



Comparison of root system architecture and rhizosphere microbial communities of Balsas teosinte and domesticated corn cultivars



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ABSTRACT

The progenitor of maize is Balsas teosinte (*Zea mays* subsp. *parviglumis*) which grows as a wild plant in the valley of the Balsas river in Mexico. Domestication, primarily targeting above-ground traits, has led to substantial changes in the plant's morphology and modern maize cultivars poorly resemble their wild ancestor. We examined the hypotheses that Balsas teosinte (accession PI 384071) has a) a different root system architecture and b) a structurally and functionally different rhizosphere microbial community than domesticated cultivars sweet corn (*Zea mays* subsp. *mays* accession PI 494083) and popping corn (*Zea mays* subsp. *mays* accession PI 542713). In a greenhouse experiment, five plants from each corn variety were grown in individual pots containing a Maury silt loam – perlite (2:1) mixture and grown to the V8 growth stage at which rhizosphere bacterial and fungal community structure was assessed using terminal restriction fragment length polymorphism and fatty acid methyl ester analysis. Functional characteristics of the rhizosphere were assayed by examining the potential activity of seven extracellular enzymes involved in carbon, nitrogen and phosphorus cycling. Root system architecture was characterized by root scans of sand grown plants at the V5 growth stage. Compared to the control the sweet corn rhizosphere had different bacterial and fungal community structure, decreased fungal diversity and increased bacterial abundance. Teosinte caused a significant change in the rhizosphere bacterial and fungal community structure and increased bacterial abundance, but no significant decrease in bacterial or fungal diversity where the former was found to be significantly greater than in the sweet corn rhizosphere. Popping corn did not trigger significant changes in the bacterial or fungal diversity and bacterial abundance in the soil. The individual popping corn plants changed the bacterial and fungal communities in different directions and the overall effect on community structure was significant, but small. Of the enzymes analyzed, potential N-acetylglucosaminidase (NAG) activity was found to contribute most to the differentiation of teosinte rhizosphere samples from the other corn varieties. The teosinte root system had proportionally more very fine (diameter < 0.03 mm) roots than popping corn and sweet corn and it developed the highest root to shoot dry weight ratio, followed by popping corn. Sweet corn had significantly lower average root diameter than popping corn and teosinte and grew proportionally the least below-ground dry mass. The results allude to functional and structural differences in the rhizosphere microbial communities of the corn varieties that, with additional research, could lead to useful discoveries on how corn domestication has altered rhizosphere processes and how plant genotype influences nutrient cycling.

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1. Introduction

Maize domestication began 9000 years ago in the early Holocene or late Pleistocene period. Archeological and genetic data suggests that the domestication processes proceeded in the central Balsas River valley in Mexico. Genetic studies have pointed to *Zea*

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mays ssp. *parviglumis*, commonly known as Balsas teosinte, to be the wild ancestor of modern corn (Doebley, 2004). Due to human selection for favorable food and seed traits, the domestication process has led to altered shoot architecture of Balsas teosinte and modification of the reproductive organs (Doebley, 2004).

Crop breeding traditionally puts emphasis on above-ground traits; however, below ground properties are equally important. The root system explores the soil to scavenge nutrients and water, thus root system architecture greatly influences how efficiently a plant acquires resources in a given environment (Pierret et al., 2007; Badri and Vivanco, 2009). Comparing a greater and a lesser yielding corn varieties Qi et al. (2012) found the greater yield potential to be associated with faster root growth and a larger root system which likely provides more water and nutrients to the shoot. Similarly, based on a modeling approach Hammer et al. (2009) found that changes in the root system architecture are an important factor in explaining the increasing corn yield in the U.S. Corn Belt during the past 70 years. Studying 74 maize inbred lines Kumar et al. (2012) concluded that total root length and root dry weight at seedling stage could be important traits for breeding programs to improve nutrient and water-use efficiency.

Root architecture is impacted by abiotic environmental factors such as soil structure, oxygen and nutrient availability, water content and temperature, as well as biotic factors like plant genetic traits and soil microorganisms. (Hodge et al., 2009; Rich and Watt, 2013). Several studies comparing different maize cultivars in laboratory or field experiments showed differences in the size and architecture of their root systems. Furthermore, differences were found between various cultivars in how these traits are affected by N-, or P application level, or plant density (Richner et al., 1997; Costa et al., 2002; Liu et al., 2004; Manavalan et al., 2011; Kumar et al., 2012; Zhang et al., 2013). Zhang et al. (2013) compared maize varieties developed at different times between the 1950s and 2000s and found trends in the change of root system characteristics over time.

