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Maize Diversity and Climate Change

White Paper for the Environmental Working Group of the UC-Mexico Initiative

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Climate change threatens maize, affecting both US economy and subsistence farming in Mexico

World populations continue to grow, requiring renewed efforts to produce more food using fewer resources. At the same time, human-mediated climate change threatens our ability to even maintain current levels of yield for many major crops.

Maize is the single most important agricultural commodity in both Mexico and the United States, but historical analyses suggest that climate change over the last 30 years has already dramatically impacted maize yields worldwide, slowing gains from breeding and management (Lobell et al., 2011). Recent work has also documented farmer-assisted migration of maize to substantially higher elevations in the Andes in response to ongoing climate change (Skarbø and VanderMolen, 2015), and that Mexican farmers in the highlands may be those most vulnerable to changing climates (Bellon et al., 2011). Here we argue that improved characterization and utilization of extant genetic diversity could facilitate maize improvement in the face of climate change.

What are the Human welfare implications?

Maize has the highest global production of any crop and, in combination with rice and wheat, accounts for 60% of the world's plant energy intake (UN-FAO). Given the importance of maize as a global staple, the human welfare implications of climate-change-induced yield reductions are profound. The impacts of yield reduction will be particularly acute in Mexico. Over 2.5 million farmers in Mexico cultivate maize and the majority of these practice smallholder, subsistence agriculture (Eakin et al., 2014). For the most part, smallholder farmers do not have access to improved varieties of maize (CIMMYT, 2016) and instead cultivate traditional landraces maintained through seed saving and seed exchange networks. The bulk of landrace harvest is directly consumed on-farm (Eakin et al., 2014) meaning farmers and their families substantially rely on maize for food security.

Over the last 10,000 years, the evolution and maintenance of landraces have been influenced both by environmental adaptation and cultural preferences. Landraces harbor greater genetic diversity than modern maize lines (Hufford et al., 2012) and may therefore have substantial adaptive potential when faced with changing climate (Hellin et al., 2014). In fact, recent research based on population genetic analyses (Takuno et al., 2015) and common garden experiments (Mercer et al., 2008) suggest that both maize landraces and their crop wild relatives (Pyhäjärvi et al., 2013) show signs of local adaptation. Unfortunately, very little effort has been directed toward understanding landrace adaptation and susceptibility to climate change, leaving the future of Mexican maize and millions of Mexicans at considerable risk. Worryingly, some of the regions with the greatest levels of maize genetic diversity — such as the highlands of Central

Mexico (Orozco-Ramírez et al., 2016) — are also those that suffer the greatest threat from changing climates (Bellon et al., 2011).

The resource in a binational context

Maize is a crop of fundamental economic and social importance for both the United States and Mexico. More than 25% of the agricultural land in the US planted to field crops[1] and sales of maize in 2015 were worth more than $67 billion dollars (USDA NASS, 2016).

Millions of Mexicans still cultivate maize for subsistence agriculture (Eakin et al., 2014), and in spite of its role as the center of domestication and origin of maize, Mexico remains the world's largest importer of maize – primarily from the United States. Indeed, bilateral trade agreements such as NAFTA may have directly impacted maize diversity, as changing markets impact the economic feasibility of smallholder maize agriculture (Dyer-Leal and Yúnez-Naude, 2003). In addition to its economic importance, maize plays an important cultural role in Mexico, and the diverse varieties of maize selected for different cultural purposes are not easily replaced by modern hybrids.

