Diversity of Maize Landraces in Germplasm Collections from South America

Diversidad de variedades criollas de maíz en colecciones de germoplasma de América del Sur

Diversidade da Coleção de Germoplasma de Variedades Crioulas de Milho de América do Sul

Editor

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Abstract

In the Southern Cone there is a wide variety of maize landraces kept by small-scale farmers, which are of interest for the development of the crop at a worldwide scale. The countries of this region hold important *ex situ* maize collections in national and international Germplasm Banks, from missions that took place before the generalization of hybrids and transgenic cultivars. In order to avoid losses of genetic diversity and to promote their use in breeding programs, it is essential that these collections are adequately known and conserved. The aim of this study was to map the geographic distribution of the collections of maize from Argentina, Bolivia, Brazil, Chile, Paraguay and Uruguay, and to analyze its diversity based on the variable kernel type. Infor-

mation about the accessions was obtained from the catalogues of maize genetic resources. The geographic distribution, Richness and Shannon Diversity Index were mapped and analyzed using software DIVA-GIS. Results show an important geographic dispersal of the accessions and concentration patterns of the different grain types (floury, flint, dent, pop and sweet). Micro-centres of maize diversity are observed in the Central regions of Chile and Bolivia, Southern Paraguay, Northern Argentina and Uruguay. This paper contributes with a broader understanding of maize diversity in the Southern Cone and seeks to revalue regions where traditional agriculture is still practiced, encouraging new prospection plans and in situ conservation strategies.
Keywords: *ex situ* conservation, kernel types, landraces, maize, *Zea mays*

Resumen

En los países del Cono Sur se encuentra una importante diversidad de variedades criollas de maíz (*Zea mays* L.), de interés para el desarrollo del cultivo a nivel mundial. Los países de la región cuentan con colecciones de germoplasma de maíz conservado *ex situ*, en bancos de germoplasma nacionales e internacionales. Estas provienen de distintas misiones de colecta que fueron realizadas previo a la difusión comercial de cultivares híbridos y transgénicos. Conocer y conservar adecuadamente estas colecciones es fundamental para evitar pérdidas de diversidad genética y promover su uso en programas de mejoramiento. El objetivo de este trabajo fue estudiar la distribución geográfica de las colecciones de maíz de Uruguay, Bolivia, Chile, Paraguay, Argentina y Brasil, y analizar la diversidad genética en función del tipo de grano. La información sobre las accesiones se obtuvo de los catálogos de recursos genéticos de maíz. Para los estudios de distribución geográfica y los análisis de Riqueza y Diversidad de Shannon se utilizó el Programa DIVA-GIS. Los resultados demuestran una dispersión geográfica importante de las accesiones y patrones de concentración de los distintos tipos de grano (harinoso, duro, dentado, pipoca y dulce). Se observan microcentros de diversidad de maíz en las regiones centrales de Chile y Bolivia, sur de Paraguay, norte de Argentina y Uruguay. Este trabajo contribuye a un conocimiento más global sobre la diversidad de maíz en el Cono Sur y busca revalorizar las regiones donde todavía existen agriculturas de tipo tradicional, favoreciendo nuevas prospecciones y estrategias de conservación *in situ*.
Palabras clave: conservación *ex situ*, maíz, tipo de grano, variedades criollas, *Zea mays*

