Accepted Manuscript
Version of Record at: https://doi.org/10.1093/jxb/erad390

Title: Root responses to abiotic stress - a comparative look at root system architecture in maize and sorghum

Running title: Changes in RSA in response to abiotic stress in maize and sorghum

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Date of Submission: 2023-09-15

Number of Tables & Figures:

- Tables: 0
- Figures: 2
- Supplemental Tables: 1

Word Count: 4,631

Highlight

Plant root systems are important for crop productivity. Here we highlight the shared and distinct responses of root systems to environmental stress conditions in maize and sorghum.

Abstract

Under all environments, roots are important for plant anchorage and acquiring water and nutrients. However, there is a knowledge gap as to how root architecture contributes to stress-tolerance in a changing climate. Two closely related plant species, maize and sorghum, have distinct root system architectures and different levels of stress-tolerance, making comparative analysis between these two species an ideal approach to resolve this knowledge gap. However, the current research has focused on shared aspects of the root system that are advantageous under abiotic stress conditions as opposed to differences. Here we summarize the current state of knowledge comparing the root system architecture relative to plant performance under water deficit, salt stress, and low phosphorus in maize and sorghum. Under water deficit, steeper root angles and deeper root systems are proposed to be advantageous for both species. In saline soils, a reduction in root length and root number has been described as advantageous, but this work is limited. Under low phosphorus (P), root systems that are shallow and wider are beneficial for topsoil foraging. Future work investigating the differences between these species will be critical for understanding the role of root system architecture in optimizing plant production for a changing global climate.

Keywords

abiotic stress, cereal crops, drought, maize, phosphorus, *Poaceae*, root system architecture, salinity, sorghum

Introduction

The function of roots remains the same regardless of growing conditions. Roots are responsible for keeping plants upright (anchorage) and acquiring water and nutrients - arguably some of the most important functions for plant survival and productivity. These functional requirements are unchanged under abiotic stressors such as water deficit (drought), salinity stress, and low phosphorus, however the functions may be optimized by targeted changes in the root system architecture.

Maize (*Zea mays*) and sorghum (*Sorghum bicolor*) are two agriculturally and economically important crops that are closely related. Both rank in the five most important cereal crops worldwide and provide food, fuel, fiber, and fodder (Rooney *et al.*, 2007; Erenstein *et al.*, 2022). While sorghum is maize's closest relative (Swigoňová *et al.*, 2004), there are differences in their root systems (Singh *et al.*, 2010). Understanding the shared and distinct responses of maize and sorghum root systems to abiotic stress will aid in the development of stress-tolerant crops, however research has primarily focused on the shared aspects, and we understand little about the distinct responses. This review highlights the current state of knowledge regarding the maize and sorghum root responses to three prevalent abiotic stressors (drought, salt, and low phosphorus).

Root system architecture in maize and sorghum

The function of roots (anchorage, water acquisition, and nutrient acquisition) is universal across plants, however the root system architecture (defined as the spatial and temporal distribution of roots (Lynch, 1995)) differs (Hochholdinger *et al.*, 2004*a*; Atkinson *et al.*, 2014; Blizard and Sparks, 2018). Monocots, like maize and sorghum, have a fibrous root system that is composed of unique root types defined by their developmental origin - seed-borne embryonic roots (primary and seminal roots), and post-embryonic roots (nodal and lateral roots) (Hochholdinger *et al.*, 2004*a*; Hochholdinger, 2009; Blizard and Sparks, 2018).

