

Architecture and distribution of maize roots grown under contrasting water regimes¹

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ABSTRACT

The root system architecture influences the spatiotemporal dynamics of the process of exploring and absorbing water and nutrients from the soil. Prospecting root phenes can help to identify genotypes adapted to restrictive soil water conditions. This study aimed to phenotype the root architecture and distribution in seedlings of three maize hybrids (BRS1010, BRS1055 and DKB390) grown under well-watered and water-restricted conditions, during early vegetative growth, comprising six treatments, in a factorial design. The nodal root insertion angle at the first and second coleoptilar nodes and the number of seminal roots, coleoptilar nodes with nodal roots and nodal roots at the first and second coleoptilar nodes were evaluated, as well as the root length density among treatments in the rhizosphere profile. No significant interaction was observed between hybrids and water regimes. The DKB390 hybrid showed the lowest number of coleoptilar nodes with roots, as well as steeper root insertion angles. The root length density decreased with increasing soil depths for all hybrids.

KEYWORDS: *Zea mays* L., water deficit, root system.

RESUMO

Arquitetura e distribuição de raízes de milho cultivado sob regimes hídricos contrastantes

A arquitetura do sistema radicular influencia na dinâmica espaço-temporal do processo de exploração e absorção de água e nutrientes do solo. A prospecção de fenes radiculares pode ajudar a identificar genótipos adaptados a condições restritivas de água do solo. Objetivou-se fenotipar a arquitetura e distribuição das raízes em plântulas de três híbridos de milho (BRS1010, BRS1055 e DKB390) cultivadas sob condições de irrigação e déficit hídrico, durante o crescimento vegetativo inicial, perfazendo seis tratamentos, em esquema fatorial. O ângulo de inserção da raiz nodal no primeiro e segundo nós coleoptilares e o número de raízes seminais, de nós coleoptilares com raízes nodais e de raízes nodais no primeiro e segundo nó coleoptilar foram avaliados, bem como a densidade de comprimento de raiz entre os tratamentos no perfil da rizosfera. Não foi observada interação significativa entre híbridos e regimes hídricos. O menor número de nós coleoptilares com raízes, assim como raízes com ângulos de inserção mais íngremes, foram obtidos no híbrido DKB390. A densidade de comprimento de raiz diminuiu com o aumento da profundidade.

PALAVRAS-CHAVE: *Zea mays* L., déficit hídrico, sistema radicular.

INTRODUCTION

Soil water deficit is the main edaphic factor limiting maize (*Zea mays* L.) yield worldwide (Chimungu et al. 2014, Ahmed et al. 2018). Therefore, ensuring an efficient exploitation of water and other soil resources via the crop root system is essential to minimize the consequences of soil water deficit (Monshausen & Gilroy 2009).

After the start of germination, maize seed develops a primary root and a variable number of

seminal roots, both of embryonic origin, which play a crucial role in determining early seedling vigor. Subsequently, numerous post-embryonic nodal roots emerge above the mesocotyl from six spirally arranged whorls, thus forming the adult root system (Hoppe et al. 1986, Hochholdinger et al. 2018).

Among the cornerstones of plant breeding is the genotype-phenotype concept, where the genotype represents genetic inheritance whose modulated expression culminates in the phenotype, encompassing metabolic, morphological, physiological, anatomical

¹ Received: Oct. 21, 2024. Accepted: Feb. 04, 2025. Published: Mar. 14, 2025. DOI: 10.1590/1983-40632025v5580906.

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and behavioral traits in an individual (Pieruschka & Porter 2012). York et al. (2013) argued that gene is to genotype as phenotype is to phenotype. As genes have variants called alleles, phenes have variants known as phenotypes. According to these authors, a given combination of phenotype states thus constitutes the phenotype of an organism.

Root system phenotyping in maize under suboptimal water availability conditions can be used as a strategy to identify phenes in maize phenotypes adapted to these conditions (Trachsel et al. 2013, York et al. 2013, Gao & Lynch 2016, Suralta et al. 2018). A few phenes exhibit plasticity in response to environmental variables (Suralta et al. 2018). Root length density is determined by an aggregate of phenes whose plasticity reflects the specific modulation of its constituent phenes (York et al. 2013, Gao & Lynch 2016). Root system phenes, such as root depth, thickness and angle (Hund et al. 2009, Lynch 2013), total root length (Zhang et al. 2009) and number of nodal roots (Gao & Lynch 2016), have been associated with drought tolerance.

Owing to limited accessibility and measurement challenges, root systems remain among the least studied and understood plant organs (Hochholdinger 2016). However, emerging technologies have made it increasingly easy to examine the root systems of plants (Tajima 2021). A root system phenotype called “steep, cheap and deep”, which integrates specific architectural and anatomical phenes that optimize soil resource exploration and acquisition, has been proposed (Lynch 2013).

