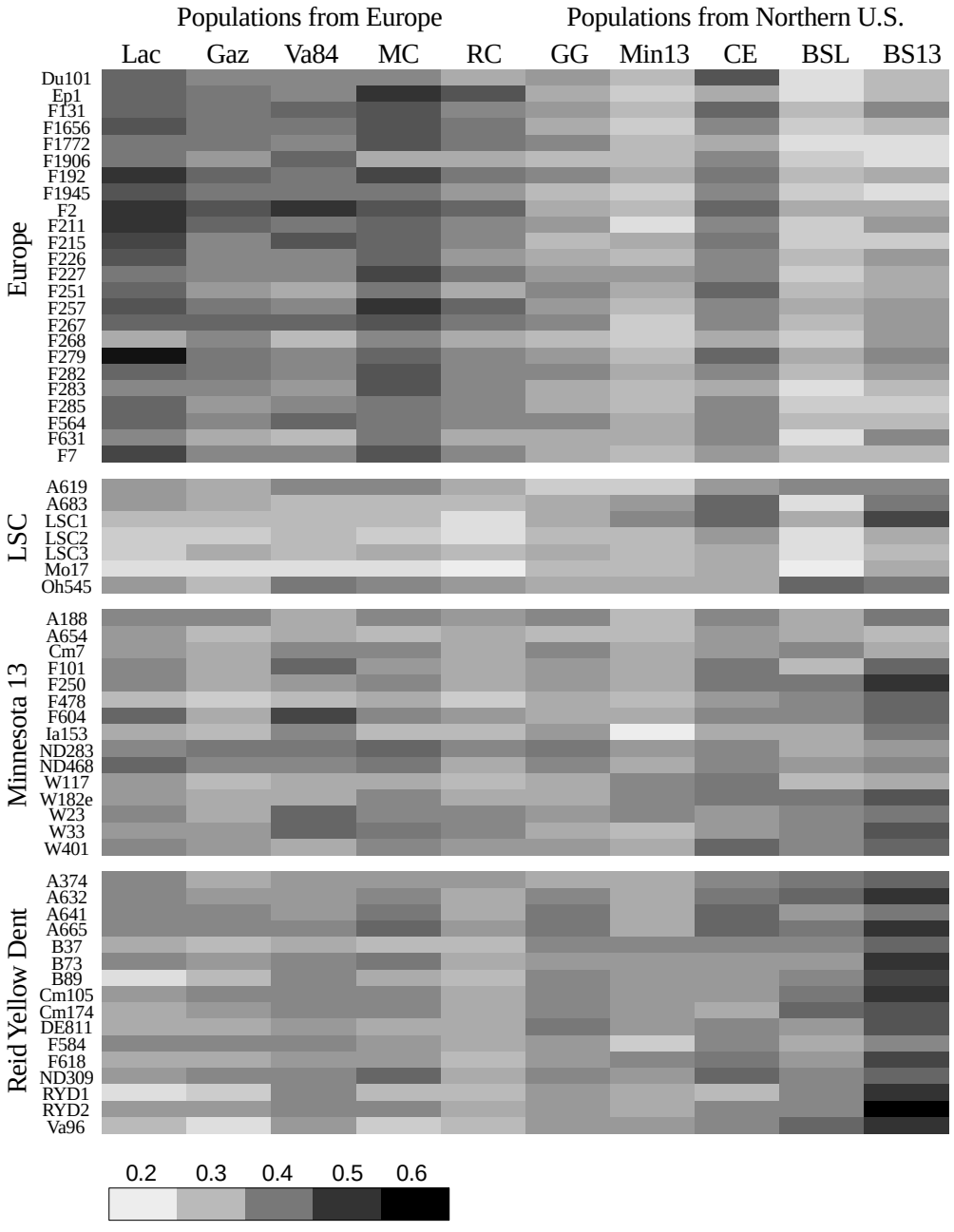

Fig. 1 Genetic similarity between lines and populations

developing first-cycle lines or in the process of maintaining the populations.

Genetic similarity between lines and populations

The genetic similarity between lines and populations ranged from 0.21 to 0.61 and is represented by shades of grey in Fig. 1. Flint lines from Europe were shown to be clearly closer to the European populations than to the U.S. ones. As expected, based on the pedigree of European flint lines, the closest population was ‘Lacaune’ with an average genetic similarity of 0.45 (Table 2). According to the SNK test used, the U.S. populations, with the exception of ‘Compton’s Early’, were on average significantly more divergent from the flint lines than their European counterparts. Surprisingly, the Northeastern flint population (i.e. ‘Compton’s Early’) was as close to the flint lines as ‘Gazost’, ‘Va84’, and ‘Roux de Chalosse’. This observation suggests that the present European heterotic group may be more related to the Northeastern U.S. germplasm than to the typical corn-belt one, provided that ‘Compton’s Early’ is a good representative of the Northeastern flint diversity.

