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ORIGINAL PAPER

Root Cortical Aerenchyma in Sorghum Increases its Root Elongation and Volume, Favoring Nutrient Uptake and Gas Exchange Compared to Maize Under Water Limitation

Jean Paulo Vitor de Oliveira[1] · Vinícius Politi Duarte[3] · Evaristo Mauro de Castro[1] · Paulo Cesar Magalhães[2] · Fabricio José Pereira[3]

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Abstract

This work investigated how root anatomical traits, such as aerenchyma development, are related to root growth and volume and nutrient acquisition capacity in maize and sorghum plants under water limitation. Experiments were conducted in a greenhouse in a factorial 2 × 2 scheme (two plant species, maize and sorghum) and two water availabilities (well-irrigated and limited irrigation) with six replicates. Leaf gas exchange, growth, aerenchyma formation, root tissues in both maturation and piliferous regions, and macro and micronutrient uptake were analyzed. Water limitation reduced maize growth with no significant changes in sorghum. Sorghum showed higher photosynthesis and transpiration compared to maize, which exhibited higher water use efficiency; nonetheless, water limitation increased the leaf water content in sorghum but not in maize. Water limitation increased the root length, volume, and aerenchyma development in sorghum plants only. Increased root elongation and volume favored macro (N, Mg, and Ca) and micronutrient (Zn, Cu, Mo, and Fe) acquisition in sorghum compared to maize. Water limitation stimulated the acquisition of B, Mn, Zn, Cu, Mg, and N in both species, but Fe and Mo contents under water limitation increased only in sorghum. Sorghum's root aerenchyma development and volume under water limitation seem related to a higher elongation capacity, favoring nutrient acquisition in this species compared with maize under water limitation.

Keywords Root water relations · Macro and micronutrients · Root volume · Water stress · *Zea Mays* L · *Sorghum Bicolor* (L.) moench

1 Introduction

In recent years, crop production regions have been facing more frequent climate variations affecting the water availability and the occurrence of drought events (Haider et al. 2024). Crop yield can be severely damaged by water limitation, causing significant economic losses (Rezaei et al. 2023). In drought-sensitive plant genotypes, water limitation limits root development, reducing root growth and, consequently, water and nutrient acquisition with negative consequences to plant growth (Díaz et al. 2018; Hemati et al. 2022). For both maize and sorghum plants, limited root growth under water limitation impairs their productivity and resilience (Pereira et al. 2008; Díaz et al. 2018; Oliveira et al. 2023). Lower root growth can restrain water uptake, causing stomatal closure and limiting photosynthesis (Díaz et al. 2018; Hemati et al. 2022; Oliveira et al. 2023). Sorghum shows the capacity to maintain its gas exchange under water limitation, favoring its photosynthesis (Oliveira et al. 2022, 2023), and this requires a stable water uptake capacity from its roots, reducing stomatal closure under water limitation and maintaining its photosynthetic capacity.

Maize and sorghum are two of the most relevant cereal crops worldwide and share traits like C_4 metabolism, Leaf

✉ Fabricio José Pereira
fabricio.pereira@unifal-mg.edu.br

[1] Universidade Federal de Lavras, Campus Universitário, Lavras, MG, Brazil

[2] Embrapa Milho e Sorgo de Sete Lagoas, Sete Lagoas, MG, Brazil

[3] Universidade Federal de Alfenas, Rua Gabriel Monteiro da Silva, 700, Centro, Alfenas, MG, Brazil

Kranz anatomy, and similar root anatomical structure. These species contrast in drought tolerance, with maize considered mostly drought-sensitive (Gong et al. 2015) and sorghum generally referred to as drought-tolerant (Impa et al. 2019). It is important to note that sorghum shows differences compared to maize, in leaf physiological and anatomical modifications to overcome water stress (Oliveira et al. 2023). For instance, the development of larger leaf intercellular spaces, particularly a larger stomatal cavity, improves leaf gas exchange in sorghum compared with maize under drought (Oliveira et al. 2022, 2023). Favorable anatomical and physiological traits to improve drought tolerance are organ-dependent, and root modifications to improve water and nutrient uptake are key features for the tolerance to water limitation in plants (Ilyas et al. 2021; Kim and Lee 2023).

Root modifications that improve drought tolerance comprehend complex changes which include distinctive traits from increased growth to cortical aerenchyma development (Díaz et al. 2018; Ilyas et al. 2021; Yao et al. 2024). Early studies associate root aerenchyma development with waterlogging due to its capacity to provide oxygen by air internal diffusion to flooded roots (Gao et al. 2025); however, the tissue was further recognized as an important drought-tolerance trait (Lenochová et al. 2009; Souza et al. 2016). Root cortical aerenchyma development under water limitation reduces the metabolic cost of roots by lowering the number of cells; this favors root growth and improves water and nutrient uptake (Lynch 2015; Schneider and Lynch 2018). Sorghum is recognized as more drought-tolerant compared to maize, and understanding its capacity to develop root cortical aerenchyma and how it correlates with water and nutrient uptake is important to crop production and breeding programs.

According to Fan et al. (2007), the development of root cortical aerenchyma in roots can reduce their hydraulic conductivity. Nonetheless, aerenchyma formation in roots can increase at the maturation region, where water and nutrient uptake are already reduced, being the development of this tissue limited at the piliferous region (Díaz et al. 2018). In maize plants grown under water limitation, aerenchyma formation increased in the maturation region but showed no significant changes in the piliferous region, and this improved root growth, water, and phosphorus uptake in drought-tolerant maize genotypes (Díaz et al. 2018). Although sorghum is a species known for its drought tolerance, how aerenchyma develops in different root regions and how this can correlate with nutrient uptake is unclear.

Understanding how aerenchyma formation differs among different root regions in maize and sorghum grown under drought and its effects on nutrient uptake in these species can elucidate important traits for crop improvement and drought tolerance. Thus, this work hypothesizes that (1) sorghum shows a higher capacity to develop aerenchyma compared with maize under water limitation, and (2) higher aerenchyma development enhances root growth and nutrient acquisition under water limitation. This work aimed to investigate the aerenchyma development in different regions of maize and sorghum roots and its relation to growth, photosynthesis, and nutrient uptake of these species under water limitation.

2 Materials and Methods

2.1 Plant Material and Experimental Design

The experiment was carried out in a greenhouse located at the Universidade Federal de Lavras, state of Minas Gerais, Brazil. *Sorghum bicolor* (L.) Moench and *Zea mays* (L.) plants were grown from seeds provided by Embrapa's National Research Centre for Maize and Sorghum, located in Sete Lagoas, Minas Gerais, Brazil.

