

**University of São Paulo  
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**Association mapping to exploit maize diversity for drought tolerance:  
landraces and early testcrosses as genetic resources**

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Thesis presented to obtain the degree of Doctor in Science.  
Area: Genetics and Plant Breeding

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**Association mapping to exploit maize diversity for drought tolerance: landraces and early  
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versão simplificada

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## RESUMO

### **Mapeamento associativo em milho para tolerância a seca: variedades crioulas e *testcross* precoces como fonte de novo alelos**

A produção de milho ao redor do mundo vem apresentando uma grande dificuldade nos últimos anos, eventos de seca estão se tornando mais frequentes e severos, principalmente em regiões tropicais e subtropicais. Além disso, as mudanças climáticas têm sugerido que isso é uma tendência real para os próximos anos. O estresse causado pela deficiência hídrica nas lavouras de milho pode resultar em grandes quebras de produtividade de grãos. O México é o centro de origem do milho, e diversos são os centros de diversidade genética espalhados pela América Latina. Toda essa diversidade deve ser explorada pelos programas de melhoramento, já que ela é uma extraordinária fonte de novos alelos que podem ter um papel fundamental nos ganhos genéticos alcançados pelo melhoramento nos próximos anos colaborando para o enfrentamento dos desafios que são previstos. Esta tese de doutorado aborda o tema em duas partes. Primeiro, apresentamos uma revisão sobre a abundante diversidade genética do milho, e o uso de variedades crioulas nos programas de melhoramento para tolerância a seca, evidenciando a importância de se desenvolver germoplasma tropical adaptado as condições de seca no intuito de contornar este problema. Ainda na revisão, nós discutimos o uso de estudos de Associação Genômica Ampla (GWAS) e seleção assistida por marcadores (MAS) neste contexto. Na segunda parte, apresentamos um trabalho onde utilizamos GWAS em um programa de pré-melhoramento de milho visando tolerância à seca, onde variedades crioulas foram usadas como fonte de diversidade genética. O objetivo foi estudar os recursos genéticos oferecidos por um painel inicial de crioulas para identificar as regiões cromossômicas associadas à tolerância à seca. Para tanto, foram utilizadas 1306 progênies oriundas de 20 populações crioulas selecionadas por seu desempenho em regiões secas da América Latina. Dados fenotípicos foram obtidos a partir de *testcross* precoces de duas gerações (RC1S1 em 2016 e RCS2 em 2017) conduzidos em dois regimes hídricos distintos, um irrigado e outro sob seca, em três locais no México. O índice de média harmônica do desempenho relativo (HMRP), calculado com base nos rendimentos de grãos em ambos os regimes de água, foi utilizado como medida de tolerância à seca dos genótipos. Os valores genotípicos foram estimados usando ajuste espacial em uma análise de dois estágios. Um conjunto final de 5695 marcadores de polimorfismo de nucleotídeo único (SNPs) foi considerado para o mapeamento associativo. Como resultados, pudemos detectar um total de 10 marcadores significativos associados ao rendimento de grãos e ao índice de tolerância à seca, e sugerimos dois genes putativos mapeados próximos a dois desses marcadores que podem ter importante participação na resposta da planta ao estresse hídrico. Além disso, para dois SNPs associados, alelos originários das variedades crioulas resultaram em um rendimento ligeiramente maior sob condições de seca. Nossos resultados indicam que a diversidade oferecida pelas variedades crioulas combinada com linhagens já melhoradas pode ter um importante papel no melhoramento de milho tropical para a tolerância à seca.

Palavras-chave: Melhoramento de plantas, GWAS, Análise espacial, Estresse abiótico, Diversidade genética

## ABSTRACT

**Association mapping to exploit maize diversity for drought tolerance: landraces and early testcross as genetic resources**

Maize (*Zea mays* L.) production worldwide have been facing a tremendous obstacle in the past years, drought events are increasing in frequency and severity, mainly in tropical and subtropical regions. Moreover, climate change forecasts this as a trend for the next few years as well. The maize production can be highly affected by water deficiency stress, resulting in losses in grain yield. Mexico is the center of origin of maize, and there are many diversity centers across Latin America. This diversity should be exploited by breeding programs once it is a source of new alleles that can be responsible for the needed genetic improvements to face the forecasting challenges. This doctoral thesis addresses the theme in two sections. First, we present a review of maize genetic diversity, the use of landraces introduction in breeding programs to improve for drought tolerance, highlighting the importance to develop improved tropical germplasm to face the drought issue. In this review we also discuss the opportunity to apply Genome-Wide Associations Studies (GWAS) and Marker-Assisted Selection (MAS) in this context. In the second section we present an original GWAS application in a pre-breeding program using selected landraces as genetic sources for drought tolerance maize improvement. The aim was to study the genetic resources of a landrace panel to identify maize chromosomal regions associated with drought tolerance. For that, we performed the GWAS in 1306 landraces progenies originated from 20 landraces populations selected due to its agricultural performance in dry regions of Latin America. Phenotypic data were obtained from early testcross trials of two generations (BC1S1 in 2016 and BCS2 in 2017) conducted in two water regimes, irrigated and drought condition, in three locations in Mexico. Harmonic Mean of Relative Performance (HMRP) of grain yield in both water regimes was used as a measure of drought tolerance of the genotypes. The genotypic values were estimated using a spatial adjustment in a two-stage analysis. A final set of 5,695 single-nucleotide polymorphism (SNPs) markers was considered for GWAS. We were able to detect a total of 10 significant markers associated with grain yield and drought tolerance index, and we suggest two putative genes mapped close to two of these markers that can be part of the plant's response to drought stress. Besides, for two associated SNPs, the alleles from landraces provided a slightly higher yield under drought conditions. Our results indicate that the diversity delivered by these landraces combined with commercial lines is an exciting strategy to improve maize for drought tolerance.

