# Isoenzymatic variation in the germplasm of Brazilian races of maize (Zea mays L.) 

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#### Abstract

There are more than 200 races of maize (Zea mays L.) divided into three groups (ancient commercial races, the recent commercial races, and indigenous races). Although the indigenous races have no commercial value, they have many important characteristics which can be incorporated into maize breeding programs. Most Brazilian indigenous germplasm race stocks were collected at least 40 years ago, and nothing is known of the genetic variability present in this germplasm. The genetic variability was assayed in 15 populations from four indigenous races of maize (Caingang, Entrelaçado, Lenha and Moroti) and five indigenous cultivars, using five isoenzymatic systems encoded by 14 loci. The analysis revealed a low level of variability among the samples studied. Overall, the mean number of alleles/ polymorphic locus was three, $64.3 \%$ of the loci analyzed being polymorphic and the estimated heterozygosity was 0.352 . The mean number of alleles/polymorphic locus per population was 1.6. A mean of $47.5 \%$ of the loci were polymorphic. The mean expected heterozygosity was 0.195 , the mean genetic identity was 0.821 and the proportion of total genetic diversity partitioned among populations (Gst) was 0.156. A founder effect could explain the low variability detected.


## INTRODUCTION

Maize (Zea mays L.) is the most important cereal crop in the world. Considerable effort has been spent in collecting and preserving varieties of maize from the Americas, in order to maintain the genetic diversity necessary for research and breeding (Paterniani and Goodman, 1978). Zea mays L. contains more than 200 races divided into three groups (ancient commercial races, the recent commercial races, and indigenous races). The conservation of the latter is particularly important since most of these materials are no longer cultivated because they have been replaced by more productive commercial hybrids. The races in the indigenous group are cultivated by Amerindians. Historically, four indigenous races (Moroti, Caingang, Lenha and Entrelaçado) occurred in Brazil.

Although they have no commercial value, the indigenous races have many important characteristics which may be incorporated into maize breeding programs, including a high level of genetic variability, a large number of kernel rows, low ear height, and high heterotic responses in some crosses (Paterniani and Goodman, 1978). Most stocks of the germplasm from indigenous races were collected at least 40 years ago, with few new additions being made to gene banks. However, nothing is known of the genetic variability present in this germplasm.

The objective of this study was to assess the genetic variability present in indigenous races using isozyme profiles.

## MATERIAL AND METHODS

## Plant material

Plants of populations from four indigenous races and five cultivars of unknown races cultivated by Amerindians in Brazil and adjacent areas were analyzed (Table I). The populations were obtained from collections maintained by AGROCERES and by CNMS (Centro Nacional de Milho e Sorgo) in Brazil. The populations from AGROCERES were formed by bulking a variable number of collections (Table I). These populations were established using morphological characters, mainly because of the unavailability of storage facilities and manpower to maintain the individual collections and because many of the races described were already represented by numerous similar collections (Paterniani and Goodman, 1978). The cultivars from unknown indigenous races were based on single accessions.

## Isozyme and electrophoretic analysis

Each plant was analyzed for five isoenzymatic systems detecting 14 loci. Coleoptiles 1.5 cm long were obtained from plants grown at $20^{\circ} \mathrm{C}$ in the dark for 4-6 days and homogenized in $30 \mu \mathrm{l}$ of extraction buffer ( $16.3 \%$ sucrose, $8.3 \%$ ascorbic acid, pH 7.4 ). The isozymes were electrophoresed in a $13 \%$ nonhydrolyzed starch (penetrose) gel. The buffer systems, electrophoretic conditions and staining techniques were described by Kephart (1990) and Stuber et al. (1988).

Table I - Number of maize plants analyzed from each of the 15 populations from the maize races Moroti, Caingang, Lenha, Entrelaçado and five indigenous cultivars.
$\begin{array}{|llcccc|}\hline \text { Race } & \text { Population } & \begin{array}{c}\text { Number of individuals }\end{array} & \begin{array}{c}\text { Collections } \\ \text { bulked to form }\end{array} & \text { Total } \\$\cline { 3 - 3 } \& \& AGR \& CNMS \& \& <br> the populations*\end{array}$]$
$\operatorname{Pr}=$ Paraná $; \mathrm{Mt}=$ Mato Grosso; RGS $=$ Rio Grande do Sul; $\mathrm{SP}=$ São Paulo; $\mathrm{Pe}=$ Pernambuco; $\mathrm{Pag}=$ Paraguay; $\mathrm{Bol}=$ Bolivia; $\mathrm{CC}=$ Caingang Composto; $\mathrm{BRA}=$ Brasil (EMBRAPA code). AGR = AGROCERES; CNMS = Centro Nacional de Milho e Sorgo; n.a. - not available. *Data from Paterniani and Goodman (1978).