Seeds were sown in 5.0 L plastic pots containing 2.0 L of sand and 800 mL of nutrient solution (Hoagland and Arnon 1950) at 40% of its ionic strength, and the seedlings were obtained according to Oliveira et al. (2023). Pots were placed in a germination chamber under 40 W m^{-2} constant light at 25 °C for 7 days, after which the seedlings had three leaves and were 10 cm in height. Seedlings were subjected to two irrigation conditions: (1) Well Irrigated (WI) and (2) Limited irrigation (LI). The well-irrigated was considered the maximum volume of water retained by 1.0 L of sand without becoming waterlogged. The volume of water applied to achieve WI was 310.0 mL water L^{-1} sand, and for LI was 155.0 mL water L^{-1} sand. For the determination of the water volume necessary to saturate 1 L of sand, this volume of sand was oven-dried at 60 °C for 24 h, and then placed in a funnel, and 500 mL of water was added to the substrate. The funnel was placed above a 500 mL graduated cylinder, which collected the water drained, and the system was maintained for 2 h in the morning, from 7 a.m. to 9 a.m., until completely drained. The volume of water collected by the graduated cylinder was measured, and the water retained by the sand was calculated as the volume added to the substrate (500 mL) minus the water collected (190 mL). The volume for the limited irrigation treatment was determined as half of the volume needed to saturate the system (310 mL). This test was performed in triplicate. The water lost by evapotranspiration was monitored by the daily difference in the weight of each pot. Water was replaced daily, and the nutrient solution was replaced weekly. The experiment was conducted in a 2×2 factorial scheme with two cereal species (sorghum and maize) and two irrigation conditions (well-irrigated and limited irrigation), with four treatments and six replicates. Each replicate comprised one plant. All the data from the analyses where multiple assessments were performed were then averaged per replicate (maintaining $n = 24$ and avoiding artificial replication). The experiment was carried out for 60 days.

2.2 Analysis of Plant Growth

Seedlings were sampled 60 days after the start of the experiment for growth analysis and varied from stages V10 to V14. Root length was measured using a metric ruler. In addition, water content (WC) in the plant and its organs was calculated using the formula: $WC = [(FM - DM)/FM] \times 100$, where FM represents the fresh mass and DM is the dry mass of the plant/organ. After these measurements, the plants were dried at 60 °C until a constant weight was achieved, and the total dry mass was determined using an analytical balance (AY220, Shimadzu, São Paulo, Brazil). The roots and shoot (stems and leaves) dry masses were measured, and the root: shoot ratio was calculated by dividing the root by the shoot dry mass.

2.3 Leaf Relative Water Content

Leaf relative water content (RWC) was measured following the methodology described by Weatherley (1950). Six leaf disk samples, approximately 0.5 cm in diameter, were taken from the median portion of the second fully expanded leaf from the top of the plant. The disks were initially weighed to determine fresh mass (FM) and then placed in Petri dishes immersed in deionized water for 24 h. After this period, they were reweighed to obtain turgid mass (TM) and subsequently dried in paper bags in a forced-air oven at 60 °C until a constant weight was achieved, determining the dry mass (DM). RWC was calculated using the formula: $RWC = [(FM - DM)/(TM - DM)] \times 100$.

2.4 Gas Exchange Analysis

Gas exchange analysis was conducted at the end of the experiment, in the morning between 8:00 and 11:00 a.m., on the first fully expanded leaf from the top of the plant. Measurements were carried out using an infrared gas analyzer (IRGA) LI-6400XT (Li-COR Biosciences, Lincoln, NE, USA), with one leaf per plant sampled. Gas exchange analyses were performed at 30 and 60 days after the start of the experiment, and data were averaged per replicate. In the measurement chamber, photosynthetically active radiation was maintained at 1000 μmol m^{-2} s^{-1} using a 6400-02B LED light source, with a reference CO_2 concentration of 392.3 μmol L^{-1}, a flow rate of 499.48 mol s^{-1}, a leaf temperature of 20.32 °C, and a vapor pressure deficit (VPD) of 0.91 kPa. The net photosynthesis (A) and transpiration (E) were evaluated.

2.5 Water-use Efficiency (WUE)

At the end of the experiment, instantaneous water-use efficiency (WUEi) was calculated following Kramer and Boyer (1995). WUE (μmol CO_2 $mmol^{-1}$ H_2O) was determined as the ratio of photosynthesis (A) to transpiration (E) values obtained from the IRGA analyses.

2.6 Plant Nutrient Analysis

For the evaluation of macro- and micronutrient concentrations, whole plants were separated, washed with running water, and dried in a forced-air oven at 60 °C for 72 h. One plant per replicate was used for this analysis. The dried material was then ground using a Willey-type knife mill, and 500 mg of dry mass was weighed on an analytical balance for nitroperchloric digestion, following the method proposed by Sarruge and Haag (1974). In this process, 10 mL of concentrated HNO_3 was added to the sample, which was left to rest for 12 h. Digestion was then carried out at 150 °C for 30 min or until the nitric acid volume was reduced by half. After this step, 1.0 mL of $HClO_4$ was added, and the digestion block temperature was increased to 210 °C for 20 min or until the solution was clarified. The digestion product was transferred to a 25 mL volumetric flask, to which 10 mL of distilled water was added, and readings were performed using a flame atomic absorption spectrophotometer.

The following macronutrients were analyzed: phosphorus (P), nitrogen (N), calcium (Ca), potassium (K), magnesium (Mg), and sulfur (S). The micronutrients analyzed included zinc (Zn), copper (Cu), manganese (Mn), iron (Fe), molybdenum (Mo), and sodium (Na).

2.7 Anatomical Analysis

At the end of the experiment (60 days), root samples were collected and fixed in 70% FAA (formaldehyde, glacial acetic acid, and 70% ethanol in a 0.5:0.5:9 ratio) for 72 h (Johansen 1940) and then stored in 70% ethanol until analysis. Hand-sectioned transverse root samples were obtained using steel blades and stained with safranin solution (0.1% safranin and 1% Astra blue in a 7:3 ratio). Semi-permanent slides were prepared following the method described by Kraus and Arduin (1997), observed under a CX31 trinocular light microscope (Olympus, Tokyo, Japan) equipped with an image capture system, and digitized for further analysis using the ImageJ software. Sections were obtained from the maturation (10 cm from the root apex) and hair (5 cm from the root apex) zones of maize and sorghum roots. Five slides and three sections were evaluated per replicate, and the data were averaged before analysis.