With respect to the American heterotic groups, we first observed that the similarities between population ‘Minnesota 13’ and lines from the corresponding heterotic group were on average particularly low. The ‘Min-

Table 2 Average genetic similarity[a] between populations and lines from the heterotic groups

Populations	Heterotic groups			
	European flint	Lancaster	Minnesota 13	Reid Yellow Dent
Europe				
Lacaune	0.454 a	0.317 a	0.379 a, b	0.353 c, d
Gazost	0.402 b	0.314 a	0.345 b, c	0.350 c, d
Va84	0.401 b	0.334 a	0.384 a, b	0.334 b, c
Moncassin	0.449 a	0.324 a	0.379 a, b	0.372 b, c
Roux de Chalosse	0.389 b	0.301 a	0.351 b, c	0.334 d
Mean	0.419	0.318	0.368	0.349
Northern U.S.				
Golden Glow	0.351 c	0.324 a	0.360 b, c	0.380 b, c
Minnesota 13	0.313 d, e	0.331 a	0.336 c	0.354 c, d
Compton's Early	0.392 b	0.376 a	0.386 a, b	0.389 b
BSL	0.293 d	0.308 a	0.367 b, c	0.397 b
BS13	0.331 c, e	0.387 a	0.414 a	0.487 a
Mean	0.336	0.345	0.373	0.401

[a] For a given heterotic group, differences between means were tested using the Student-Newman-Keuls method. Means with the same letters are not significantly different at the 0.05 probability level

nesota 13' lines were shown significantly more related to other populations, including some European flint populations. This result may be related to the fact that the lines analyzed were not selected directly from the 'Minnesota 13' population. Moreover, the actual genetic background of the Minnesota 13 heterotic group does not trace back exclusively to the 'Minnesota 13' germplasm. The use of lines developed from populations of miscellaneous origins has been mentioned to have contributed to the establishment of this group, which is confirmed by its high internal genetic diversity (Dubreuil et al. 1996) and the fact that the mean co-ancestry coefficient among the 'Minnesota 13' lines is very low (0.043) (Dubreuil 1996). Some lines such as A374, were selected from Reid Yellow Dent populations (Gerdes et al. 1993), which could explain why rather high values of genetic similarity were observed between some lines included into the 'Minnesota 13' heterotic group and the 'BS13-S-C4' population.

Similarly, the lines from the Lancaster Sure Crop (LSC) heterotic group appeared to be more closely related to the Reid Yellow Dent (RYD) population ('BS13-S-C4') than to the Lancaster one ('BSL-S-C4'), even if the too small sample of LSC lines prevented the SNK multiple comparison test from revealing significant differences among the populations. This feature particularly concerns the lines from the C103 family (Mo17 and its relatives A683, LSC1, LSC2, and LSC3), whereas Oh545 and A619, both related to the Oh43 line, have a higher genetic similarity with the population 'BSL-S-C4'. Gerdes *et al.* (1993) have depicted the pedigree relationships of the lines from the Lancaster heterotic group, showing that this group has been developed by an increasing use of lines from a mixed origin. Lines originally developed out of a pure Lancaster germplasm were improved by crossing with RYD lines less sensitive to field stalk lodging (Jenkins 1978). Thus, while the selection for lodging resistance was progressing, the LSC background was likely progressively displaced by the RYD background in the further cycle LSC lines. This could be the case for the Mo17 line, which derived from a mixed cross between a RYD-related line (i.e., CI 187-2) and a first-cycle LSC line (i.e. C103).

In contrary to the previous results, strongly contrasted values of genetic similarity were obtained for the RYD lines. The genetic relatedness between these lines and the 'BS13-S-C4' population was clearly evidenced by the high values of genetic similarity estimated (0.487). This result is related to the fact that the RYD lines were mostly derived from crosses between a few progenitors, namely, B14, B37, and B73 lines, which in turn were selected from a single population (i.e., the Iowa Stiff Stalk Synthetic population) from which the 'BS13-S-C4' population was directly derived (Eberhart et al. 1973; Lamkey 1992). The close genetic relationships among the RYD lines was further proved by a mean co-ancestry coefficient that was higher (0.174) than those estimated for the other heterotic groups (0.147, 0.129, and 0.043 for the Lancaster Sure Crop, the European flint, and the Minnesota 13 heterotic groups, respectively) (Dubreuil 1996).