Theoretical framework

While maize is an extremely high-yielding crop, modern maize hybrids are extremely narrowly adapted. The highest-yielding Iowa hybrids, for example, do not fair well in Georgia or upstate New York, let alone the coastal tropics or central highlands of Mexico. This narrow adaptation to environment also suggests a vulnerability to rapidly changing climates. Fortunately, given its global importance as a food source and commodity and its rapid adaptation to environments across the globe (Hake and Ross-Ibarra, 2015) there is great potential for adapting maize to changing climate. As genome-wide data have become available for a number of species, the uncommon level of genetic diversity within maize has become increasingly clear. In fact, when DNA sequences of two individuals of maize are compared, more differences are found than are observed between a human and a chimpanzee, species that diverged several million years ago Sequencing and Consortium (2005); Tenaillon et al. (2001). The vast genetic diversity of maize has most certainly contributed to its historical adaptation to a number of habitats and has been an important resource for plant breeders during the era of modern crop improvement. However, much of the genetic potential of maize has yet to be well exploited. For example, van Heerwaarden and co-authors 2012 recently determined that the ancestry of modern maize in the United States can be largely traced to two common landraces that were commonly grown in the U.S. Corn Belt at the onset of breeding programs. To place this in context, at least 59 distinct landraces of maize have been identified in Mexico alone Vielle-Calzada and Padilla (2009), and even cursory genetic analyses of maize landraces and their wild relatives readily identify a number of genetic variants absent in modern breeding material (e.g. Fang et al., 2012; Takuno et al., 2015; Pyhäjärvi et al., 2013; Hufford et al., 2013). Characterization of this untapped diversity

could identify alleles that are adaptive across numerous environmental conditions including those predicted in the future. Breeding programs such as the Germplasm Enhancement of Maize (GEM, (Carena, 2013)) could then incorporate adaptive alleles into both modern maize varieties and farmer landraces in order to minimize the global decreases in yield predicted for maize under climate change models.

Policy responses and challenges

The importance of maize landraces as a source of agricultural biodiversity has long been recognized. Until recently, the primary focus has been on *ex situ* conservation of landraces. For example, the Maize Germplasm Bank at the International Maize and Wheat Improvement Center (CIMMYT) in Mexico houses over 28,000 unique accessions of maize from 88 countries. This massive effort toward protection of landraces has established a valuable resource for combating climate change, but in order for the potential of the resource to be realized, landraces must first be characterized and utilized. With this in mind, the Seeds of Discovery (SeeD) project was spearheaded by CIMMYT and Mexico's Ministry of Agriculture, Livestock, Rural Development, Fisheries and Food (SAGARPA). Several thousand maize landrace accessions have now been genotyped at high density and utilized to produce "bridging germplasm" through crosses with elite maize lines. These landraces are also being evaluated in field sites across Mexico in order to determine their performance in disparate environments.

Less effort, however, has focused on *in situ* conservation of diversity on farms. The most detailed longitudinal study to date, however, suggests that landrace diversity is declining (Dyer et al., 2014) (but see (Brush et al., 2015)), highlighting the need to characterize existing diversity.

In addition to encouraging both scientific efforts to characterize diversity and identify potentially useful variation as well as the continued conservation of diversity *in situ*, the economic impacts of any number of other policy decisions will likely change the rate of loss of maize diversity via impacts on immigration and subsistence agriculture.

Scientific/historical background: What do we know?

Maize (*Zea mays* ssp. *mays*) was domesticated in the lowlands of southwest Mexico from the narrowly distributed teosinte *Zea mays* ssp. *parviglumis* (Matsuoka et al., 2002). Since domestication, maize has spread worldwide, and now exhibits the greatest global geographic breadth of 16 staple crops (Hake and Ross-Ibarra, 2015): maize is cultivated on six continents, ranging from southern Chile to Canada and from sea level to well over 3000m in elevation (Tenaillon and Charcosset, 2011).

Although there has been considerable effort to identify the genetic basis of many agronomically important traits in modern breeding material (e.g. Wallace et al., 2014), we know relatively little about how maize has adapted to new environments. We are only

beginning to understand, for example, how maize was able to adapt to temperate regions (Unterseer et al., 2016), but even this work focuses on extremely coarse environmental differences and still focuses on mostly modern breeding germplasm.