## Data analysis

The genotypes were inferred based on the band patterns and the genetic control of the loci analyzed, as described by Stuber et al. (1988). The data were analyzed using the program BIOSYS (Swofford and Selander, 1989). The number of alleles per locus (total number of alleles in the polymophic loci/number of polymorphic loci), the percentage of polymorphic loci (number of polymorphic loci/total number of loci analyzed), and the expected heterozygosity ( $\mathrm{H}=1-\Sigma \mathrm{p}_{\mathrm{i}}{ }^{2}$, with $\mathrm{p}_{\mathrm{i}}$ being the mean frequency of the i allele in a locus) were calculated for each population. Nei’s genetic diversity statistic (Nei, 1972) was used to apportion the genetic diversity within and among populations. The genetic identities between all possible pairs of populations were computed following Roger (1972). A tree was generated using the unweighted pair-group method algorithm - UPGMA (Sneath and Sokal, 1973).

## RESULTS

A mean of 30.95 plants were analyzed per population. Nine of the 14 loci were polymorphic (Table II) when all the populations are analyzed as a whole (a polymorphic locus is one at which the most common allele has a frequency <0.99). Loci Est8, Got2, Got3, Mdh3 and $M d h 6$ were monomorphic. Overall, 27 alleles were found in the nine polymorphic loci analyzed, with an average of
three alleles per locus. The average number of alleles per locus per population was 1.59 , and ranged from 1.4 for population Mt III to 1.8 for population RGS XX. Few alleles were rare, having frequencies of 0.01 or less (Table III). The average locus heterozygosity per population was 0.195 in the nine polymorphic loci analyzed. The mean expected heterozygosity per population $(\mathrm{Hp})$ varied from 0.019 for $M d h 4$ to 0.459 for Acp 4 .

The frequencies of most of the alleles were similar in most of the populations (Table II). However, some alleles were found in only one population, or occurred in two or three populations at very high frequencies. Allele Acp4-5 was detected only in population CC from CNMS (Table II). Allele $I d h 1-3$ showed a very high frequency in population BRA 017574, but was detected at very low frequencies in two other populations (RGS XX and BRA 017568).

Populations formed by one to three collections were sometimes more variable than populations formed by more than three collections. On average, $84 \%$ of the genetic variation occurred within populations (Table IV). The variation among populations ranged from 5 to $32 \%$.

The mean genetic similarity was 0.821 (Table V). The values varied from 0.746 between populations BRA 017574 and SP XIV to 0.944 between populations BRA 014148 and PeI.

Figure 1 summarizes the relationships between the populations. In general, populations from the same races were not grouped together.

Table II - Allele frequencies of the 14 loci analyzed in 15 populations of maize
from the races Moroti (M), Caingang (C), Lenha (L), Entrelaçado (E) and five indigenous cultivars (IC).