Multivariate structure of the diversity

Association among lines and populations as depicted through principal component analysis was shown in Fig. 2. The first axis, which accounted for 6.2% of the total variation, exhibited a major separation between European and North-American germplasms, which was consistent with previous results (Dubreuil et al. 1996; Dubreuil and Charcosset 1998). Axis 2 (3.7%) resolved different genetic backgrounds. Within European germplasm, it clearly distinguished between populations from the Pyrenees and both 'Lacaune' and 'Va84'. Within the American germplasm, a marked separation between the Reid Yellow Dent population ('BS13-S-C4') and the others was observed.

Groupings of lines and populations mainly concured with expectations based on pedigrees and genetic ori-

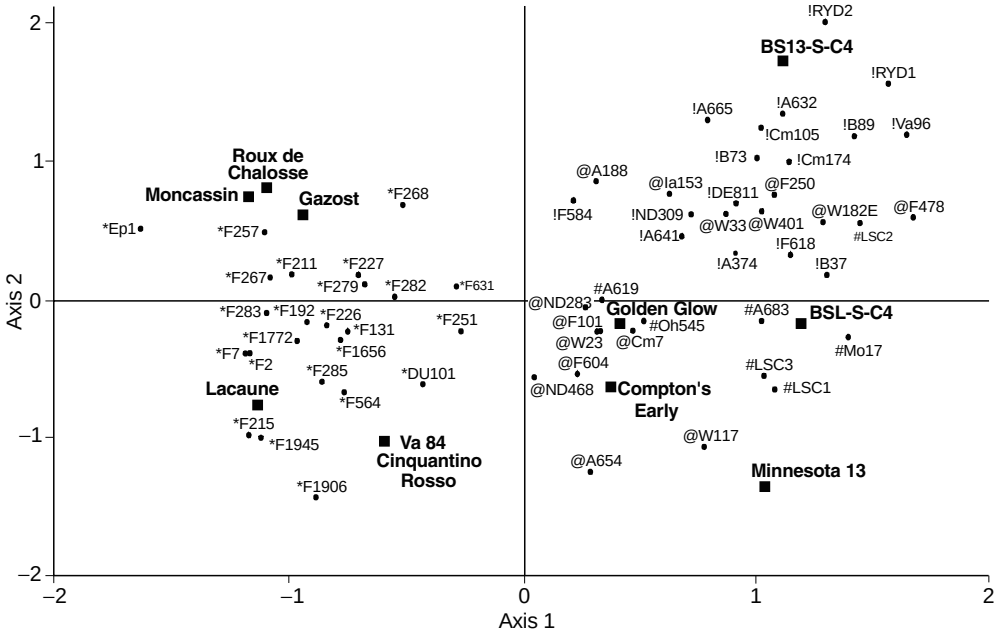

Fig. 2 Scatter diagram from principal component analysis: *Axes 1* and *2* were first and second principal components, respectively, which together account for about 10% of the total variation. Lines marked with an *, @, *!*, and # are classified into the European flint, Minnesota 13, Reid Yellow Dent, and Lancaster Sure Crop heterotic groups, respectively

gins. Lines F2 and F7 were located in the vicinity of the 'Lacaune' population from which they were selected, whereas the Spanish Ep1 line and its derivatives were close to the Pyrennean populations. Similarly, most of the Reid Yellow Dent lines clustered around the population from the same genetic origin (i.e. 'BS13-S-C4'), and the Lancaster Sure Crop lines from the C103 family were located near the Lancaster related population (i.e. 'BSL-S-C4'). The close association between the Lancaster population and the C103 family contrasts with the low estimates of similarity obtained. Nonetheless, the first two principal components only explained a small portion of the total variation (see above). The third principal component (3.4%) definitely distinguished between the Lancaster lines from the C103 family and those from the Oh43 family (data not shown), with the former being clearly separated from the 'BSL-S-C4' population, while the latter were closely associated with this population, consistent with estimates of similarity. The location of 'Compton's Early' also did not reflect its genetic similarity with flint lines, probably for the same reason. The Minnesota 13 germplasm appeared to be more scattered than the other North American germplasms, even if consistent associations were observed between (1) the 'Golden Glow' population and some Minnesota 13 lines (especially W23 which has been directly developed from 'Golden Glow'), and (2) the Minnesota 13 population and the line W117 which derives from that population.