The following anatomical parameters were evaluated: total root area, cortical region area, cortical aerenchyma proportion (CA%), vascular cylinder area, epidermis thickness, exodermis thickness, endodermis thickness, cortex thickness, and xylem vessel diameter. CA% = (cortical aerenchyma area/cortex area)/*100. Additionally, root volume was calculated using the formula: RV= [(HA + MA)/2]*RL, where RV = root volume; HA = total area of the root hair zone; MA = total area of the maturation zone; RL = root length; for this calculation, all measurements were converted to square millimeters.

2.8 Statistical Analysis

The data were checked for normality using the Shapiro–Wilk test and subjected to analysis of variance (two-way ANOVA), and the means were compared by the Scott–Knott test for $p < 0.05$ using the SISVAR statistical software (Ferreira 2011).

3 Results

There was significant interaction between plant species and irrigation for the root length and plant dry mass, but no significant interaction was found for the root dry mass, root: shoot ratio, and root and leaf water contents (Fig. 1). Water limitation increased the root length by 95% from sorghum only (Fig. 1). Maize showed longer roots at well irrigated condition but under limited irrigation both maize and sorghum showed similar root length (Fig. 1A). Water limitation promoted no significant changes in the root dry mass and maize showed 50% larger root dry mass compared with sorghum at both well-irrigated and limited irrigation treatments (Fig. 1B). Water limitation reduced the total dry mass of maize by 50%; in addition, Maize plants showed twice dry mass as compared to Sorghum at well irrigated treatment but, under limited irrigation, reduced total dry mass of Maize caused this variable to exhibit similar values to sorghum (Fig. 1C). Maize root: shoot ratio 50% greater compared with sorghum and water limitation promoted no significant changes in this variable (Fig. 1D). Sorghum showed root water content 14.28% higher compared to maize but water limitation promoted no significant changes in this parameter (Fig. 1E). Maize showed leaf water content 15.3% higher compared to sorghum but the limited irrigation treatment promoted no significant changes in this variable (Fig. 1F).

No significant interaction between plant species and irrigation was found for photosynthesis, transpiration, and water use efficiency but a significant effect occurred for leaf relative water content (Fig. 2). Sorghum showed photosynthesis 40% higher than maize and water limitation promoted no significant effect in this parameter (Fig. 2A). Transpiration was 73.4% higher in sorghum compared to maize but irrigation promoted no significant effect in this parameter (Fig. 2B). The water use efficiency was 28.6% higher in maize compared to sorghum but water irrigation promoted no significant effect in this parameter (Fig. 2C). Limited irrigation increased the leaf relative water content by 38.46% in sorghum only (Fig. 2D). Maize showed leaf relative water content 46.15% higher than sorghum under well-irrigated conditions but under limited irrigation, both species showed similar means (Fig. 2D).

No significant interaction between plant species and irrigation was observed for the macronutrient content (Fig. 3). The P content was similar in both irrigation treatments and also between maize and sorghum (Fig. 3A). The limited irrigation treatment increased the N content by 27.3% and sorghum showed N content 33.3% higher than maize (Fig. 3B). Sorghum showed Ca content 77.8% larger compared with maize but irrigation treatments did not modify this parameter (Fig. 3C). The K content was similar between maize and sorghum and was not modified by irrigation treatment (Fig. 3D). Limited irrigation increased the Mg content by 20% and this parameter was 31.6% greater in sorghum compared to maize (Fig. 3E). The S content was not modified neither by irrigation treatments nor plant species (Fig. 3F).

Regarding the micronutrients, there was significant interaction for irrigation treatments and plant species only for Fe and Mo contents (Fig. 4). Limited irrigation increased the Zn content by 88.9% and this variable was 1.4 times bigger in sorghum compared to maize (Fig. 4A). The Cu content increased by 150% under limited irrigation and sorghum showed 2.7 times greater Cu content than maize (Fig. 4B). Limited irrigation increased the Mn content by 36.1% but no significant differences were found between sorghum and maize (Fig. 4C). Limited irrigation increased the Fe content by 68% in sorghum but decreased this parameter by 20% in maize (Fig. 4D). Under well-irrigated conditions maize and sorghum showed similar Fe content; however, under limited irrigation sorghum Fe content 75% larger than maize (Fig. 4D). Limited irrigation increased the B content by 47.8% but no significant differences were found between sorghum and maize (Fig. 4E). Limited irrigation increased the Mo content in sorghum by 28.6% but reduced this parameter in maize by 38.6% (Fig. 4F). Sorghum showed higher Mo content than maize in both irrigation treatments, being 61.5% larger in the well-irrigated treatment and 2.6 times bigger than maize under water limitation (Fig. 4F). The Na content was not significantly modified neither by irrigation treatments or plant species (Fig. 4G).