Despite many similarities, some root architectural traits have diverged between maize and sorghum resulting in different development and morphology (**Figure 1**). For both species, the embryonic primary root emerges first. In maize this emergence is followed by embryonic seminal roots, whereas sorghum lacks seminal roots altogether (Singh *et al.*, 2010; Hochholdinger *et al.*, 2018). In maize, the transition between the embryonic root system being the dominant root type and post-embryonic root system being the dominant root type occurs by the vegetative leaf 6 (V6) stage (Hochholdinger *et al.*, 2004*a*,*b*). Due to the lack of seminal roots in sorghum, one might expect that the nodal roots would develop earlier in sorghum to compensate for the function of the seminal roots. Instead, the post-embryonic nodal roots develop much later in sorghum compared to maize (Singh *et al.*, 2010). These differences in root architecture persist throughout maturity with maize developing a denser root system than sorghum (**Figure 2**), however it is unknown if these differences are due to slower node development or slower root development. Counterintuitively, despite a lower root density (and a longer period of reliance on the primary root), sorghum has greater tolerance to abiotic stress than maize (Pardo and VanBuren 2021). We propose that the differences in root architecture between maize and sorghum are likely to contribute to the differences in abiotic stress tolerance. However, there is currently little data assessing the impact of these differences on stress tolerance – most studies have focused on shared responses.

The sequential emergence of roots based on their developmental timing likely influences their functional importance. Yet, there have been limited studies that investigate root type specific function across plant growth and development. The few studies that have assessed different root types (Ahmed et al. 2016; Ahmed et al. 2018), have looked at only water uptake in young maize plants grown in controlled environments. While findings from these studies show that root type matters, there was no temporal aspect to these studies to understand how root function changes over plant growth stages. Thus, more research is needed to elucidate root type specific function across different developmental phases of the plant in both optimal and stressed conditions. It is further unknown how the differences in developmental timing between maize and sorghum root development impacts root function.

Although the differences between maize and sorghum are likely of critical importance, the shared aspects have been the focus of the literature. For example, recent research has highlighted some shared genetic control of root system architecture between maize and sorghum (Zheng *et al.*, 2020). Using a root excavation and analysis pipeline, the authors identified SNPs associated with root traits of maize and sorghum by Genome Wide Association (GWA) analyses. A comparison of the GWA hits identified seven syntenic genes between maize and sorghum with root trait association (Zheng *et al.*, 2020). While this demonstrates a level of strong genetic conservation, each individual species had additional unique gene associations that may be responsible for the differences in root system architecture (Singh *et al.*, 2010; Hochholdinger *et al.*, 2018) and stress tolerance thresholds. However, these divergent gene associations remain to be investigated. The mechanism by which shared and divergent genetic landscapes lead to the differences between sorghum and maize and how these traits correlate to abiotic-stress tolerance remains unclear.

Impact of abiotic stress on root system architecture in maize and sorghum

Understanding the root response to different abiotic stresses is challenging. While field experiments are highly applicable, many factors are uncontrollable, making it difficult to quantify the response to individual environmental cues. Adding to the complexity, assessing root system architecture in the field is limited by poor resolution (e.g., mini-rhizotrons) or destructive (e.g., root crown excavation) approaches (Clark *et al.*, 2020). To overcome these challenges, many researchers opt for greenhouse or growth chamber systems. Yet studies show that results from greenhouse studies are not directly interpretable in the field setting (Poorter et al. 2016; Rich et al. 2020).

For the purposes of this review, we focus on a subset of prevalent abiotic stresses (water deficit, high salt, and low phosphorus) that are perceived by root systems and summarize the architectural changes that occur in maize and sorghum under these conditions. Most of the published research in this area has been completed in maize, with fewer studies in sorghum and even less work attempting to compare the two species or determine the mechanism for differential stress tolerance mechanisms.

Drought

Water deficit, often referred to as drought, affects plant growth, development, and productivity. Drought is one of the leading causes of yield loss worldwide, making this abiotic stressor a major concern for the growing population (Lamaoui *et al.*, 2018; Iqbal *et al.*, 2020). Since water availability is not always readily solved through management practices (i.e., irrigation), there has been a significant focus on developing new drought-tolerant plant varieties. The development of drought-tolerant varieties, with a focus on optimizing roots for water use efficiency, would be an ideal approach since roots are the first organ to sense, signal, and respond to water deficits. However, most of the research has focused on improving drought tolerance via aboveground phenotypes. In this section, we review what is known about the constitutive and inducible traits of maize and sorghum root systems in response to drought.