Resumo

Os países do Cone Sul apresentam uma grande diversidade de variedades crioulas de milho conservadas por pequenos agricultores, que são de interesse para o desenvolvimento da cultura em escala mundial. Esses países mantêm importantes coleções ex-situ de milho em Bancos de Germoplasma nacionais e internacionais, de missões que ocorreram antes da difusão dos híbridos e dos transgênicos. O conhecimento e a conservação adequados dessas coleções são essenciais para evitar perdas da diversidade genética e promover seu uso em programas de melhoramento. Compreender as condições ecogeográficas dos locais de coleta é uma questão fundamental, uma vez que essas condições geralmente estão associadas a padrões de diversidade genética. O objetivo deste estudo foi mapear a distribuição geográfica das coleções de milho da Argentina, Bolívia, Brasil, Chile, Paraguai e Uruguai e analisar sua diversidade com base na variável tipo de grão. As informações sobre os acessos foram obtidas nos catálogos de recursos genéticos do milho. O software DIVA-GIS foi utilizado para estudar e mapear os índices de distribuição geográfica, riqueza e diversidade. Os resultados mostram uma dispersão geográfica importante dos acessos e padrões de concentração dos diferentes tipos de grãos (farináceo, duro, dentado, pipoca e doce). Concentrações de diversidade de milho são observadas nas regiões centrais do Chile e Bolívia, sul do Paraguai, norte da Argentina e Uruguai. Este artigo contribui para uma compreensão mais ampla da diversidade de milho no Cone Sul e busca reavaliar regiões

onde a agricultura tradicional ainda é praticada, incentivando novos planos de prospecção e estratégias de conservação in situ.
Palavras-chave: *ex situ* conservação, milho, variedades crioulas, *Zea mays*

1. Introduction

Maize (*Zea mays* L.) is cultivated in almost every continent, showing specific adaptations to different climates and soils[1][2]. In the Southern Cone (Argentina, Brazil, Bolivia, Chile, Paraguay and Uruguay) there is a wide variety of maize landraces[3][4] that have been kept by small-scale farmers in traditional ways over the centuries[5]. The region has been a meeting place of different ethnicities, through the colonization and immigration of different cultures[6]. This fact has led to an important development of maize landraces, evolving into a secondary center of genetic diversity of the crop[7][8][9].

A comprehensive study of the races of maize that were grown in the South America lowlands[4] identified 19 races and 15 sub-races. Since this classification, which was later expanded by Sánchez and others[10], broad studies on the racial diversity of *Zea mays* L. in this wide geographic area have not been executed[11]. Recent studies with high sampling intensity in micro-regions in southern Brazil revealed a currently greater number of races of maize[5][12]. Furthermore, the presence of wild relatives of maize in sympatric coexistence with landraces, along with the identification of new races[12], has led to the indication of micro-centers of diversity[2].

The lowland middle South America region holds an important locally adapted maize gene pool[13], with many traits of agronomic interest that can be incorporated in breeding programs. This is the case of the *Catetos*, a group of races that shows high protein and carotenoid contents, aluminum tolerance[14] among other qualities. Another race that has shown outstanding performance in grain production and forage yield is *Blanco Dentado*[15][16][17].

The countries of the Southern Cone keep important *ex situ* maize collections in Germplasm Banks. Most of these collections were carried out in farmers' fields in the 1970s, before the generalization of hybrids and transgenic cultivars. Ecogeographic data associated to the origin of the accessions has proved useful for germoplasm classifications in several crops[18][19][20][21][22][23]. In Brazil, ecogeographic origin and kernel type, a highly discriminant variable[24], were used to classify maize landraces[25][26] and select the Brazilian core collection[27]. This paper describes geographical patterns of diversity in maize germplasm collections from the Southern Cone, to contribute to its conservation and use. The aim of this study was to map the geographic distribution of these collections and to analyze its genetic diversity based on kernel type.

2. Materials and Methods

2.1 Collection databases

The databases used are the Maize Genetic Resources Catalogues from Uruguay, Chile and Bolivia[15][28][29]. Databases from Argentina and Paraguay were provided by partners from the *Instituto Nacional de Tecnología Agropecuaria* (INTA) and the *Centro Regional de Investigación Agrícola* (CRIA), respectively (2003 conversation with A. Hourquescos; unreferenced; 2003 conversation with O. Noldin; unreferenced). The database from Brazil proceeds from the Banco Ativo de Germoplasma (BAG), and was supplied by M. L. Burle (2004 conversation with M. L. Burle; unreferenced). The total number of accessions assessed in this research was 7,680. The Uruguayan collection consists of 852 accessions, the Chilean collection consists of 898; Bolivia has 601 accessions; Argentina has 2,111; Paraguay has 467, and the

Brazilian collection consists of 2,751 accessions.