| Populations | Allele | Est 9 | Est 8 | Got 1 | Got2 | Got3 | Idh 1 | $I d h 2$ | Acp 1 | Acp4 | Mdh1 | Mdh2 | Mdh3 | Mdh4 | Mdh6 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Pr II-M | 1 | 0.750 | 1.000 | 0.529 | 1.000 | 1.000 | 0.917 | 1.000 | 0.729 | 0.708 | 0.295 | 0.432 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.250 |  | 0.471 |  |  | 0.083 |  | 0.146 | 0.167 | 0.659 | 0.568 |  |  |  |
|  | 3 |  |  |  |  |  |  |  | 0.125 | 0.125 | 0.045 |  |  |  |  |
| Bol II-M | 1 | 0.919 | 1.000 | 0.597 | 1.000 | 1.000 | 0.694 | 1.000 | 0.661 | 0.339 | 0.040 | 0.200 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.081 |  | 0.403 |  |  | 0.306 |  | 0.339 | 0.661 | 0.960 | 0.800 |  |  |  |
| Bol IIB-M | 1 | 0.784 | 1.000 | 0.477 | 1.000 | 1.000 | 0.909 | 1.000 | 0.727 | 0.420 | 0.148 | 0.148 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.216 |  | 0.523 |  |  | 0.091 |  | 0.205 | 0.580 | 0.852 | 0.739 |  |  |  |
|  | 3 |  |  |  |  |  |  |  | 0.068 |  |  | 0.114 |  |  |  |
| Pe I-M | 1 | 0.797 | 1.000 | 0.266 | 1.000 | 1.000 | 0.766 | 1.000 | 0.922 | 0.438 | $0.242$ | $0.484$ | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.203 |  | 0.734 |  |  | 0.234 |  | $0.047$ | 0.563 | $0.758$ | $0.516$ |  |  |  |
|  | 3 |  |  |  |  |  |  |  | 0.031 |  |  |  |  |  |  |
| Mt III-M | 1 | 0.625 | 1.000 | 0.375 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.094 | 0.063 | 0.563 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.375 |  | 0.625 |  |  |  |  |  | 0.906 | 0.937 | 0.437 |  |  |  |
| Pag VI-M | 1 | 0.952 | 1.000 | 0.484 | 1.000 | 1.000 | 0.839 | 1.000 | 0.484 | 0.452 | 0.439 | 0.606 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.048 |  | 0.516 |  |  | 0.161 |  | 0.516 | 0.516 | 0.561 | 0.394 |  |  |  |
|  | 3 |  |  |  |  |  |  |  |  | 0.032 |  |  |  |  |  |
| Pag VII-M | 1 | 0.667 | 1.000 | 0.333 | 1.000 | 1.000 | 0.875 | 1.000 | 1.000 | 0.604 | 0.229 | 0.208 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.333 |  | 0.667 |  |  | 0.125 |  |  | 0.292 | 0.688 | 0.417 |  |  |  |
|  | 3 |  |  |  |  |  |  |  |  | 0.104 | 0.083 | 0.375 |  |  |  |
| Bol I-M | 1 | 0.775 | 1.000 | 0.700 | 1.000 | 1.000 | 0.625 | 0.775 | 0.900 | 0.450 | 0.075 | 0.425 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.225 |  | 0.300 |  |  | 0.375 | 0.225 | 0.100 | 0.525 | 0.925 | 0.575 |  |  |  |
|  | 3 |  |  |  |  |  |  |  |  | 0.025 |  |  |  |  |  |
| Pag VIA-M | 1 | 0.964 | 1.000 | 0.714 | 1.000 | 1.000 | 0.893 | 1.000 | 0.643 | 0.536 | 0.393 | 0.929 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.036 |  | 0.286 |  |  | 0.107 |  | 0.357 | 0.464 | 0.607 | 0.071 |  |  |  |
| Pr III-C | 1 | 0.788 | 1.000 | 0.621 | 1.000 | 1.000 | 0.500 | 0.833 | 0.848 | 0.576 | 0.280 | 0.420 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.212 |  | 0.379 |  |  | 0.500 | 0.167 | 0.030 | 0.424 | 0.560 | 0.580 |  |  |  |
|  | 3 |  |  |  |  |  |  |  | 0.121 |  | 0.000 |  |  |  |  |
|  | 4 |  |  |  |  |  |  |  |  |  | 0.160 |  |  |  |  |