In the absence of rain or irrigation, water can be found in deep soil layers, thus deeper root systems are proposed to be advantageous for plants under drought because they are able to access this water (Lynch, 2007, 2013; Lynch *et al.*, 2014; Lynch and Wojciechowski, 2015). The concept of deeper rooting has played a big role in the development of the “steep, cheap, and deep” model that was first described in maize (Lynch, 2013). Root systems that have increased growth of nodal roots (e.g., crown roots) (Saengwilai *et al.*, 2014) or steeper angles of the primary root (Trachsel *et al.*, 2011; Burton *et al.*, 2014; Schneider *et al.*, 2020) enable plants to reduce the metabolic cost of soil exploration (e.g., through low-cost root cortical aerenchyma formation) while increasing water extraction from deep soil layers (Lynch 2013; Zhan et al. 2015). Notably, a single-gene associated with steeper root angles, DEEPER ROOTING 1 (DRO1), was first identified in rice to promote steeper root angles and increase plant performance under drought (Uga *et al.*, 2013). This gene has conserved function across species such as *Arabidopsis thaliana*, *Prunus* species, and even maize (Guseman *et al.*, 2017; Feng *et al.*, 2022). For maize, the expression of DRO1 under an ABA-inducible promoter led to changes in root angle and increased drought tolerance (Feng *et al.*, 2022). A meta-analysis of quantitative trait loci (QTL) associated with root-related drought stress adaptation across species, identified syntenic regions for DRO1 in wheat, barley, maize, and sorghum (Siddiqui *et al.*, 2021). This conservation is consistent with the shared genetic basis of maize and sorghum root architecture identified in Zheng *et al.* (2020). Collectively, these studies demonstrate the power of cross-species analysis and show promise that there are some pathways that provide universal control of root architecture that can be used to develop drought tolerant varieties. However, there are likely additional genes that can fine-tune this response in different species, which remain to be identified.

The premise of steeper root angles and increased drought tolerance is built upon the idea of a constitutive type of root architecture; however root systems are plastic and responsive to their environment (Schneider and Lynch 2020; Lynch 2007). Maize shows a decrease in crown root number in response to water deficit in both greenhouse and field studies (Gao and Lynch 2016; Sebastian et al. 2016). In fact, Sebastian *et al*. (2016) show that this suppression of crown roots post-emergence in response to water deficit occurs not only in maize, but also other members of *Poaceae* like *Setaria viridis*, sorghum, *Brachypodium distachyon*, and *Panicum virgatum*. This means that if drought occurs at early stages, root growth will be suppressed, and a steeper growth angle would not help even with the right genetics (unless alleles favoring crown root growth under water deficit are identified). Another example of root system plasticity in response to drought that has been broadly attributed to several plant species is a reduction in the number and growth of lateral roots (Xiong *et al.*, 2006). While this has been confirmed in maize (Zhan *et al.*, 2015), there is no published study assessing the lateral root response to drought in sorghum. Again, these studies have focused on the shared responses, and differences remain to be defined.

In addition to the DRO1 studies highlighted above, there are other association studies that have attempted to link root traits with plant performance under drought stress. Most of these studies have focused on aboveground phenotypes as a measure of plant performance under drought stress. One of these phenotypes is the stay-green trait, which is when plant leaves continue to photosynthesize and remain green during the grain filling period providing an advantage under drought conditions (Borrell et al. 1999;

Borrell et al. 2014; Borrell et al. 2022). In sorghum, a bi-parental QTL for nodal root angle overlaps with QTL for stay-green (Mace *et al.*, 2012). This finding is supported by other studies that found that sorghum with steeper root angles were also more drought tolerant (Singh *et al.*, 2011; Lopez *et al.*, 2017). A similar QTL analysis was performed in maize and showed that QTL for root traits overlapped with QTL for shoot traits (Li *et al.*, 2018). Collectively, these data highlight the potential for cross-species analyses to provide insight into shared physiological constraints that impact plant performance under abiotic stress.