2.2 Geographic coordinate assignment

The different catalogues presented differences at the level of accuracy of their geographic coordinates: Paraguay and Brazil displayed accuracy at the level of seconds; Bolivia and Argentina at the level of minutes, and Chile and Uruguay at the level of degrees. In the case of the Uruguayan database, additional information regarding descriptions of the collection sites was available[30]. Thus, an ex post assignment of the approximate geographic coordinates was made, taking into account three sources of information: 1) *gazetteers* available on the internet[31], 2) maps in paper format, where routes, roads and locations were positioned, and 3) a digital map of the world, Map Source[32], where distances were measured and geographically located. As for Chile, in order to assign the geographic coordinates, gazetteers and country maps were used to identify the different locations (towns or villages).

2.3 Geographic analysis

The software DIVA-GIS[33] was used to map the geographic distribution of the accessions. Richness and Shannon Diversity Indices according to grain type (kernel type) were performed. Richness is defined as the *Number of different classes*: different classes of a variable (e.g. the different grain types in a dataset) present in each grid cell[33].

The Shannon Index (H) is defined as:

$$H = - \sum p_i \ln p_i$$

Where p_i is the proportion of observations of kernel type i[34].

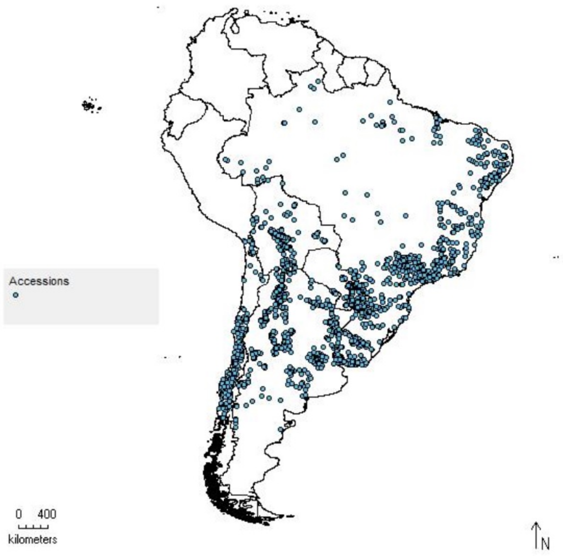
The study area was divided into equally sized rectangles (grids). A grid divides a geographic region into equal-sized cells. The advantage of using grids is that cells of the same size and shape allow more objective comparisons[33].

3. Results

3.1 Geographic distribution of maize collections

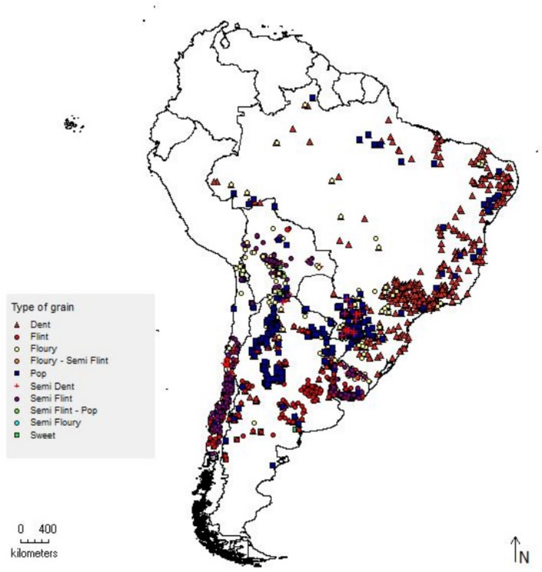
The location of the collection site of one or several accessions is represented by a point on the map, and represents the maize collection of the countries of the Southern Cone (Figure 1). In the Uruguayan collection, accessions concentrated mainly in three regions: departments of Canelones and San José (South of the country); Tacuarembó and Rivera (Northeast), and Soriano and Colonia (West). Chile showed a concentration of accessions in the Central zone (los Lagos, Araucanía, Bio Bio, Maule, Libertador O' Higgins, Metropolitana de Santiago, Valparaíso, Coquimbo and Atacama). In the Bolivian collection, accessions concentrated in the Central and Southern regions (Cochabamba, Chuquisaca and Tarija). As for Paraguay, the East part of the country is subdivided in four regions: North (Concepción and San Pedro), Center-South (Caaguazu, Guaira, Paraguari, Caazapa and Misiones); Northeast (Amambay and Canindeyu) and Southeast (Alto Paraná and Itapua), where accessions showed a relatively uniform distribution. Accessions from the Argentinian collection mainly concentrated in the provinces of Jujuy, Salta, Catamarca, La Rioja, Misiones and Buenos Aires. In Brazil, accessions concentrated in the Southeast, South and Northeast of the country (states of Sao Paulo, Minas Gerais; Río Grande do Sul and Northeast of Bahía, Alagoas, Pernambuco, Paraiba and Ceará).