| SPXIV-C | 1 | 0.586 | 1.000 | 0.586 | 1.000 | 1.000 | 1.000 | 0.638 | 0.172 | 1.000 | $0.089$ | $0.429$ | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.414 |  | 0.414 |  |  |  | 0.362 | 0.690 |  | $0.911$ | $0.571$ |  |  |  |
|  | 3 |  |  |  |  |  |  |  | 0.138 |  |  |  |  |  |  |
| CC-C | 1 | 0.692 | 1.000 | 0.385 | 1.000 | 1.000 | 0.872 | 0.782 | 0.603 | 0.275 | 0.286 | 0.500 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.308 |  | 0.615 |  |  | 0.128 | 0.218 | 0.397 | 0.550 | 0.679 | 0.500 |  |  |  |
|  | 3 |  |  |  |  |  |  |  |  | 0.175 | 0.000 |  |  |  |  |
|  | 4 |  |  |  |  |  |  |  |  |  | 0.000 |  |  |  |  |
|  | 5 |  |  |  |  |  |  |  |  |  | 0.036 |  |  |  |  |
| CC-C | 1 | 0.639 | 1.000 | 0.583 | 1.000 | 1.000 | 0.806 | 0.583 | 1.000 | 0.000 | 0.542 | 0.292 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.361 |  | 0.417 |  |  | 0.194 | 0.417 |  | 1.000 | 0.458 | 0.375 |  |  |  |
|  | 3 |  |  |  |  |  |  |  |  |  |  | 0.333 |  |  |  |
| RGS XX-E | 1 | 0.783 | 1.000 | 0.652 | 1.000 | 1.000 | 0.913 | 0.130 | 1.000 | 0.563 | $0.450$ | 0.250 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.217 |  | 0.348 |  |  | 0.065 | 0.435 |  | 0.396 | 0.550 | 0.500 |  |  |  |
|  | 3 |  |  |  |  |  | 0.022 | 0.435 |  | 0.042 |  | 0.250 |  |  |  |
| Mt VI-L | 1 | 0.849 | 1.000 | 0.267 | 1.000 | 1.000 | 0.837 | 0.756 | 0.721 | 0.477 | 0.287 | 0.538 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.151 |  | 0.733 |  |  | 0.163 | 0.244 | 0.093 | 0.372 | 0.712 | 0.463 |  |  |  |
|  | 3 |  |  |  |  |  |  |  | 0.186 | 0.151 |  |  |  |  |  |
| O17586-IC | 1 | 0.483 | 1.000 | 0.417 | 1.000 | 1.000 | 0.883 | 1.000 | 0.900 | 0.483 | $0.000$ | $0.417$ | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.517 |  | 0.583 |  |  | 0.117 |  | 0.100 | 0.450 | $1.000$ | $0.583$ |  |  |  |
|  | 3 |  |  |  |  |  |  |  |  | 0.067 |  |  |  |  |  |
| 017568-IC | 1 | 0.830 | 1.000 | 0.947 | 1.000 | 1.000 | 0.798 | 0.766 | 0.957 | 0.755 | 0.000 | 0.533 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.170 |  | 0.053 |  |  | 0.160 | 0.234 | 0.043 | 0.245 | 1.000 | 0.467 |  |  |  |
|  | 3 |  |  |  |  |  | 0.043 |  |  |  |  |  |  |  |  |
| 017574-IC | 1 | 0.925 | 1.000 | 0.125 | 1.000 | 1.000 | 0.066 | 0.600 | 1.000 | 0.375 | 0.013 | 0.850 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.075 |  | 0.875 |  |  | 0.303 | 0.400 |  | 0.625 | 0.988 | 0.150 |  |  |  |
|  | 3 |  |  |  |  |  | 0.632 |  |  |  |  |  |  |  |  |
| 017581-IC | 1 | 0.696 | 1.000 | 0.429 | 1.000 | 1.000 | 0.768 | 1.000 | 1.000 | 0.393 | 0.196 | 0.821 | 1.000 | 0.714 | 1.000 |
|  | 2 | 0.304 |  | 0.571 |  |  | 0.232 |  |  | 0.607 | 0.804 | 0.179 |  | 0.286 |  |
| 014148-IC | 1 | 0.847 | 1.000 | 0.347 | 1.000 | 1.000 | 0.875 | 0.986 | 0.764 | 0.389 | 0.069 | 0.639 | 1.000 | 1.000 | 1.000 |
|  | 2 | 0.153 |  | 0.653 |  |  | 0.125 | 0.014 | 0.236 | 0.611 | 0.847 | 0.361 |  |  |  |
|  | 3 |  |  |  |  |  |  |  |  |  | 0.000 |  |  |  |  |
|  | 4 |  |  |  |  |  |  |  |  |  | 0.083 |  |  |  |  |