In optimizing root systems for drought tolerance, both constitutive and plastic responses should be considered. While a steeper growth angle and deeper root systems are likely to be advantageous for water acquisition under drought, the emergence of roots is equally important for other root functions. Current research points to a shared optimization mechanism between maize and sorghum, however there is limited work in this area and more research is needed. It is unknown how the differences in constitutive root architecture and different stress tolerance thresholds contribute to drought-tolerance in maize and sorghum.

Salinity

Soil salinization is another prevalent abiotic stress that negatively impacts crops. Soil salinity is a complex problem arising from both natural and human factors, and in agriculture soil salinization typically worsens because of irrigation (Smedema and Shiati, 2002). With salinity stress, roots must be able to take up enough water to support the demands of the plant (osmotic stress tolerance) while also excluding salt ions (ionic stress tolerance). For some plant species, and even varieties within a species, osmotic stress is more detrimental to plant productivity than ionic stress and for other plants the opposite is true (Munns and Tester 2008). The different perception of stresses (osmotic vs ionic) imposed by high salinity can impact the optimal root system architecture to be targeted for salinity tolerance. Thus, understanding root system responses is important for identifying candidate genes and traits to incorporate into breeding programs.

Between the two crops discussed here, sorghum is considered a salt tolerant crop (Igartua *et al.*, 1995; Huang, 2018), whereas maize is considered a salt sensitive crop (Maas and Hoffman, 1977; Maas *et al.*, 1983; Rodriguez *et al.*, 1997; Chinnusamy *et al.*, 2005; Munns and Tester, 2008; Shelden and Munns, 2023). In most species, including maize and sorghum, the shoot growth is negatively impacted to a greater extent than the root growth under salinity stress, resulting in a reduced shoot-to-root ratio (Weimberg *et al.*, 1984; Munns and Termaat, 1986; Wang *et al.*, 2020; Shelden and Munns, 2023). In both sorghum and maize, the primary root length decreases, with a greater reduction occurring at higher salt concentrations and extended durations of salt exposure (Kandil *et al.*, 2012; Rajabi Dehnavi *et al.*, 2020; Wang *et al.*, 2020; Li *et al.*, 2021*b*). For both species, the roots of the salt tolerant genotypes were able to maintain primary root growth under salinity more than the salt sensitive genotypes (Rajabi Dehnavi *et al.*, 2020; Wang *et al.*, 2020).

Beyond the primary root, the response of other root types has been limited to studies in maize. In maize, the primary root length is more tolerant to salt stress than other root types (Rodriguez *et al.*, 1997; Zhang *et al.*, 2015; Wang *et al.*, 2020; Li *et al.*, 2021*a*). Specifically, there is up to a 60% reduction in seminal root lengths (Rodriguez *et al.*, 1997; Zhang *et al.*, 2015) and up to a 70% reduction in crown root lengths compared to less than a 10% reduction in primary root lengths (Zhang *et al.*, 2015). There is also up to a 54% reduction in nodal root numbers under salinity stress (Wang *et al.*, 2020). While these data suggest a root-type specific response to salinity stress, the experimental design or timing of stress may impact this interpretation (Shavrukov, 2013). Some studies introduced high concentrations of salts in a single dose (Zhang *et al.*, 2015; Li *et al.*, 2021*b*,*a*) while others gradually increased salts to the desired concentration, and no single study has reported a comprehensive root-type comparison under different salinity stress conditions.

In mapping the genetic basis of salt-tolerance for both maize and sorghum, results show an overlap in salt-tolerance QTL with root trait QTL (Luo *et al.*, 2019; Hostetler *et al.*, 2021*a*). Additionally, there are overlaps in the response of root system architecture to drought stress and salt stress (**Figure 1**). Since salt stress has both an osmotic and ionic stress phase, the impacts of osmotic stress are expected to phenocopy drought stress, which is an osmotic stress. Yet, it remains unclear how roots distinguish between the osmotic and ionic stresses imposed by salinity (Munns and Tester, 2008; Shelden and Munns, 2023), and how this impacts root architectural responses. It is further unclear how this leads to salt sensitivity in maize and salt-tolerance in sorghum.