This study aimed to phenotype root architecture and distribution in the seedlings of three maize hybrids grown under contrasting water availability conditions during early vegetative growth.

MATERIAL AND METHODS

The experiment was performed in an aphid-proof screenhouse at the Universidade Estadual de Montes Claros, in Janaúba, Minas Gerais state, Brazil, from July to September 2017.

Commercial maize hybrids were grown in a nursery for three consecutive cycles, with planting dates spaced a week apart, in a factorial design, with six treatments comprising three hybrids and two water regimes. The treatments included cultivating BRS1010, BRS1055 and DKB390 hybrids under well-watered and water-restricted conditions.

The plants were grown in polyvinyl chloride (PVC) tubes (1.0 m in height × 0.1 m in diameter) lined with plastic film and filled with quartz sand. Each experimental unit consisted of a growth column containing one plant.

At sowing, pots under well-watered conditions received water up to the field capacity (1.64 L), whereas water-restricted treatments received 30 % of this volume with no further irrigation. Two seeds were sown per pot at a depth of 5 cm, and, after emergence, only one seedling was maintained.

Upon reaching the V5 growth stage (Abendroth et al. 2011), plants were harvested by removing the shoots and PVC tubes. The root system enclosed by the plastic film was then divided into 10-cm-long cylindrical sections. A subsample (100 cm³) was collected from each section, weighed to obtain the fresh mass, and then oven-dried to constant weight, to determine the dry mass and available water content.

The cylindrical root sections at each depth were dismantled and washed under running water to remove the substrate. The roots were carefully separated and stored in plastic bags containing a 70 % ethanol solution. The root system architecture was evaluated for number of seminal roots and of coleoptilar nodes with nodal roots, nodal root insertion angle at the first and second coleoptilar nodes, and number of nodal roots at the first and second coleoptilar nodes. The data were analyzed using the multivariate analysis of variance (Manova) with the Pillai's trace test at $\alpha = 0.05$ in the Stats software. The canonical correlation analysis was performed using the Candisc package (Friendly & Fox 2024) after confirming the absence of multicollinearity.

The root length density (cm cm⁻³) at all soil depths was determined using the WinRHIZO Pro 2007 software (Regent Instr. Inc.) and analyzed using the univariate analysis of variance with a factorial design. Means were compared using the Tukey test at 5 % of significance. All statistical analyses were performed using the R software (R Core Team 2016) with the ExpDes.pt package.

RESULTS AND DISCUSSION

The principal component analysis was performed to identify the phenotype groupings most closely associated with drought performance. The Manova results for root phenes revealed no significant

interaction effects ($p \leq 0.05$) between the hybrids and water regimes (Table 1).

The first two canonical varieties accounted for 93.8 % of the total variation, enabling their representation in a two-dimensional scatter plot (Figure 1). The first canonical variable explained 60.34 % of the total variation, primarily because of the root angle at the first and second coleoptile nodes and the number of coleoptile nodes with nodal roots (Table 2).

The scatter plot (Figure 1) shows that the DKB390 hybrid grown under water restriction exhibited lower estimates for the first canonical variable (Table 2), showing wider root angles at both evaluated nodes and fewer coleoptilar nodes with nodal roots. On the contrary, hybrids grown under well-watered conditions exhibited positive scores for the first canonical variable. According to Chaudhary et al. (1985), root growth angles tend to be steeper in plants in low-density soils than in those in high-density ones. Lynch (2013) stated that a steep root system would be beneficial under conditions where water and soluble nutrients are predominantly present in relatively deep soil layers, such as during terminal drought and in soils with low water and nutrient retention capacity. These findings support the results of the present study, where quartz sand was used as a substrate, exhibiting the aforementioned characteristics.

The second canonical variable accounted for 33.46 % of the variation among the treatments, particularly regarding the number of nodal roots at the second coleoptile node in the BRS1055 hybrid. Field and greenhouse studies have demonstrated that the production of nodal root varies among maize genotypes, ranging from 5 to 70 (Burton et al. 2013). A reduced number of nodal roots leads to enhanced dispersion

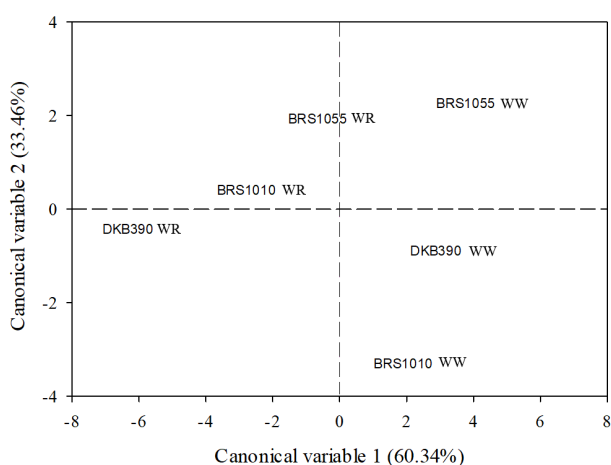


Figure 1. Graphical dispersion of the scores relative to the axes of the first two canonical variables, for six root system phenotypes in three corn hybrids grown under two water regimes: well watered (WW) and water restricted (WR).