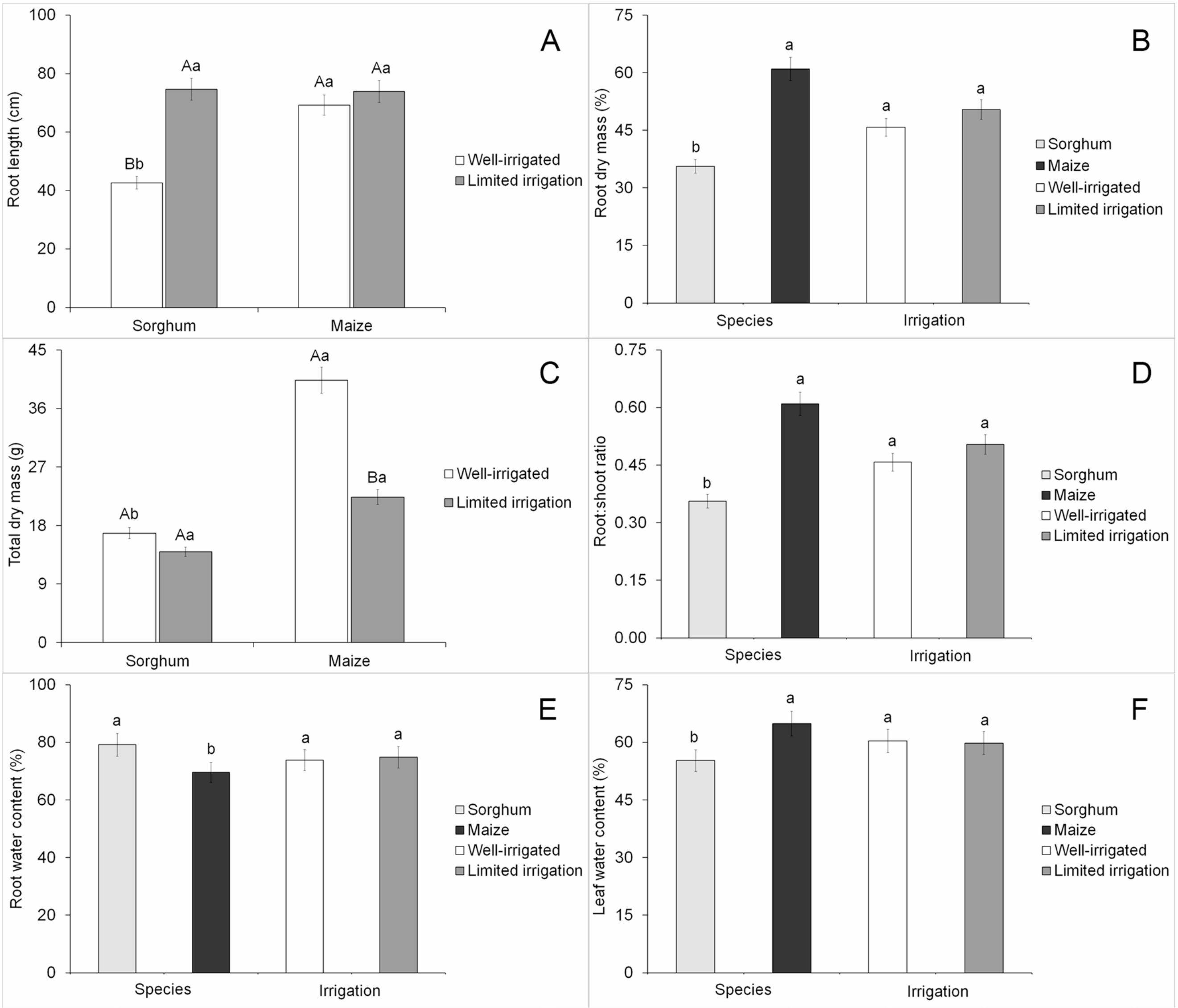

Fig. 1 Growth parameters of *Sorghum bicolor* and *Zea mays* under different irrigation conditions. Interaction between plant species and irrigation was significant ($p < 0.05$) for the root length (**A**) and total dry mass (**C**); however, no significant interaction was observed for root dry mass (**B**), root: shoot ratio (**D**), root water content (**E**), and leaf water content (**F**). The lowercase letters compare plant species, and the uppercase ones compare water conditions for panels A and C, while for panels B, D, E, and F, lowercase letters compare means within each factor. The same letter shows no significant differences according to the Scott-Knott test at $p < 0.05$. Bars = standard errors

There was a significant interaction between irrigation and plant species for aerenchyma proportion and root volume (Table 1). Limited irrigation inhibited aerenchyma formation in maize at both piliferous and maturation regions but promoted no significant effect in sorghum (Table 1; Fig. 5, and Fig. 6). Under well-irrigated conditions maize and sorghum showed similar aerenchyma proportion at both maturation and piliferous regions but under limited irrigation sorghum showed higher aerenchyma proportion than maize (Table 1; Fig. 5, and Fig. 6). Limited irrigation decreased the average root volume from maize by 46.4% but doubled the size of this parameter in sorghum (Table 1; Fig. 5, and Fig. 6). Under well-irrigated conditions maize showed average root volume the double of the size compare with sorghum; however, under limited-irrigation this was inverted and sorghum showed root volume 86.7% larger than maize (Table 1; Fig. 5, and Fig. 6).

There was significant interaction for irrigation and plant species for most anatomical parameters at the root piliferous region, except for epidermis and endodermis thicknesses (Fig. 7). Limited irrigation increased the total root area from sorghum by 66.7% but reduced this parameter in maize by 57.6% (Figs. 5 and 7A). Under well-irrigated conditions maize showed the total root area double the size compared to sorghum, but under limited irrigation this inverted and sorghum showed means double the size of maize (Figs. 5