For abbreviations see legend to Table I.

Table III - Genetic variability of the nine polymorphic loci analyzed in 15 populations of indigenous races of maize (Moroti, Caingang, Lenha and Entrelaçado) and five indigenous cultivars.

| Races | Populations | Number <br> of plants | Total number <br> of alleles | Number <br> of alleles/locus | Polymorphic <br> loci $(\%)$ | Expected <br> heterozygosity |
| :--- | :--- | :---: | :---: | :---: | :---: | :---: |
| Moroti | Pr II | 24 | 24 | 1.7 | 50.0 | 0.210 |
|  | Bol II | 31 | 21 | 1.5 | 42.9 | 0.171 |
|  | Bol II - CNMS | 44 | 23 | 1.6 | 50.0 | 0.187 |
|  | Pe I | 32 | 22 | 1.6 | 50.0 | 0.187 |
|  | Mt III | 16 | 19 | 1.4 | 35.7 | 0.127 |
|  | Pag VI | 31 | 22 | 1.6 | 42.9 | 0.208 |
|  | Pag VII | 24 | 23 | 1.6 | 42.9 | 0.201 |
|  | Bol I | 20 | 23 | 1.6 | 57.1 | 0.214 |
|  | Pag VIA | 28 | 21 | 1.5 | 42.9 | 0.163 |
|  | Pr III | 33 | 24 | 1.7 | 57.1 | 0.247 |
|  | SPXIV | 29 | 21 | 1.5 | 42.9 | 0.186 |
|  | CC | 24 | 1.7 | 57.1 | 0.252 |  |
|  | CC - CNMS | 16 | 21 | 1.5 | 42.9 | 0.215 |
|  | RGS XX | 22 | 25 | 1.8 | 50.0 | 0.234 |
| Entrelaçado | Mt VI | 47 | 24 | 1.7 | 57.1 | 0.235 |
| Lenha | BRA 017586 | 30 | 21 | 1.5 | 42.9 | 0.176 |
| Indigenous cultivars | BRA 017568 | 47 | 22 | 1.6 | 42.9 | 0.146 |
|  | BRA 017574 | 40 | 22 | 1.6 | 42.9 | 0.151 |
|  | BRA 017581 | 28 | 21 | 1.5 | 50.0 | 0.201 |
|  | BRA014148 | 36 | 23 | 1.6 | 50.0 | 0.183 |
|  | Mean | 31 | 22.3 | 1.6 | 47.5 | 0.195 |

For abbreviations see legend to Table I.

Table IV - Genetic diversity of nine polymorphic loci in 15 populations and five cultivars of the indigenous races of maize analyzed.

| Loci | $\mathrm{H}(\mathrm{s})$ | $\mathrm{H}(\mathrm{t})$ | $\mathrm{D}(\mathrm{st})$ | $\mathrm{G}(\mathrm{st})$ |
| :--- | :---: | :---: | :---: | :---: |
| Est 9 | 0.314 | 0.343 | 0.029 | 0.084 |
| Got 1 | 0.419 | 0.498 | 0.079 | 0.159 |
| Idh1 | 0.275 | 0.369 | 0.094 | 0.255 |
| Idh2 | 0.191 | 0.255 | 0.064 | 0.251 |
| Acp 1 | 0.232 | 0.343 | 0.111 | 0.324 |
| Acp 4 | 0.459 | 0.538 | 0.079 | 0.149 |
| Mdh1 | 0.303 | 0.338 | 0.035 | 0.104 |
| Mdh2 | 0.451 | 0.463 | 0.012 | 0.026 |
| Mdh4 | 0.019 | 0.020 | 0.001 | 0.050 |
| Average | 0.295 | 0.352 | 0.056 | 0.156 |

$\mathrm{H}(\mathrm{s})$ - Mean within-population genetic diversity; $\mathrm{H}(\mathrm{t})$ - total genetic diversity for the species; $\mathrm{D}(\mathrm{st})$ - mean among-populations genetic diversity; $G(s t)$ - proportion of total genetic diversity partitioned among populations.