Phosphorus

In addition to water and salt, roots are also faced with nutrient stresses. Nutrient stresses have been mostly alleviated by the copious use of fertilizer; however, this approach is unsustainable and there is a move toward more nutrient-use efficient crops. The major nutrients required for plant growth are nitrogen (N) and phosphorus (P). There have been extensive reviews written on the root responses to N (Lynch, 2013; Yu *et al.*, 2014, 2019; Sun *et al.*, 2020), but less on P. Thus, we elected to focus on the current state of knowledge for maize and sorghum root responses to P deficiency.

Although soil P availability mediates the below ground P-acquisition strategies of root systems, the responses are complex and not uniform (spatially and temporally) (Wen *et al.*, 2019). P deficiency compromises plant growth in the early developmental stages, while only moderately impacting growth during mature stages (Colomb *et al.*, 2000). The severity of P deficiency has differential effects on root system architecture in plants, with moderate P deficiency stimulating root growth and more severe P deficiency impairing root growth entirely (Wissuwa and Ae, 2001; Liu *et al.*, 2004; Rose *et al.*, 2013). Under low P, uptake is restricted by the size of the root system, thus small increases in the uptake of P will stimulate root growth and consequently elevate P uptake (Wissuwa, 2003). The distribution of roots close to the nutrient-rich zone favors P uptake and the establishment of plants. Under low P, a shallow root system, which involves changes in seminal and lateral root growth (Zhu & Lynch, 2004; Zhu et al., 2005; Zhu et al., 2006; Bayuelo-Jiménez et al., 2011; de Sousa et al., 2012; Postma et al., 2014; Azevedo et al., 2015; Xucun et al., 2018; Perkins & Lynch, 2021; Alden et al., 2021; Zhang & Ning, 2023; Ribeiro et al., 2023) and crown root angle (Baoru et al., 2018; Parra-Londono et al., 2018; Campolino et al., 2023), in addition to enhanced proliferation of root hairs, provide potential adaptation to P scarcity through topsoil foraging (Ho *et al.*, 2005; Lynch, 2011; López-Arredondo *et al.*, 2014). Maize and sorghum, genotypes with higher grain yield have wider crown root angle (Campolino *et al.*, 2023). Despite these similarities, maize and sorghum have differences in their mining strategies, presumably with different costs (e.g., resources and energy) and benefits. Maize plants present microorganism diversity and foraging traits (more compact, bushy and shallow root system) and wider root angle than sorghum (Campolino *et al.*, 2023)(**Figure 2**).

Several mapping strategies have been applied to dissect the genetic complexity of root morphology and architecture related to P deficiency in maize (Cai *et al.*, 2012; Kumar *et al.*, 2014; Burton *et al.*, 2014; Pace *et al.*, 2015; Zurek *et al.*, 2015; Azevedo *et al.*, 2015; Song *et al.*, 2016; Ren *et al.*, 2022; Ribeiro *et al.*, 2023) and sorghum (Hufnagel *et al.*, 2014; Parra-Londono *et al.*, 2018; Bernardino *et al.*, 2019, 2021). One example in maize suggests that different root plasticity mechanisms exist for adaptation to low P conditions, with greater lateral root length and root surface (de Sousa et al., 2012; Azevedo et al., 2015; Zhang & Ning, 2023) being significantly impacted as a result of P level in all three genetic groups (Ribeiro *et al.*, 2023). In sorghum, a GWA study revealed significant QTL associated with several root traits, indicating hotspots controlling root system development (Parra-Londono *et al.*, 2018). At low P, the extent of the root system was larger, likely due to more lateral roots and greater root length, whereas at high P levels, roots were thicker. Interestingly, when looking at root system architecture by cluster analysis, (Parra-Londono *et al.*, 2018) identified three distinct rooting types (small, exploratory, and compact and bushy), which would each be favorable in different environmental conditions. These results further show that root systems are plastic and that there is a lot of phenotypic and genetic variability in root system architecture, which is important for breeding P-tolerant lines.