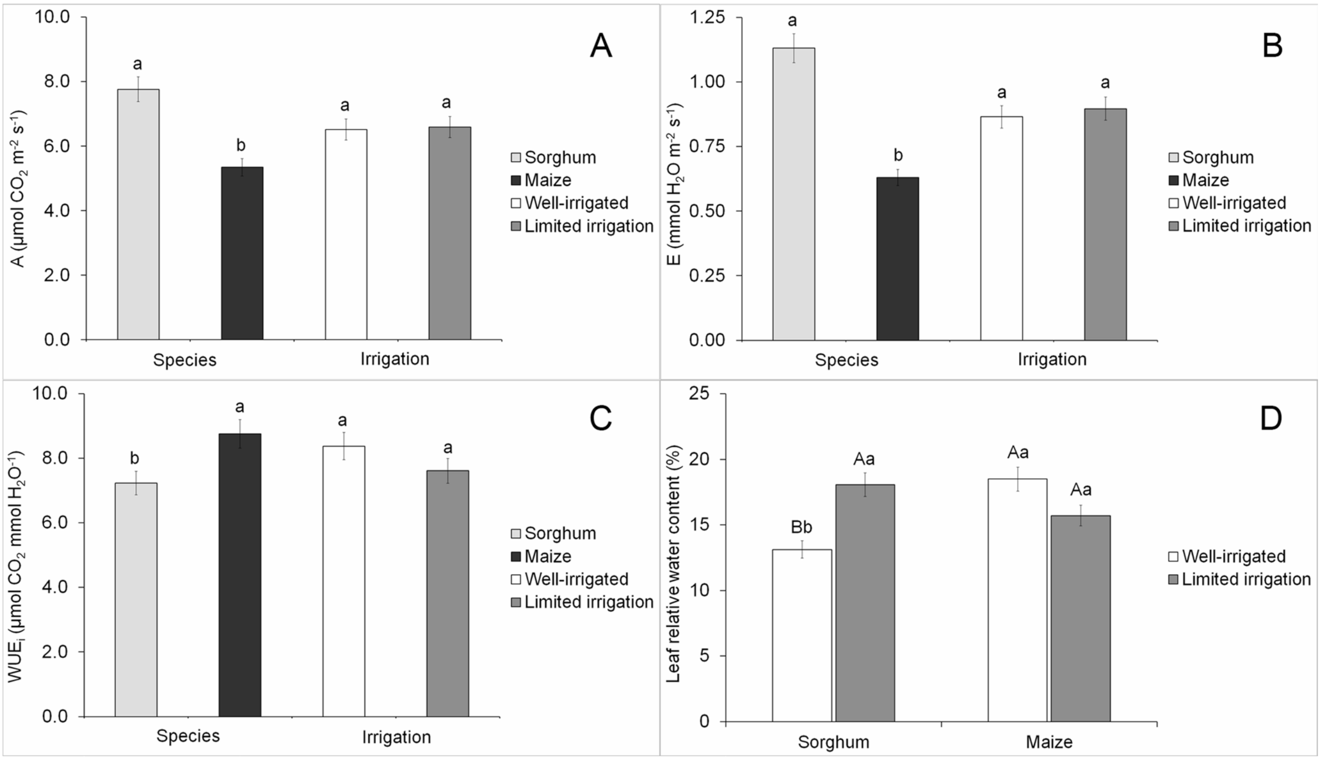

Fig. 2 Leaf gas exchange and leaf relative water content parameters of *Sorghum bicolor* and *Zea mays* under different irrigation conditions. Interaction between plant species and irrigation was significant ($p<0.05$) for the leaf relative water content (**D**); however, no significant interaction was observed for the net photosynthesis (**A**), transpiration (**B**), and water use efficiency (**C**). The lowercase letters compare plant species, and the uppercase ones compare water conditions for panel D, while for panels A, B, and C, lowercase letters compare means within each factor. The same letter shows no significant differences according to the Scott-Knott test at $p<0.05$. Bars = standard errors

and 7A). The area of the vascular cylinder showed similar results, being increased 1.3 times under limited irrigation in sorghum and reduced by 53.3% in maize (Figs. 5 and 7B). The area of the vascular cylinder was double the size in maize compared to sorghum under well-irrigated conditions; however, under limited irrigation, this inverted and this parameter was the twice the size in sorghum compared to maize (Figs. 5 and 7B). Limited irrigation reduced the cortex thickness from maize by 46.7% but caused no significant effect in sorghum (Figs. 5 and 7C). Under well-irrigated conditions maize and sorghum showed similar cortex thickness but under limited irrigation maize showed 40% thinner cortex (Figs. 5 and 7C). Limited irrigation increased the xylem vessel diameter from sorghum by 52.9% but reduced this parameter in maize by 30% (Figs. 5 and 7D). Under well-irrigated conditions, maize and sorghum showed similar xylem vessel diameter but under limited irrigation sorghum showed xylem vessels 60% larger compared with maize (Figs. 5 and 7D).

At the piliferous root region, the epidermis thickness was not significantly modified by irrigation or plant species (Figs. 5 and 7E). Limited irrigation increased the exodermis thickness from sorghum by 42% but reduced this parameter in maize by 32.4% (Figs. 5 and 7F). Under well-irrigated conditions maize showed exodermis twice the thickness compared to sorghum, but at limited irrigation both species showed similar means (Figs. 5 and 7F). The endodermis thickness was not significantly modified neither by irrigation or plant species (Figs. 5 and 7G). Limited irrigation increased the root cortex area from sorghum by 78.6% but reduced this parameter in maize by 63.7% (Figs. 5 and 7H). Under well-irrigated conditions maize showed root cortex area twice the size compared with sorghum but under limited irrigation this inverted and sorghum cortex area doubled the size compared with maize (Figs. 5 and 7H).

At the root maturation region there was not a significant interaction between irrigation and plant species for most parameters, except for the cortex thickness and xylem vessel diameter (Fig. 8). There was no significant effect from irrigation or plant species for the total root area (Figs. 6 and 8A) and vascular cylinder area (Figs. 6 and 8B). Limited irrigation reduced the cortex thickness by 32% only from maize (Figs. 6 and 8C). Under well-irrigated conditions maize and sorghum showed similar means for the root cortex thickness; nonetheless, under limited irrigation maize cortex was 30% thinner than sorghum (Figs. 6 and 8C).