Work to date focusing on maize landraces and wild relatives have identified considerable evidence of local adaptation (Pyhäjärvi et al., 2013). Perhaps the most striking findings have been that alleles utilized by natural selection are often found segregating at low frequencies in populations in other environments (Takuno et al., 2015), that landraces and wild relatives harbor novel adaptive diversity completely absent in modern maize breeding (Hufford et al., 2013; Fang et al., 2012; Takuno et al., 2015; Pyhäjärvi et al., 2013) and that gene flow from wild crop relatives has historically allowed maize to adapt to new extreme climates such as those found in the highlands of Central Mexico (Hufford et al., 2013). Together, these results point to the utility of characterizing genetic diversity and the potential for such diversity to contribute to maize improvement.

Unanswered questions, research void

Current models predict the world's climate to change significantly within the next 50 years. Given the diversity of cultivated environments in Mexico, and associated crop genetic richness, we can be cautiously optimistic that the agroecosystem as a whole possesses the flexibility to maintain productivity if effectively managed. And yet, if climate change drives shifting practice, or displacement of crop populations, what will be the longer term consequences in terms of genetic or cultural erosion? For the present, increased adoption of commercial hybrid varieties notwithstanding, the great majority of the maize cultivated area in Mexico remains given over to farmer-saved seed. For as long as such large-scale cultivation is maintained, landrace maize as a whole can be considered relatively secure. The fate of any given variety, however, is far from certain: a landrace that ceases to be productive will not be maintained long in cultivation Mercer and Perales (2010).

Landrace populations arise from a combination of direct (farmer-mediated) selection for traits of agronomic interest, and indirect (natural) selection for adaptation to the local environment. The action of direct selection is clearly evident in the diversity of maize ear morphology. Indeed, ear characteristics form the basis for race definition in traditional farming practice and formal classification alike, and can be maintained by strong divergent selection even in the face of considerable gene flow Pressoir and Berthaud (2004). In contrast, local adaptation and the role of indirect selection are more difficult to assess, and their importance has largely been inferred on the basis of landrace distribution Ruiz Corral et al. (2008) and overall genetic diversity. To understand local adaptation, it will be important to characterize plants in their native environment, considering traits not in isolation, but with reference to the total phenotype that they collectively define. Indeed, trade-off among traits is predicted to drive local adaptation, and will impact the outcome of climate change.

Thinking ahead: Priorities for future binational research and training initiatives

Genomics-enabled resources, including whole genome sequence and high-density marker platforms, are providing unprecedented information on the diversity of Mexican maize. And yet, without the incorporation of phenotypic data, obtained from plants grown in the appropriate environments, genomics data alone have limited power to identify functionally important variation or to inform strategies for future responsible use and conservation of Mexican landrace maize. The synergy of genomic and phenotypic approaches is greatest when efforts are coordinated: common sets of material are characterized; genomics data is used to select material for evaluation; phenotypic data is used to select material for genomic analysis. In order to infer climatic effects on plant performance evaluation must be conducted in multiple environments. While it is natural to focus on adaptive variation, characterization of maladaptive genetic variants acting outside the adaptive zone are of equal, if not greater, importance in an understanding of landrace distribution and responses to climate change.

Understanding local adaptation and functional diversity in Mexican landrace maize will require the collaboration of multidisciplinary research teams to generate and integrate the necessary genomic and phenotypic data. This work requires a range of capacities that have traditionally been separated at the institutional level, between so-called "basic" and "applied" research institutions, and between academic and public sector agricultural institutions such as USDA and INIFAP. This divide is less evident in the US, where the land grant universities have long provided a valuable bridge between basic research and agronomic application. The experience of such institutions would be invaluable in realizing the potential of the Mexican research base. A clear priority is to promote initiatives that enable the adoption of genomic techniques by Mexico's extensive public sector agronomy infrastructure. Institutions such as Mexico's National Laboratory of Genomics for Biodiversity (LANGEBIO) are training a new generation of young scientists familiar with genomic techniques. As yet, however, there are few opportunities for the application of their skills within public or private sector agriculture.

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1. Includes area planted to corn, sorghum, oats, barley, rye, winter wheat, Durum wheat, other spring wheat, rice, soybeans, peanuts, sunflower, cotton, dry edible beans, potatoes, canola, proso millet, and sugarbeets↵

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