Nevertheless, there are not many genes directly linked to root system architecture and P acquisition, particularly in crop species cultivated in soils with low P availability.

However, one example in rice was identified as being a key player in P-deficiency tolerance (Wissuwa *et al.*, 2002). Rice lines overexpressing Phosphorus-starvation tolerance 1 (PSTOL1), a receptor-like cytoplasmic kinase, were shown to have greater total root length and surface area, P uptake, and grain yield under low P conditions compared to the control (Wissuwa *et al.*, 2002; Gamuyao *et al.*, 2012). In sorghum, multiple homologs of OsPSTOL1 have been shown to modify root system architecture leading to increase in grain yield and biomass accumulation (Hufnagel *et al.*, 2014; Bernardino *et al.*, 2019, 2021). Specifically, greater P uptake in low P environments was associated with greater root length (primary and crown roots), smaller root diameter. In maize, homologs of OsPSTOL1 that were preferentially expressed in roots and co-localized with QTLs associated with root morphology and P acquisition traits (Azevedo *et al.*, 2015), mapped in the same region of QTLs for grain yield in a low P soil (Mendes *et al.*, 2014). Collectively this data shows that PSTOL1 is important in modulating total root length (primary, seminal, and crown) and surface area in P-deficient environments across species.

Another gene associated with root morphology is the maize transcription factor ROOTLESS CONCERNING CROWN AND SEMINAL ROOTS (RTCS), which contains a Lateral Organ Boundaries (LOB) domain. RTCS is responsible for the initiation of embryonic seminal and postembryonic shoot-borne roots (Hetz *et al.*, 1996; Taramino *et al.*, 2007; Xu *et al.*, 2015). RTCS is highly expressed in a P efficient maize genotype under low P conditions when compared to a P inefficient genotype (de Sousa *et al.*, 2012), indicating that it is modulated under low P and again emphasizing the importance of root system size for P acquisition.

In contrast to drought and salt, the root system architecture that is advantageous for low P is topsoil foraging, which requires shallow root systems and wider root angles (**Figure 2**). However, there is little knowledge about the root-type specific responses of maize and sorghum to low P. This knowledge will be critical for future crop improvement aimed at optimizing crops for multiple abiotic stressors.

Functional trade-offs

Optimizing root system function is necessary to support plant growth, development, and productivity in a changing environment. Throughout this review, we have focused on the impact of abiotic stress on root system architecture primarily in the context of water and nutrient acquisition, however, the impact of these changes on plant anchorage was not discussed and is often overlooked. A failure of plant anchorage, called root lodging, has significant detrimental impacts on crop yield (Carter and Hudelson, 1988; Rajkumara, 2008; Tirado *et al.*, 2021). Plant anchorage is a complex trait defined by the strength of the roots, the spatial and temporal distribution of the roots within the soil (root system architecture), the strength of the root-soil adhesions, and the presence of microbial communities (Ennos and Pellerin 2000). Of these, the root system architecture is thought to be the most important for root anchorage. In maize, genotypes that have greater root anchorage and are considered root lodging resistant, also have wider brace root angles (Hostetler et al. 2022). However, a GWA analysis showed that root system architecture only explains a portion of the root lodging characteristics (Zheng *et al.*, 2023). Thus, understanding the complexities of root anchorage is important for future root optimization.

It's also interesting to consider how optimizing for different functions may influence other functions. For example, studies in maize have shown that deeper and steeper root systems are important for accessing water from deep soil layers (Lynch 2013), but other results suggest that steep growth angles would compromise anchorage (Hostetler et al. 2022). Given the complex nature of root anchorage, more research is needed to determine if anchorage could be improved without compromising other root functions (e.g., water and nutrient uptake).