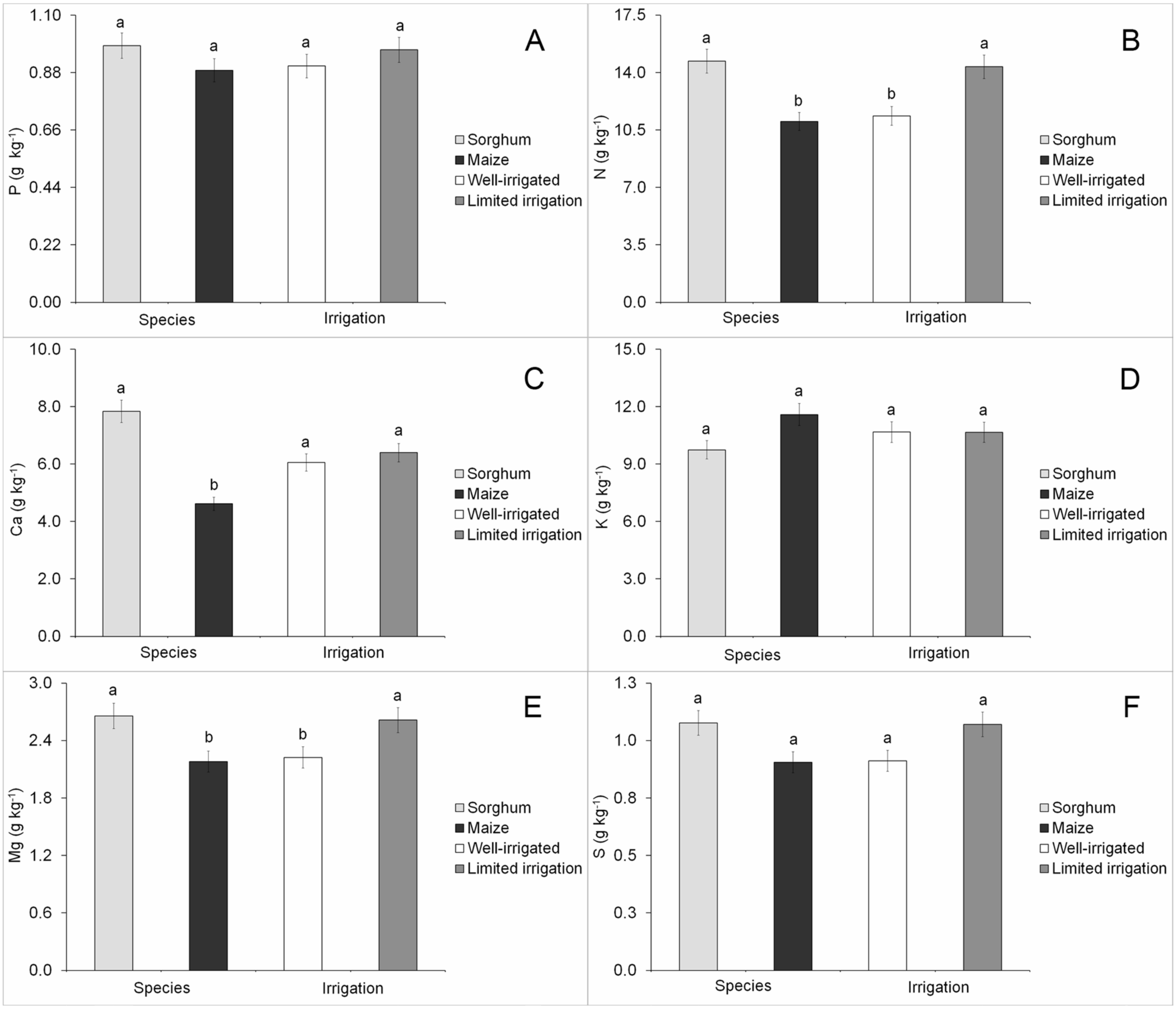

Fig. 3 Macronutrient content of *Sorghum bicolor* and *Zea mays* under different irrigation conditions. Interaction between plant species and irrigation was not significant ($p < 0.05$) for P (**A**), N (**B**), Ca (**C**), K (**D**), Mg (**E**), and S (**F**) contents; lowercase letters compare means within each factor. The same letter shows no significant differences according to the Scott-Knott test at $p < 0.05$. Bars = standard errors

Limited irrigation increased the xylem vessel diameter by 41.6% in sorghum but had no significant effect in maize (Figs. 6 and 8D). Under well-irrigated conditions maize and sorghum showed similar xylem vessel diameter but under limited irrigation, sorghum showed xylem vessels 80% larger (Figs. 6 and 8D). Limited irrigation promoted no significant modification in the epidermis thickness but maize showed epidermis 46.2% thicker compared with sorghum (Figs. 6 and 8E). At the root maturation region neither irrigation nor plant species showed significant modifications in the exodermis thickness (Figs. 6 and 8F), endodermis thickness (Figs. 6 and 8G), and root cortex area (Figs. 6 and 8F).

4 Discussion

Maize and sorghum belong to the same family (Poaceae) among monocotyledons and contrast in drought tolerance (Oliveira et al. 2023). Maize plants are bigger than sorghum (Oliveira et al. 2023) and under well-irrigated conditions, these plants showed larger biomass because of these natural size differences as shown by variables related to plant dry mass (Fig. 1). Nonetheless, maize reduced its total dry mass under limited irrigation while sorghum kept its growth, this is a typical tolerance response from sorghum that is often classified as drought-tolerant species (Gong et al. 2015) and the lower growth of maize corroborate its response as