Figure 1. Geographic distribution of maize accessions from Southern Cone countries.



The distribution of kernel types is represented on the map in Figure 2. Floury kernel types were mainly distributed in Central areas of the Southern Cone. Important concentrations of floury types were found in Paraguay, Bolivia, and North and Central Chile. In Argentina, this type of grain was restricted to areas bordering Uruguay (Buenos Aires province) and areas bordering Paraguay and Brazil (Chaco and Misiones). On the other hand, flint kernels were distributed throughout the entire region. In Brazil, an important group was observed in the Southeast and some accessions were scattered along the Atlantic coast. In Uruguay, flint kernels represented more than half of the collection, and were distributed throughout the country. In Chile, flint kernel type represented approximately forty percent of the national collection, with a dispersed distribution. In Argentina, these types were restricted to Buenos Aires province and to the North of the country. Dent kernel types concentrated along the Atlantic coast from Brazil to Uruguay. A small number of representatives of this grain type were registered in Bolivia and Chile. In Argentina and Uruguay dent kernel types were found in an isolated manner. Pop kernel types concentrated in areas that were formerly occupied by Guaraní indians. This type of grain was also found in the Central areas of Chile and Argentina, and in a scattered way in Brazil and Uruguay.

Figure 2. Distribution of maize accessions from Southern Cone countries according to grain type.



3.2 Richness and Diversity analysis

Red cells on the map show the areas where the highest Richness and Shannon Diversity Index values for kernel type were registered; whereas green cells reflect the lowest values (Figures 3 and 4). The maximum Richness values (7 different kernel types) were observed in the central region of Bolivia (Cochabamba, Chuquisaca, Potosí) and in the O'Higgins region in Chile. In Uruguay, up to six different kernel types were found in the South (departments of Canelones and San José), Northeast (Tacuarembó and Rivera) and West of the country (Soriano and Colonia) (Figure 3). The Shannon Diversity Index shows a similar pattern, with the highest values found in Chile (1.676), Bolivia (1.535 and 1.523), Paraguay (1.486), North of Argentina (1.386) and Uruguay (1.255) (Figure 4).

Figure 3. Richness analysis for grain type of maize accessions from Southern Cone countries.