Most studies highlighted in this review have focused on primary roots, nodal roots, or not distinguished the root type. Of note, there is a little focus on the unique aboveground roots (brace roots) that are found in maize and sorghum (Hostetler *et al.*, 2021*b*). While these roots are important for anchorage (Reneau *et al.*, 2020; Obayes *et al.*, 2022; Hostetler *et al.*, 2022), there is limited information on how they respond to stresses. Thus, brace roots may be a critical way to overcome these tradeoffs by providing anchorage, while enabling the belowground root system to respond advantageously to abiotic stresses.

Conclusion

The spatial and temporal arrangement of roots is important for optimizing root function while also minimizing the negative effects of abiotic stresses. In this review, we discuss the constitutive and plastic responses of root system architecture in maize and sorghum in response to drought, salt stress and low phosphorus. Under drought, there is little known about how different root types respond and the potential for alleles that are advantageous. However, constitutively steeper root angles and deeper root systems are proposed to be important for drought tolerance in both maize and sorghum. In contrast, there is no constitutive root system architecture proposed to optimize for high soil salinity. This is likely because salt stress is a dual stress, which has both an osmotic and ionic component. It is possible that the osmotic stress can be mitigated through similar responses as drought stress, however more research is needed. In regard to low P, a constitutive root system architecture proposed to be advantageous to tolerant genotypes includes root systems that are wide and shallow to promote P acquisition via topsoil foraging. Yet none of the work to-date allows us to link different root system architectures with the differential stress tolerance of maize and sorghum. We propose that comparative work focus not just on shared aspects, but also divergent aspects that could elucidate different mechanisms of stress tolerance.

When considering the root system architecture that is advantageous under each of these stressors, it is important to consider that there are both overlapping and distinct features. However, each of these stresses has been studied in the absence of others, and in a changing global climate there is a need to understand how to optimize plants for multifaceted stressors. Moreover, root system architecture optimization is primarily focused on nutrient and water acquisition, yet by only focusing on one root function, other root functions such as anchorage could be compromised. Given that anchorage is partially determined by root system architecture, there is an opportunity to compensate for any compromised anchorage by targeting specific root traits. Overall, more research is needed to understand the functional trade-offs associated with breeding for abiotic-tolerant crops, especially in important cereal crops like maize and sorghum.

Acknowledgements

We thank Dr. Lindsay Erndwein of Illustrations by LindZeaMays for illustrating Figure 1 from this article. We thank members of the Sparks Lab, Eva Birtell, Teclemariam Weldekidan, Irene Ibiwari Ikiriko, Thanduanlung Kamei, and Dave Griffin, for providing comments and suggestions on this manuscript. We also thank two anonymous reviewers and the associate editor for their suggestions.

Author Contributions

All authors contributed to the writing and editing of the manuscript.

Conflict of Interest

No Conflict of Interest has been declared.

Funding

This work was supported by a United States Department of Agriculture (USDA) National Institute of Food and Agriculture (NIFA) Postdoctoral Fellowship awarded to ANH (grant no. 2022-67012-36840); Empresa Brasileira de Pesquisa Agropecuária - Embrapa (grant no. 20.20.03.024.00.00) awarded to SMDST; and Fundação de Amparo à Pesquisa do Estado de Minas Gerais - Fapemig (grant no. APQ-00606-21) awarded to SMDST.