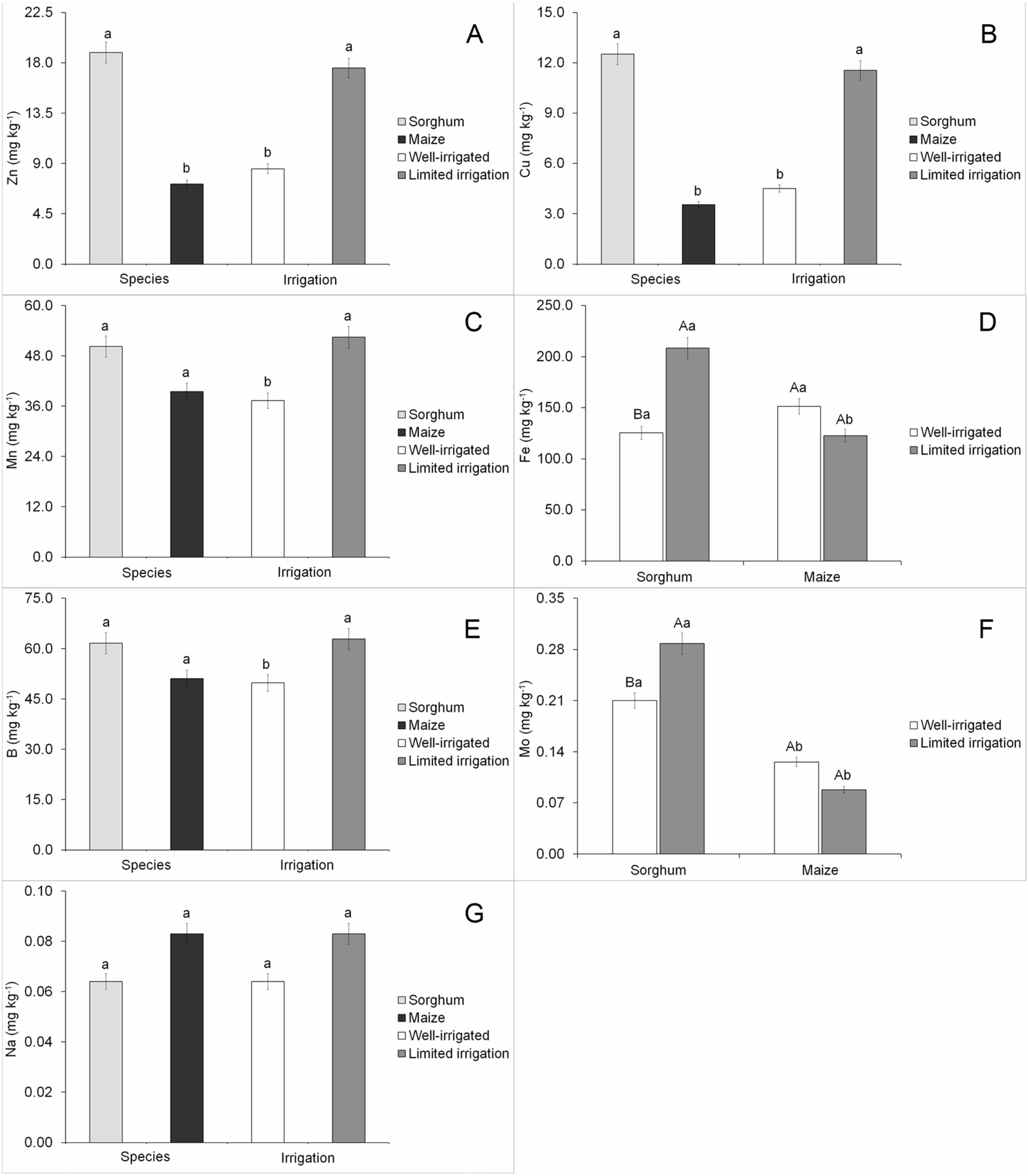

Fig. 4 The micronutrient content of *Sorghum bicolor* and *Zea mays* under different irrigation conditions. Interaction between plant species and irrigation was significant ($p<0.05$) for the Fe (**D**) and Mo (**F**) contents; however, no significant interaction was observed for the Zn (**A**), Cu (**B**), Mn (**C**), B (**E**), and Na (**G**) contents. The lowercase letters compare plant species, and the uppercase ones compare water conditions for panels D and F, while for panels A, B, C, E, and G, lowercase letters compare means within each factor. The same letter shows no significant differences according to the Scott-Knott test at $p<0.05$. Bars = standard errors

Table 1 Cortical root aerenchyma proportion and average root volume of *Sorghum bicolor* and *Zea Mays* under different water conditions. Data is shown as mean ± standard deviation

Aerenchyma (%) from the piliferous region		
	Maize	Sorghum
Well-irrigated	13.58 ± 11.6Aa	18.70 ± 13.3Aa
Limited irrigation	0.00 ± 0.00Bb	19.86 ± 15.27Aa
Aerenchyma (%) from the maturation region		
	Maize	Sorghum
Well-irrigated	27.31 ± 11.74 Aa	32.69 ± 27.2Aa
Limited irrigation	0.00 ± 0.00Bb	39.96 ± 8.48Aa
Average root volume (mm^3)		
	Maize	Sorghum
Well-irrigated	366.49 ± 96.64Aa	179.81 ± 129.56Bb
Limited irrigation	196.33 ± 57.90Bb	366.46 ± 84.78Aa

Interaction was significant ($p < 0.05$) for all variables. The lowercase letters compare plants, and the uppercase ones compare water conditions. The same letter shows no significant differences according to the Scott-Knott test at $p < 0.05$

a drought-sensitive crop (Impa et al. 2019). In addition to stable biomass production under drought, only sorghum plants increased their root length, improving their capacity to acquire water and nutrients compared to maize.

One important variable that contributes to facilitating root growth is aerenchyma formation, which was inhibited in maize under limited irrigation, but sorghum maintained its development. Root cortical aerenchyma formation can be stimulated by flooding (Gao et al. 2025) and drought (Souza et al. 2016), being also constitutive, and always present, in aquatic plants like *Typha domingensis* Pers. (Corrêa et al. 2015; Duarte et al. 2021). Aerenchyma formation reduces the number of cells in the root cortex, reducing its metabolic cost and favoring root growth (Lynch 2015; Schneider and Lynch 2018; Kalra et al. 2024). Thus, the capacity of sorghum plants to maintain the root cortical aerenchyma development under limited irrigation favored their capacity to obtain water and nutrients compared with maize.

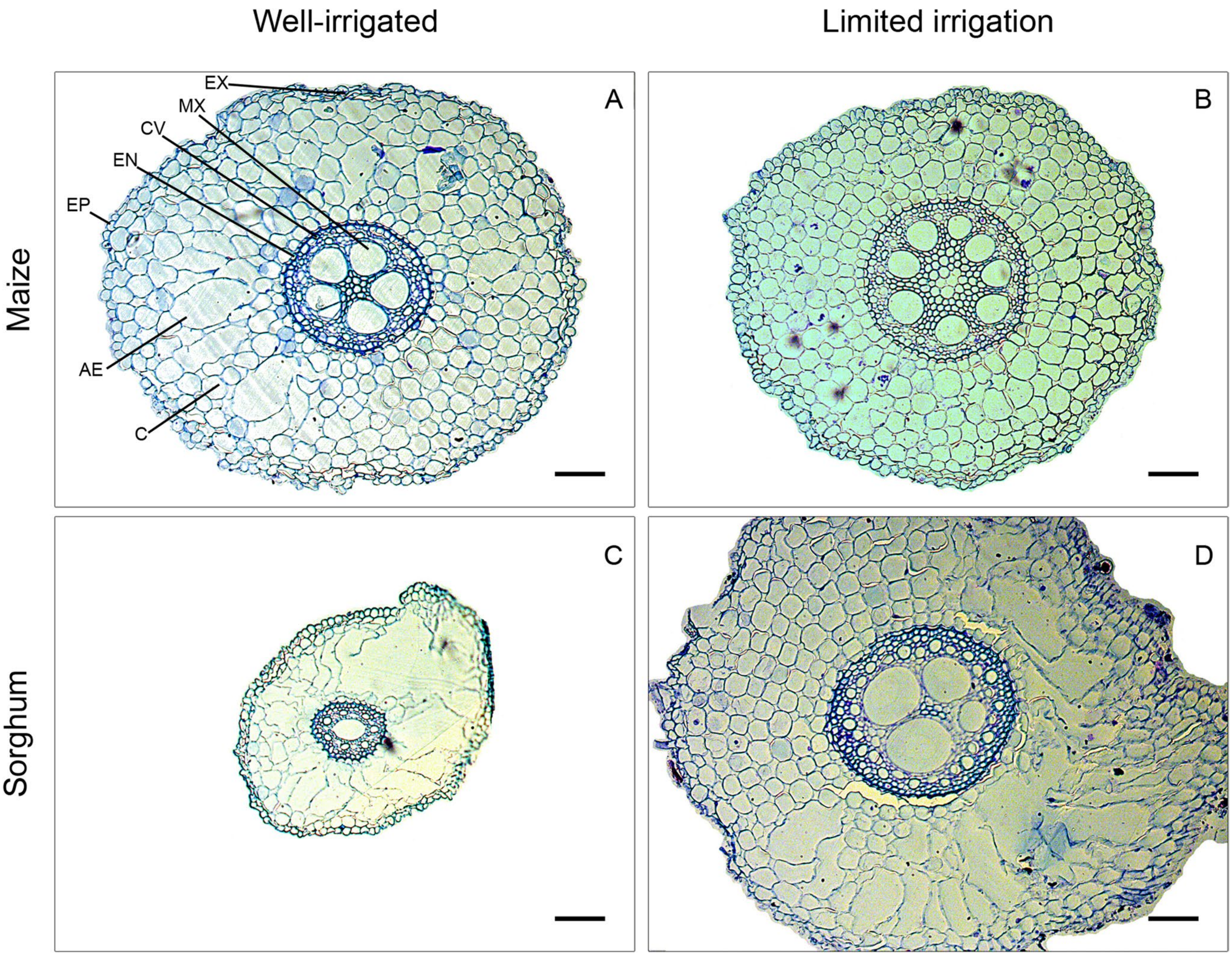

Fig. 5 Transversal sections of *Sorghum bicolor* and *Zea mays* root piliferous under different water conditions. EP = Epidermis cells; EX = Exodermis cells; AE = Cortical aerenchyma; EN = Endodermis cells; CV = Vascular cylinder; C = Córtex; MX = Metaxylem vessel; Bars = 100 µm