Table 1. Summary of the analysis of variance for three corn hybrids (BRS1010, BRS1055 and DKB390) grown under well-watered and water-deficit regimes.

Source of variation	Degrees of freedom	Pillai	Approx F	Num Df	Den Df	Pr ($> F$)
Hybrid (H)	2	1.39994	2.333	12	12	0.078259 ^{ns}
Water regime (WR)	1	0.94645	14.7277	6	5	0.004835**
Block	2	1.1462	1.3425	12	12	0.308981 ^{ns}
H x WR	2	1.37893	2.2203	12	12	0.090752 ^{ns}

** $p \leq 0.01$; * $p < 0.05$; ^{ns} $p > 0.05$.

Table 2. Correlations between the first two canonical variables in six phenes of commercial corn hybrids growing under well-watered and water-restricted regimes.

Quantitative descriptors	Canonical variables	
	1	2
Nodal root angle at the first node	-0.94737	-0.11947
Nodal root angle at the second node	-0.83768	0.132856
Number of seminal roots	0.663424	0.479086
Number of coleoptilar nodes	0.922121	-0.38222
Number of nodal roots at the first node	-0.02224	0.10449
Number of nodal roots at the second node	0.651202	0.629585

in soil resource exploration, making plants relatively more susceptible to lodging (Hetz et al. 1996). On the contrary, if nodal roots are excessively numerous, they may compete with each other for internal metabolic and soil resources, compromising their elongation and wasting resources under stress conditions (Lynch 2013). Gao & Lynch (2016) proposed an intermediate number of nodal roots, arguing that the soil type and the intensity of biotic and abiotic stresses must be considered while sizing the nodal roots (Saengwilai et al. 2014). Gao & Lynch (2016) cultivated pure maize lines under contrasting water regimes and supported the hypothesis that, under water deficit, a reduced number of nodal roots leads to resource exploitation in deep soil layers, enhancing water content, stomatal conductance and photosynthesis, and reducing the carbon proportion allocated to root respiration. In the present study, the DKB390 hybrid produced fewer coleoptilar nodes with nodal roots than those in the BRS hybrids, demonstrating its adaptation to water-limiting conditions.

Moreover, the root length densities in the rhizosphere profile differed among the treatments (Figure 2). The use of phenes, which completely deplete resources within a given soil volume, optimize absorption rates by increasing root density (number of roots or length per unit volume) through enhanced nodal root development, lateral branching or absorbent hairs (York et al. 2013), thus maximizing resource exploitation and acquisition. According to these authors, variations in root length density have been documented in both embryonic and adventitious roots in maize.

In the present study, DKB390 exhibited the lowest root length density among the three cultivars (Figure 2A). For all hybrids, the estimated root length density was higher at 20-40 cm depths than at the other depths. At 30-60 cm depths, DKB390 and BRS1055 exhibited similar root length densities, but lower than those of BRS1010, whereas all hybrids exhibited decreasing root length density values below 70 cm depths.

According to Bolaños et al. (1993), plants adapted to drought conditions typically exhibit reduced root mass in the upper 50 cm of the soil profile. According to Gao & Lynch (2016), during drought progression, soil desiccation begins at the surface, exposing upper roots to water stress, whereas deeper roots can continue accessing soil water for plant growth.