## DISCUSSION

There was a mean of three alleles per locus, with nine polymorphic loci among the 14 loci analyzed. An isoenzymatic analysis of Mexican germplasm, where a mean of 32.8 individuals were analyzed, showed a mean of 7.09 alleles in the 23 loci analyzed, with $95.3 \%$ of the loci polymorphic and a total genetic variability of 0.251 (Doebley et al., 1985). A study of maize from Bolivia, where a mean of 39 individuals were analyzed, showed a mean of 5.17 alleles in the 23 loci analyzed, with $86.9 \%$
of the loci polymorphic (Goodman and Stuber, 1983). Based on the loci analyzed in all three studies (Est8, Got1, Got2, Got3, Idh1, Idh2, Mdh1, Mdh2, Mdh3 and Mdh4), the mean number of allele/locus for the Mexican maize study would be $6,4.9$ for the Bolivian and 2.2 in this study. A reduction in variability in the sample analyzed may have occurred by a founder effect, as indicated by the high frequency of allele $I d h 1-3$ in population BRA 017574 (Table II) and its low frequency in two other populations (RGS XX and BRA 017568). The lack of variation between maize from different cultural groups may be a consequence of the small sample size collected and of the founder effects (Doebley et al., 1983). According to Heywood and Fleming (1986), low variability within populations may occur as a result of recent founding of a population from a small number of individuals, a recent reduction in the population size or a restricted genetic flow among populations. Since the populations in our study were cultivated under the same environmental conditions, environment is unlikely to account for the variable frequency of $\operatorname{Idh} 1-3$.

Despite the low allelic diversity detected, the mean expected heterozygosity was higher than that reported by Gottlieb (1981) for outcrossing plants. According to Futuyma (1992), the level of heterozygosity in a derived population is nearly as high as in the original population because rare alleles contribute little to the level of heterozygosity, and such alleles are also likely to be absent in the derived population.

The lack of correlation between the number of collections used to form the populations and the genetic vari-

Table V - Matrix of Rogers' identity (below the diagonal) and distance (above the diagonal) among the
15 populations and five indigenous cultivars of the four indigenous races of maize (Moroti, Caingang, Lenha and Entrelaçado) studied.