Discussion

Our purpose was to investigate genetic diversity as revealed by RFLPs among lines and populations considered together in order to assess the usefulness of (1) traditional germplasm as a potential source of new alleles and (2) such an approach to elucidate genetic relationships between the heterotic groups and corresponding traditional populations.

By comparing numbers of alleles specific to each type of germplasms, we found a net deficit of alleles within lines accounting for about 22% of the total allelic richness of the populations. Despite the fact that this value may be poorly estimated, it shows a clear trend towards an erosion of genetic diversity from populations to lines. Although, this can be partly explained by genetic improvement itself, this result confirms that populations represent significant reservoirs of diversity that breeders could benefit from by increasing their use in breeding programs since elite germplasm is not likely to contain all useful alleles. The french OPVs from the Pyrennees ('Moncassin', 'Gazost' and 'Roux de Chalosse') and the Northern U.S. 'Minnesota 13' and 'Golden Glow' populations, which exhibited the highest number of unique alleles, should be worthwhile to this end. Moreover, multivariate analysis of molecular diversity revealed consistent associations among lines and populations. This approach proved to be useful (1) to better understand the way the heterotic groups have been developed and (2) from a practical point of view, to aid in choosing lines and populations to be crossed with as potential donors of favorable alleles. The use of a larger set of populations should provide a comprehensive picture of genetic relationships among the elite and traditional germplasms.

Through the analysis of genetic similarity between lines and populations, this study also revealed interesting

patterns of genetic diversity that lead one to question the phylogenetic relationships among maize germplasm. Its main outcome is that the Northeastern U.S. 'Compton's Early' population was shown to be significantly as closely related to the European heterotic group as typical flint OP varieties from south-western France and northern Italy. Although, this relatedness should be further investigated using other Northeastern U.S. flint populations, a brief review of the history of maize introductions in Europe may help to propose scenarios that could explain this relationship.

As described by Brandolini (1969, 1971) and Gerrish (1982), maize was imported from different geographical origins that roughly correspond to a few distinct waves of introduction. The first maize imported to Europe was observed in the vicinity of Seville (Spain) in 1494, 2 years after the new world was discovered by Columbus. Although there is general agreement on the fact that this West-Indian flint maize was the primary origin of European maize, the genetic basis that allowed the expansion of maize through the Mediterranean bassin and then northward remains a matter of controversy. Brandolini (1969, 1971) argues that maize spread throughout Europe on the sole basis of early introductions, whereas Gerrish (1982) advocates that the Carribean flint maize and the high altitude flint maize introduced shortly afterwards from the Andean valley and highland Mexico likely remained confined to a restricted area because they were mostly daylength sensitive and thus unadapted to temperate-zone climatic conditions. According to this author, early maize imported from South America by the Portugese during the 16th century was more likely to contribute efficiently to the development of maize in the north of Europe. Nonetheless, under these previous hypotheses on the genetical background of Northern European germplasm, how can the European heterotic group be so significantly closer to the Northeastern flint 'Compton's Early' populations than to the other U.S. populations?

Although it cannot be ruled out that maize plants described in Germany as early as 1539 by the herbalist J. Bock (Finan 1950) were brought into this country from southern Europe as a botanical curiosity, it also cannot be seriously questioned that maize was common in northern Europe before the late introductions of maize from northeastern USA (18th century). Therefore, in our opinion two scenarios can be proposed to explain the genetic similarity between the European flint lines and the Northeastern U.S. 'Compton's Early' population. First, the Northeastern U.S. flint populations imported during the 18th century could have progressively displaced through hybridization the maize already present in the north of Europe at this time. Alternatively, maize from northeastern USA may have been introduced in Europe long before the French and British people was settled in these areas. These regions were indeed discovered as soon as 1497 by the explorer J. Cabot (Duby 1989). On the one hand, this seems somewhat unlikely because such event would have been certainly more documented if it really occured. On the other hand, Finan (1950) emphasizes that European maize pictured in the great herbals of the Renaissance (16th century) and the Northeastern U.S. flints resemble each other, especially for their lack of prop-roots, thus giving more credit to this latter hypothesis. The sample of populations analyzed and historical evidence are yet too small to assert that early European flint germplasm directly derives from early introductions of Northeastern U.S. flint populations. Moreover, this apparent relatedness between the European and Northeastern U.S. flints has not been previously observed for as yet unclear reasons by comparing directly the genetic distances among populations (Dubreuil and Charcosset 1998). Even so, this scenario would deserve more investigation by analyzing on a large scale the genetic diversity among distinct germplasms, including populations from different parts of Europe, and their presumed origins.

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