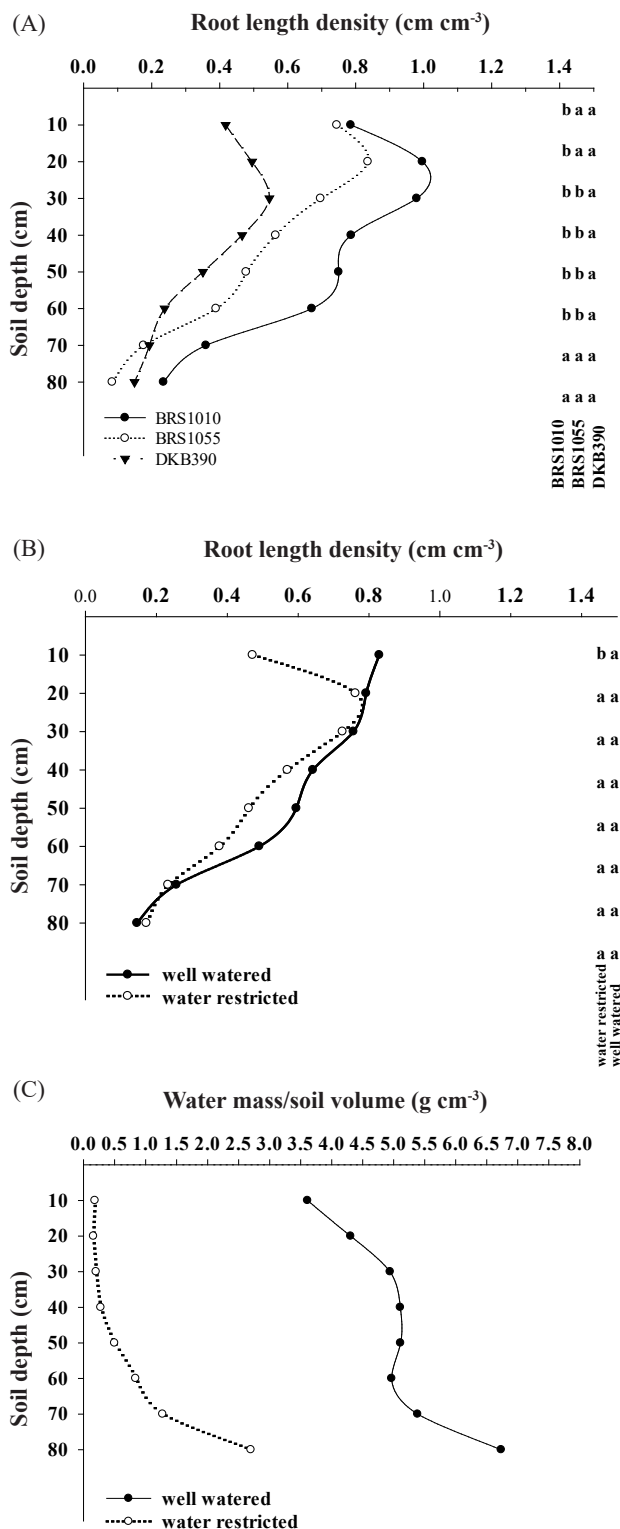


Figure 2. Root length density in the rhizosphere profile of maize hybrids (A) and in well-watered and water-restricted maize (B), and water mass (without statistics) in the rhizosphere profile under two water regimes (C). Means followed by the same letter for hybrids and water regime do not differ from each other by the Tukey test at 5 % of significance.

The root length density decreased with depth and exhibited no significant differences among the treatments involving contrasting water regimes at most depths, except at 10 cm (Figure 2B). Under well-watered conditions, the soil water content in the rhizosphere profile (Figure 2C) was higher than that under water-restricted conditions and increased with depth in both water regimes (Figure 2C). The decrease in root length density with depth (Figure 2A) indicates that the expansion of the root system decreases with increasing water availability (Figure 2C) across all studied hybrids, particularly DKB390, which exhibited the lowest root length density throughout most of the soil profile among all hybrids.

Regarding root system depth in natural biomes, Hund et al. (2009) indicate that root systems in arid and semi-arid regions tend to be deeper than those in humid environments. These authors also observed a decrease in root length density in maize as water availability increased. According to Trachsel et al. (2013), nodal root angle is significantly associated with root depth in the soil.

The results of the present study suggest that the groupings of root system architecture phenes in maize hybrids exhibit distinct patterns when grown under contrasting water regimes. The lack of significant interaction between hybrid and water regime suggests that the differences reported herein are intrinsic to hybrid variations, regardless of the applied water regime. However, future studies employing more restrictive water availability conditions will be necessary to confirm whether the variable groupings employed herein truly respond to contrasting water regimes.

For the DKB390 hybrid, the presence of steeper nodal root insertion angles demonstrates its ability to explore deeper soil layers in search of mobile resources such as water. The lower root length density of DKB390 in surface layers, when compared to the BRS hybrids, suggests the involvement of unexplored genes, such as those controlling root hair density and length or aerenchyma formation, which could explain its reduced biomass allocation to root system expansion, if identified in future studies.

CONCLUSIONS

1. The increase in water availability with depth results in a lower root length density, regardless of the water regime;

2. The DKB390 hybrid expressed a lower number of coleoptilar nodes with roots, as well as nodal roots with steeper insertion angles, when compared to the BRS1010 and BRS1055 hybrids.

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Pesquisa Agropecuária Tropical

vol. 55, e80906, 2025

Escola de Agronomia/UFG,

ISSN: 1517-6398

ISSN-E: 1983-4063

DOI: <https://doi.org/10.1590/1983-40632025v5580906>