| Populations | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 Pr II | **** | 0.113 | 0.067 | 0.080 | 0.119 | 0.090 | 0.075 | 0.103 | 0.103 | 0.086 | 0.122 | 0.086 | 0.159 | 0.123 | 0.080 | 0.083 | 0.112 | 0.223 | 0.124 | 0.091 |
| 2 Bol II | 0.887 | **** | 0.062 | 0.099 | 0.128 | 0.100 | 0.142 | 0.083 | 0.118 | 0.114 | 0.171 | 0.115 | 0.171 | 0.175 | 0.132 | 0.106 | 0.135 | 0.183 | 0.137 | 0.086 |
| 3 Bol II - CNMS | 0.933 | 0.938 | **** | 0.068 | 0.099 | 0.092 | 0.088 | 0.090 | 0.118 | 0.109 | 0.155 | 0.089 | 0.153 | 0.134 | 0.098 | 0.074 | 0.134 | 0.195 | 0.108 | 0.061 |
| 4 Pe I | 0.920 | 0.901 | 0.932 | **** | 0.085 | 0.090 | 0.073 | 0.080 | 0.124 | 0.090 | 0.186 | 0.081 | 0.145 | 0.142 | 0.059 | 0.074 | 0.118 | 0.147 | 0.075 | 0.056 |
| 5 Mt III | 0.881 | 0.872 | 0.901 | 0.915 | **** | 0.136 | 0.097 | 0.121 | 0.163 | 0.155 | 0.175 | 0.102 | 0.122 | 0.174 | 0.122 | 0.074 | 0.142 | 0.171 | 0.095 | 0.077 |
| 6 Pag VI | 0.910 | 0.900 | 0.908 | 0.910 | 0.864 | **** | 0.125 | 0.129 | 0.064 | 0.122 | 0.166 | 0.081 | 0.162 | 0.153 | 0.092 | 0.120 | 0.153 | 0.199 | 0.123 | 0.073 |
| 7 Pag VII | 0.925 | 0.858 | 0.912 | 0.927 | 0.903 | 0.875 | **** | 0.128 | 0.141 | 0.121 | 0.176 | 0.101 | 0.127 | 0.117 | 0.094 | 0.080 | 0.135 | 0.195 | 0.103 | 0.094 |
| 8 BolI | 0.897 | 0.917 | 0.910 | 0.920 | 0.879 | 0.871 | 0.872 | **** | 0.132 | 0.058 | 0.146 | 0.101 | 0.139 | 0.125 | 0.099 | 0.086 | 0.074 | 0.155 | 0.121 | 0.100 |
| 9 Pag VI-A | 0.897 | 0.882 | 0.882 | 0.876 | 0.837 | 0.936 | 0.859 | 0.868 | **** | 0.129 | 0.190 | 0.117 | 0.182 | 0.150 | 0.123 | 0.144 | 0.143 | 0.197 | 0.126 | 0.097 |
| 10 Pr III | 0.914 | 0.886 | 0.891 | 0.910 | 0.845 | 0.878 | 0.879 | 0.942 | 0.871 | **** | 0.167 | 0.112 | 0.141 | 0.117 | 0.096 | 0.117 | 0.111 | 0.184 | 0.139 | 0.122 |
| 11 SP XIV | 0.878 | 0.829 | 0.845 | 0.814 | 0.825 | 0.834 | 0.825 | 0.854 | 0.810 | 0.833 | **** | 0.136 | 0.201 | 0.185 | 0.158 | 0.143 | 0.149 | 0.254 | 0.216 | 0.172 |
| 12 CC | 0.914 | 0.885 | 0.911 | 0.919 | 0.898 | 0.919 | 0.899 | 0.899 | 0.883 | 0.888 | 0.864 | **** | 0.131 | 0.145 | 0.062 | 0.095 | 0.135 | 0.186 | 0.117 | 0.076 |
| $13 \mathrm{CC}-\mathrm{CNMS}$ | 0.841 | 0.829 | 0.847 | 0.855 | 0.878 | 0.838 | 0.873 | 0.861 | 0.818 | 0.859 | 0.799 | 0.869 | **** | 0.112 | 0.150 | 0.162 | 0.172 | 0.203 | 0.154 | 0.166 |
| 14RGS XX | 0.877 | 0.825 | 0.866 | 0.858 | 0.826 | 0.847 | 0.883 | 0.875 | 0.850 | 0.883 | 0.815 | 0.855 | 0.888 | **** | 0.134 | 0.155 | 0.139 | 0.218 | 0.175 | 0.163 |
| 15 Mt VI | 0.920 | 0.868 | 0.902 | 0.941 | 0.878 | 0.908 | 0.906 | 0.901 | 0.877 | 0.904 | 0.842 | 0.938 | 0.850 | 0.866 | **** | 0.106 | 0.107 | 0.153 | 0.124 | 0.073 |
| 16017586 | 0.917 | 0.894 | 0.926 | 0.926 | 0.926 | 0.880 | 0.920 | 0.914 | 0.856 | 0.883 | 0.857 | 0.905 | 0.838 | 0.845 | 0.894 | **** | 0.115 | 0.184 | 0.105 | 0.078 |
| 17017568 | 0.888 | 0.865 | 0.866 | 0.882 | 0.858 | 0.847 | 0.865 | 0.926 | 0.857 | 0.889 | 0.851 | 0.865 | 0.828 | 0.861 | 0.893 | 0.885 | **** | 0.179 | 0.152 | 0.122 |
| 18017574 | 0.777 | 0.817 | 0.805 | 0.853 | 0.829 | 0.801 | 0.805 | 0.845 | 0.803 | 0.816 | 0.746 | 0.814 | 0.797 | 0.782 | 0.847 | 0.816 | 0.821 | **** | 0.151 | 0.143 |
| 19017581 | 0.876 | 0.863 | 0.892 | 0.925 | 0.905 | 0.877 | 0.897 | 0.879 | 0.874 | 0.861 | 0.784 | 0.883 | 0.846 | 0.825 | 0.876 | 0.895 | 0.848 | 0.849 | **** | 0.084 |
| 20014148 | 0.909 | 0.914 | 0.939 | 0.944 | 0.923 | 0.927 | 0.906 | 0.900 | 0.903 | 0.878 | 0.828 | 0.925 | 0.834 | 0.837 | 0.927 | 0.922 | 0.878 | 0.857 | 0.916 | **** |

For abbreviations see legend to Table I.