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Figure Legends

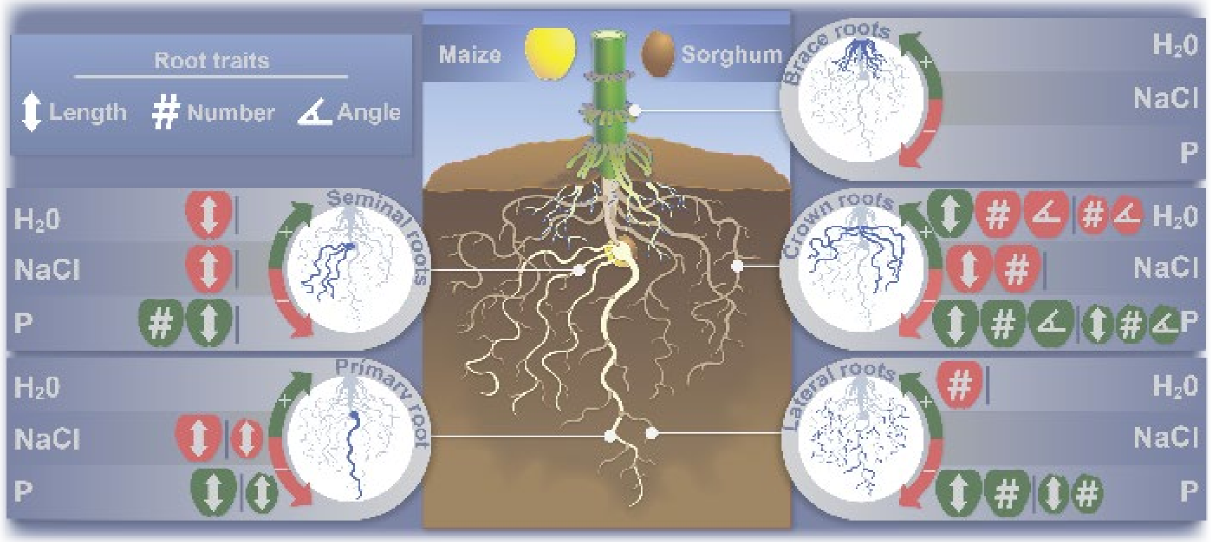

Figure 1 Changes in root system architecture of maize and sorghum plants in response to drought, salt, and low phosphorus. The maize and sorghum root systems are comprised of embryonic and post-embryonic root types. In maize, the embryonic root system includes both primary and seminal roots, whereas in sorghum, the embryonic root system lacks seminal roots. Both the sorghum and maize post-embryonic root systems consist of nodal and lateral roots. Nodal roots can be further divided into roots that emerge from nodes below the soil, called crown roots, and roots that emerge from nodes above the soil, called brace roots. For each of the root types (primary, seminal, crown, brace, and lateral), changes in root traits (root length, root number, and root angle) were described as increasing (green icons) or decreasing (red icons) in response to drought, salt, and low phosphorus. For each root type, changes in maize root traits are illustrated to the left of the line with a larger maize seed icon. Changes in sorghum root traits are illustrated to the right of the line with a smaller sorghum seed icon. When interpreting changes in root angle, we considered the ground as 90-deg, therefore a steeper root angle would be considered a decrease. See

Supplemental Table S1 for more information regarding references used for the generation of Figure 1.

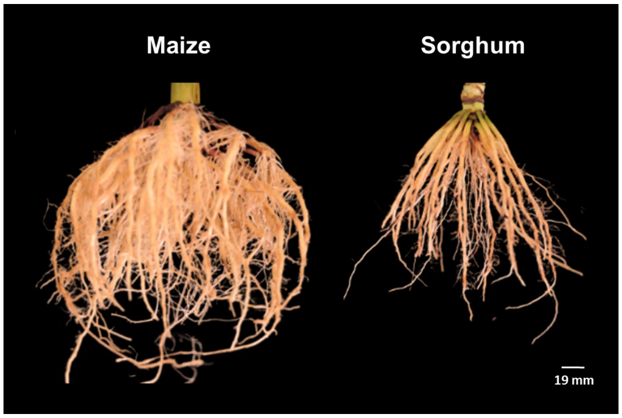

Figure 2 The maize and sorghum root systems are distinct. The maize root system is denser with wider root angles compared to the sorghum root system. Images are from field grown plants collected via shovelomics at 60-70 days after planting. Sorghum genotype -1G100 (Pioneer); Maize genotype - 1M1752 (Embrapa Maize and Sorghum)