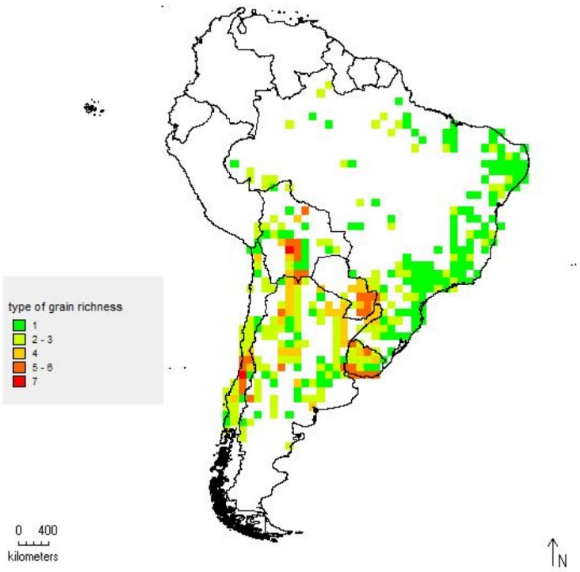
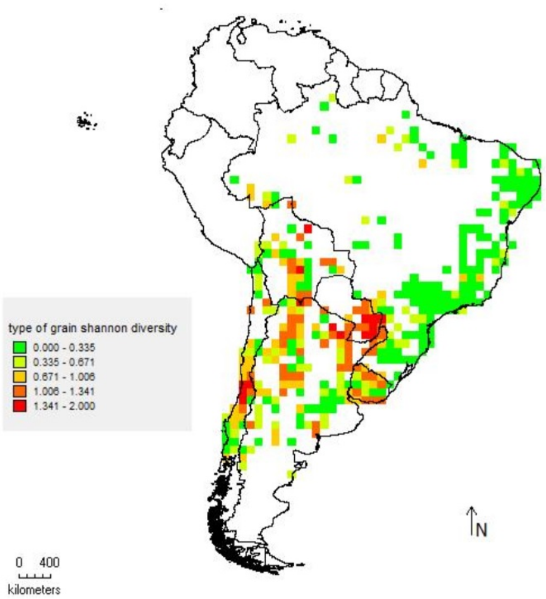


Figure 4. Shannon Diversity Index for grain type of maize accessions from Southern Cone countries.



4. Discussion

Maize diversity is associated with farmers' preferences and environmental conditions[1][35][36][37]. The distribution of kernel types (*pop*, *flint*, *floury*, *dent* and *sweet*) is related to different stages in the process of domestication of the crop; it is assumed that primitive maizes were pop types, then appearing flints, floury types and dents[3][38]. According to Paterniani and Goodman,[4] Guaraní Indians grew a floury maize belonging to the *Avatí Morotí* race, a white flint from the *Avatí Tupí* race and two kinds of pop: one with rounded grains (*Avatí Pichingá Ihú*) and the other with pointed grains (*Avatí Pichangá*). As a general rule, floury types prevail among populations of indigenous descent, whereas most of the materials used in breeding programs are dents and flints that evolved in North and Central America.

The distribution of maize diversity is not homogenous throughout the Southern Cone; micro-centres of diversity are verified in the Central regions of Chile and Bolivia, Southern Paraguay, North of Argentina and Uruguay. The diversity values registered in this study are comparable to those obtained by Li and others[39], who recorded average Shannon Index values of 1.408 for American countries, 1.077 for accessions from Europe, and 1.370 for Asia, Africa and Oceania. The results obtained in this work are consistent with the notion that the crop experienced a post-domestication diversity increase in this region[40]. Ecogeographic conditions define that certain genotypes are best adapted than others, in some cases due to long periods of interaction with the environment[41]. Socio-economic factors (including field size, grain destination and selection practiced by farmers, among others) have also been identified as of great significance in defining genetic diversity in crops[41][42].

Bolivia presents drastic variations in climates and elevations, with altitudes ranging from 100 to 6000 meters above sea level. An important cultural and linguistic diversity is found in this country, with the most important agricultural regions situated in the Altiplano and in the Temperate and Tropical Highland Valleys[43]. The country has the largest number of maize races recorded in America (77 races), surpassing Mexico, that has 65 races[44]. In Chile, mountains make up about 70 percent of the country, with elevations ranging from sea level to more than 6000 meters. Chile has a rich cultural pattern and agricultural system. Most of its agriculture is confined to the Central Valley, where Indians traditionally cultivated maize as one of the most important staple crops[45]. Paraguay is naturally divided by the Paraguay River into two distinct regions: The Eastern and the Western region (the Chaco region). There are substantial geographic, topographic and climatic differences between these two regions[46]. Conditions in the eastern region are generally favorable for maize production[47]. Maize has historically been one of the most important agricultural crops in Paraguay. Production practices and farming systems vary considerably in this country. In this sense, small-scale farmers, which cultivate landraces of maize as a subsistence crop coexist with medium to large-size famers, which grow this crop mainly for animal feed[46]. According to Morris and Alvarez[47], by the year 1991 around 48 percent of the maize area was planted with local varieties, known by their Guaraní language names, whereas improved varieties and hybrids occupied 25 and 27 percent, respectively.