Figure 1 - Phenogram constructed by UPGMA clustering of a matrix of Roger's distance (1972), derived from the mean allelic frequencies of 15 populations from the races Moroti (M), Caingang (C), Lenha (L), Entrelaçado (E) and five indigenous cultivars (IC) of maize. For abbreviations see legend to Table I.
ability found in the resulting populations may be because: 1) the original collections had different levels of variability, 2) some collections were better sampled than others, and 3 ) the populations formed by a large number of collections had their variability reduced due to phenomena such as bottleneck or founder effects. With regard to the latter possibility, our results suggested a founder effect as one probable cause for the lack of correlation mentioned above. No inferences can be made about hypotheses 1 and 2 because comparisons between the studied and the original populations would be necessary. This is no longer possible since the original populations and collections are no longer available.

More than $83.3 \%$ of the genetic variation $(\mathrm{Hs} / \mathrm{Ht})$ was within the populations. An analysis of Mexican germoplasm showed that $72 \%$ of the variation occurred within the collections and $28 \%$ was due to differences between them (Doebley et al., 1985). In conifers, this value usually exceeds $90 \%$ (Guries and Ledig, 1982; Dancik and Yeh, 1983; Moran et al., 1988). According to Hamrick and Loveless (1986), there is a general tendency for outcrossing plant species to show little or no differentiation among populations.

In our study, populations from different races were more similar to each other than populations from the same race. For instance, the populations of Bol I, which belongs to Moroti race, and Pr III, which belongs to the Caingang race, were more similar to each other ( $\mathrm{I}=0.886$ ) than were CC (CNMS) and SP XIV, which belong to the Caingang race. A lack of well-defined racial groups was also observed in the analysis of Mexican maize germplasm (Doebley et al., 1985). On the other hand, an analysis of the races of maize in Bolivia showed that racial similari-
ties defined based on ear morphology, general plant agroecological adaptation, and geographical source are also valid for isoenzymes (Goodman and Stuber, 1983). The divergence between morphological and isoenzymatic data is not surprising since morphological characteristics are chosen for their taxonomic constancy and not for indicating strong genetic differentiation (Gottlieb, 1974). Lewandowski and Mejnartowicz (1991) suggested that differences between morphological and isoenzymatic data reflect the fact the evolutionary forces act differently on those two parameters; isozyme alleles may have no evolutionary significance.

The genetic similarity among populations collected in different geographic regions, as in the case of Pr II and Mt VI, was sometimes higher than that among populations from the same race, collected at sites very close to each other. This suggests that there is little correlation between the geographic and genetic distances among populations. This same lack of correlation has also been found in populations of Desmodium nudiflorum, an annual allogamous and herbaceous plant (Schaal and Smith, 1980). The presence of such correlation between plant populations often indicates that the differentiation results from geographic isolation (Wendel and Parks, 1985). The lack of correlation between these two distances in the populations analyzed suggests that the populations could not be characterized because of the loss of genetic variation.

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## RESUMO

Existem mais de 200 raças de milho (Zea mays L.), as quais são divididas em três grupos (raças comerciais antigas, raças comerciais recentes e raças indígenas). As raças indígenas, embora não tenham valor comercial, possuem muitas características importantes que podem ser utilizadas em programas de melhoramento de milho. A maior parte do germoplasma brasileiro das raças de milho indígena foi coletada, no mínimo, 40 anos atrás e nada é conhecido sobre a variabilidade presente neste germoplasma. Quinze populações de 4 raças indígenas de milho (Caingang, Entrelaçado, Lenha e Moroti) e 5 cultivares indígenas foram analisados utilizando-se 5 sistemas isoenzimáticos codificados por 14 locos. A análise revelou um baixo nível de variabilidade entre as amostras estudadas. O número médio de alelos/loco foi três, com $64,3 \%$ de locos polimórficos e uma heterozigosidade média esperada de 0,352 . Por população, a média de número de alelos por loco polimórfico foi 1,6 , em média $47,5 \%$ dos locos foram
polimórficos e a heterozigosidade média foi 0,195 . A distância genética média entre as populações foi 0,821 e a proporção da variabilidade genética, que é atribuída ao componente entre populações (Gst), foi 0,156 . Os dados sugerem que um efeito de fundador poderia explicar a baixa variabilidade detectada.

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