Beside root architecture the ability of a plant to mine nutrients from the soil depends on its uptake systems and the conversion of less plant-available nutrients to more accessible forms. All of these factors are influenced by the rhizosphere microbiota and its interactions with the plant (Wissuwa et al., 2009). Several recent studies investigated whether the rhizosphere microbial community shows characteristics specific to corn variety: Picard et al. (2008) found differences in how two inbred maize lines and their hybrid stimulate the populations of antibiotic producing bacteria, diazotrophs and arbuscular mycorrhizal fungi in the soil. In a field experiment Aira et al. (2010) demonstrated that corn genotype can have significant effect on the microbial community structure in the rhizosphere. In accordance with these findings Bouffaud et al. (2012) were able to show differences in the composition of the rhizosphere microbiota of ten maize cultivars representing the five major genetic groups of corn lines. Similarly, comparing 27 inbred lines Peiffer et al. (2013) concluded that plant genotype has a significant influence on the bacterial diversity in the rhizosphere.

These findings suggest that breeding new varieties had significant effects on the characteristics of the corn root system and rhizosphere and raise the question to what extent do these below-ground traits of modern cultivars differ from their ancestor's, Balsas teosinte. In their review Wissuwa et al. (2009) raised the concept that developing modern crop cultivars in highly fertilized agricultural environments may potentially result in the loss of beneficial plant–microbe interactions and in the decrease of the efficiency of plant nutrient acquisition. Comparing the root system and rhizosphere characteristics of Balsas teosinte with domesticated maize

varieties can reveal if this was the case during corn domestication, and may assist with the development of new cultivars more efficient in nutrient acquisition, abiotic or biotic stress tolerance.

In this study we examined the hypotheses that Balsas teosinte has a) a different root system architecture and b) a structurally and functionally different rhizosphere microbial community than domesticated cultivars. Balsas teosinte and two domesticated maize lines were grown in a greenhouse and their root architecture and the structure and function of their rhizosphere microbiota were compared using root scans, terminal restriction fragment length polymorphism, fatty acid methyl ester analysis and enzyme assays.

2. Materials and methods

2.1. Maize cultivars and teosinte

Seeds from the following three maize varieties used in this study were obtained from the North Central Regional Plant Introduction Station, Ames, Iowa: *Zea mays* subsp. *parviglumis* accession PI 384071 (Mexico, Guerrero, pit name Wilkes 10), a wild collection of Balsas teosinte, in the following referred to as teosinte. *Zea mays* subsp. *mays* accession PI 494083 (Chile, pit name Amarillo dulce (yellow sweet corn)) open pollinated population. In the following this cultivar is referred to as sweet corn. *Zea mays* subsp. *mays* accession PI 542713 (Nebraska, pit name YPI LFWS(1)), also a population, in the following referred to as popping corn. This cultivar was selected for resistance against Stewart's bacterial wilt (*Pantoea stewartii* (Smith)).

2.2. Soil properties

Soil was prepared by mixing two parts 2 mm sieved, air dried Maury Silt Loam soil (fine, mixed, semiactive, mesic Typic Paleudalf) collected from the surface 30 cm of a fescue pasture at Spindletop Farm, Lexington KY, and one part perlite (Therm-O-Rock West Inc., Chandler, AZ). The perlite in the growth medium served to aerate the soil and provide adequate drainage. Samples from the Maury Silt Loam were sent to the University of Kentucky Regulatory Services Soil Testing Laboratory for analysis of basic soil properties (<http://soils.rs.uky.edu/tests/methods.php>).

The soil was classified as a silt loam (14% sand, 72% silt, 14% clay) with 4.11% organic matter content, CEC of 19.64 meq 100 g⁻¹, base saturation of 38.03% and a pH of 5.22. Total N was found to be 0.231%, and Mehlich III extractable (mg kg⁻¹) P, K, Ca, Mg and Zn were 76.5, 60, 1173, 160.5, and 3.1, respectively.

2.3. Plant growth conditions and rhizosphere sampling

Five seeds of each cultivar (teosinte, popping corn and sweet corn) were individually planted in 15 cm, 2 L black plastic pots at a depth of 1 cm. Pots were filled with soil and maintained at 75% field capacity for two weeks prior to planting. Immediately after planting, 200 ml of water was supplied to each pot. The plants were watered 3 times a week, with equal amounts of nutrient (Floragro™ 2-1-6, pH 6.5) supplementation every third watering. The amount of water or nutrients added to the pots increased from ~50 ml to ~200 ml three times per week as the plants grew larger. The cumulative amount of water needed to reach V8 growth stage for a 113 day corn hybrid (for example) in Kentucky is equal to ~ 5.5 inches (personal communication, Dr. Chad Lee UK extension agronomist) which equates to ~2474 cm³ (i.e. $\pi(7.52 \text{ cm})^2 \times 14 \text{ cm}$), or ~2.5 L for the pots used in this study. Over the duration of the study ~3 L of water on average was added per pot which, according to these calculations, is a sufficient amount to ensure that the plants

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