Keywords: Plant breeding, GWAS, Spatial analysis, Abiotic stress, Genetic diversity.

## 1. INTRODUCTION

Maize (*Zea mays* L.) is a major crop cultivated worldwide and it plays a central role in human food security and economic development. It corresponded to about 13,6% of the whole area destined for agriculture in 2018 (FAOSTAT, 2018). The production of this cereal is to a large extent concentrated in tropical and subtropical regions, such as Central and South America, Africa and Southeast Asia. However, studies coordinated by the Intergovernmental Panel on Climate Change forecasts an increase in the frequency and severity of drought events in these regions (IPCC, 2007). As maize is a high water-demanding plant, these drought events have caused significant losses in grain yield.

In this context, plant breeding has an important participation in the solution to provide new drought-tolerant cultivars. Maize is a highly variable species and genetic diversity is the base to develop improved crops, what enables breeding as an essential tool to overcome the effects of climate change in agriculture (Bedoya et al., 2017; Fisher et al., 2015; Warburton et al., 2008). A constant challenge is to develop and apply the best strategies to incorporate this diversity into breeding programs. Exploit the diversity of landraces is one exciting approach for that (Gorjanc et al., 2016; Mayer et al., 2017).

Villa et al., (2005) defined the term landrace as “a dynamic population of a cultivated plant that has a historical origin, a distinct identity and lacks formal crop improvement, as well as often being genetically diverse, locally adapted and associated with traditional agricultural systems”. Due to these characteristics, landraces play an important role in studies of evolution, conservation, and diversity (Matsuoka et al., 2002), as well as being sources of alleles of interest for breeding programs. The terms local, traditional or creole varieties are sometimes used to characterize landraces populations, mainly in anthropological studies (Costa, 2013). These terms could be treated differently, depending on the area of study. In the present research, landraces will be a population of cultivated maize that had not undergone a formal breeding program.

Plant breeding, as genetics science in general, had rapid progress in recent decades. One of the advances was the use of Genome-wide Association Studies (GWAS) in plant breeding, which has the main purpose to find genomic regions associated with a phenotypic trait. With the advent of new high-throughput DNA sequencing technologies, GWAS become an extensively used tool for several studies in humans, animals, and plants (Brachi et al., 2011). For plant breeding studies it is useful for identifying natural genetic variants that are related to complex traits (Huang and Han, 2014), and has been used to a better understanding of drought tolerance in maize (Farfan et al., 2015; Hao et al., 2011; Setter et al., 2011; Xiao et al., 2017).

The thesis contains two sections, in the first we provide a review and discussion about the maize diversity and how the breeding programs have dealt with it, especially to improve for drought tolerance in tropical regions, as well as how GWAS have been used in this context. Afterward, in the second section, we report an original GWAS performed with landrace progenies, using phenotypic data from early testcrosses of a current breeding program to drought tolerance. We aim to study the genetic resources of the landrace panel to identify new beneficial variants in chromosomal regions associated with drought tolerance.

## **1.1. CONCLUSIONS**

### **1.1.1. Conclusion of Section 1**

Despite the natural high diversity of maize, breeding programs should always be aware of the narrow genetic base resulted from consecutive years of intense selection. Tropical regions, thus developing countries, will face more often the increase in the frequency of drought events. In the same way, growing demand for food in this region is forecast, thus, it must be a constant concern for the international scientific community, requiring that they keep going with coordinate actions and efforts to face this issue. Furthermore, the maize yield in developing countries is still much lower than in the developed ones, therefore, there is an opportunity for rapid increases. Many breeding strategies and genome approaches were developed. A combination of excellence phenotyping strategies and genome-wide associations studies for correct identification of genome regions associated with grain yield and drought tolerance is a useful tool available to assist the breeders with this task.

### **1.1.2. Conclusion of Section 2**

The genome-wide association study (GWAS) was able to identify genomic regions in early testcrosses associated with drought tolerance, although they were not stable over generations and irrigation treatments. Furthermore, two promising putative genes that encode proteins associated with physiological plant response to abiotic stress are located close to the significant SNPs found in this study. Additionally, some alleles from the landraces provide a slightly higher yield under drought treatments. Thus, these results indicate that the diversity delivered from landraces x elite inbred line crosses is an exciting breeding strategy for improving maize for drought tolerance and for trait introgression bringing new superior allelic diversity from landraces to breeding populations.

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## Section 1

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