In the pre-Columbian era, a trail referred to as *Peabiru path* was constructed, connecting the Atlantic and the Pacific Oceans. A study of alcohol dehydrogenase 2 (ADH2) allele sequences[48][49] in landraces from Peabiru and archaeological specimens from the Andes suggests an early exploitation of maize around this historical path, involving Incas and Guaraní indigenous peoples, in the transition area around the Brazil-Paraguay border[50]. This proposed path displays a similar pattern as the observed concentrations of maize diversity based on kernel type.

Patterns of diversity can also be explained by the effect of sampling density. Uruguay occupies approximately 1,3 percent of the territory and contains 11 percent of the total accessions. This represents an important sampling density and possibly explains the high diversity registered. Brazil, on the other hand, occupies 65 percent of the area and holds 35 percent of the accessions. Therefore, a low sampling density could explain the lower observed diversity in this country, in comparison to the rest of the region. Apart from this, popcorn races were not included in the phenotypic evaluations performed by Paterniani and Goodman[4], as it was considered at that time that pop grain types did not have immediate use for breeding programs in Brazil.

A broader understanding of maize diversity in the Southern Cone can increase the accessibility of *ex situ* collections[41][51] by encouraging germplasm use in breeding programs. This can lead to the development of new cultivars, with specific adaptations to environmental conditions, disease and pest resistance or improved quality or yield. Landraces are significantly more diverse than cultivars[52], and can show adaptations to marginal environments, constituting an important resource for agriculture under adverse conditions[53], including climate change scenarios[54]. Crops and agricultural systems are continuously evolving, and this has profound implications for the conservation of biological diversity[55]. At present, in many regions of South America, maize is grown in large extensions for animal feed, replacing traditional farmer's landraces with hybrid cultivars and transgenics, leading to a decrease in the overall genetic diversity. A practical application for this research is to propose prospection plans and *in situ* conservation strategies for the traditional varieties that are still being grown. Also, local characterizations of maize diversity through census of diversity could be performed, which is perceived as a crucial step for strengthening *on farm* conservation strategies[2]. This paper contributes with a broader understanding of maize diversity in the Southern Cone and seeks to revalue micro-centres where traditional agriculture is still practiced. Integrating different types of information allows a more rational use, and contributes to the establishment of adequate conservation goals.

5. Conclusion

Maize germplasm collections from the countries of the Southern Cone show an important dispersion, covering different geographic areas. The kernel type distribution (*floury, flint, dent, pop* and *sweet*) shows patterns of concentration. A general observation is that floury and pop accessions are principally found in areas that were inhabited by different Indian groups (Guaraní, Tupí Guaraní, Caingang and Chavante). Flint maize is dispersed throughout the region, and predominates in Southeastern Brazil and along the Atlantic coast. Dent maize distributes along the Atlantic coast, and was presumably introduced from the United States. Based on kernel type, maize diversity is not evenly distributed throughout the Southern Cone, and micro-centres of diversity can be identified in the Central regions of Chile and Bolivia, Southern Paraguay, North of Argentina and Uruguay. It is assumed that geographic and socio-economic factors play a significant role in determining the distribution of genetic diversity. This research contributes to a broader understanding of maize diversity in the Southern Cone and seeks to highlight the strategic value of maize genetic resources, enhancing regions where traditional agriculture is still practiced.

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Author contribution statement

MV: wrote the manuscript and participated in the experimental design; performed the analysis and interpretation of results. RV: participated in writing the manuscript and analysis and interpretation of results. TA: conceived and designed the analysis, participated in writing, analysis and interpretation of results.

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