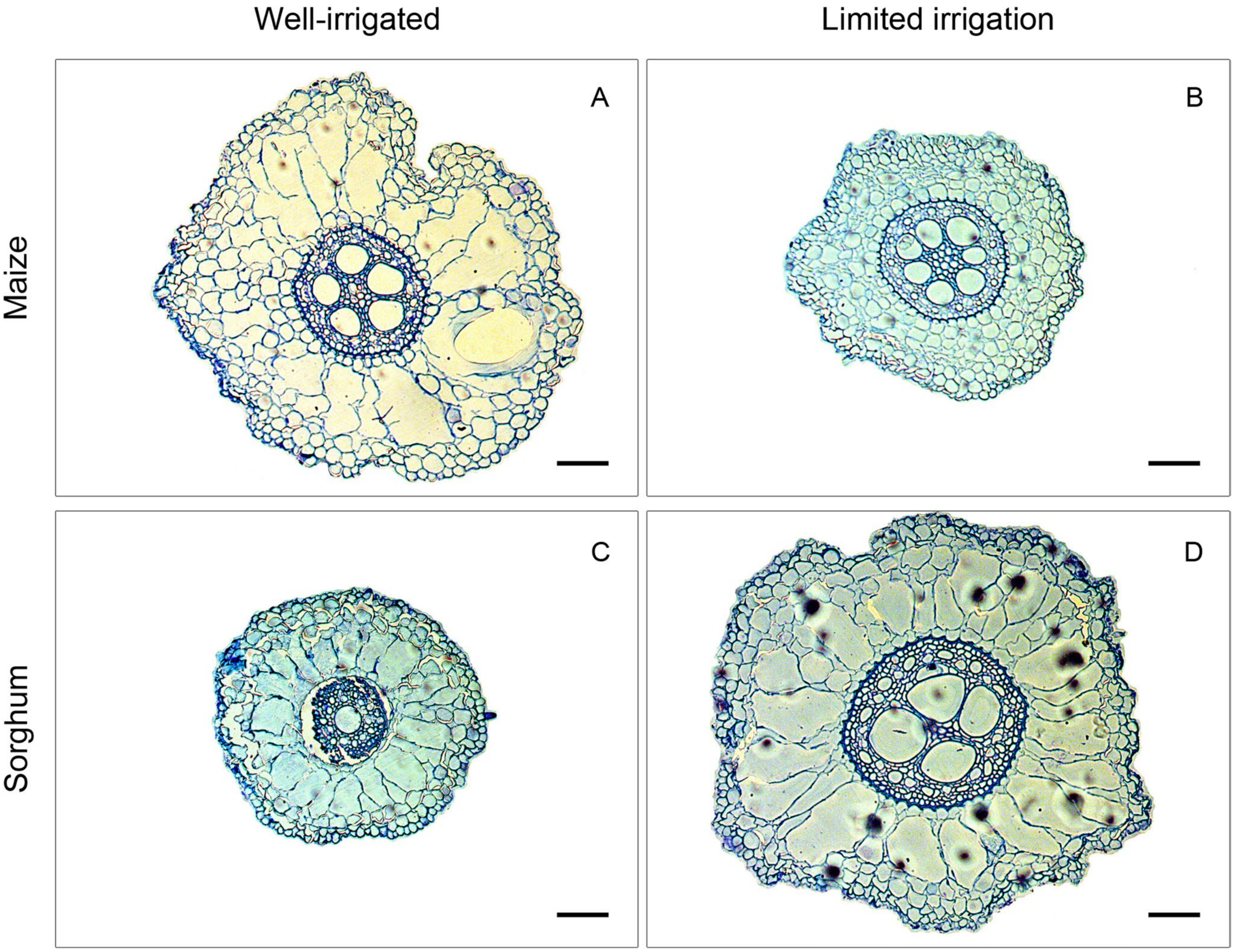

Fig. 6 Transversal sections of *Sorghum bicolor* and *Zea mays* root maturation region under different water conditions. Bars = 100 µm

Aerenchyma formation, despite its benefits for root growth, can be a factor that reduces the root hydraulic conductance, but sorghum roots did not show such a limitation; they improved water and nutrient acquisition under limited irrigation, and sorghum showed improved nutrient uptake compared to maize. According to Fan et al. (2007), increased root cortical aerenchyma influences nutrient uptake. In addition, Díaz et al. (2018) showed that maize roots develop a higher aerenchyma percentage at the maturation region compared to the piliferous region, benefiting from reduced metabolic cost and avoiding a limitation to water and nutrient uptake. The three main water and nutrient uptake pathways present in roots are apoplastic, symplastic, and transcellular (Wang et al. 2023). All these pathways depend on cells for water movement, being through their cell walls (apoplastic) or cytoplasm (symplastic and transcellular). Thus, reduced cell number is expected to reduce water and nutrient uptake, but this did not occur in sorghum, suggesting that roots from this species show some compensation mechanism to avoid such a limitation.

Sorghum roots were longer and showed a larger area compared to maize, and these parameters increased the total root volume, which may be related to a larger external area for trichome formation and water and nutrient uptake compared to maize under limited irrigation. This can be an important mechanism for drought tolerance in sorghum because of increased capacity to uptake water and nutrients under limited water availability, improving the efficiency of root function. Sorghum showed higher root water content, transpiration, and leaf relative water content compared to maize (Fig. 2) and showed higher N, Mg, Ca, Zn, Cu, Mo, and Fe compared to maize. In addition, under limited irrigation, only sorghum increased the Mo and Fe acquisition. These results indicate that sorghum roots showed no limitation for water and nutrient uptake, although with high aerenchyma development, their nutrition and water content seem higher than these parameters in maize. Higher hydration

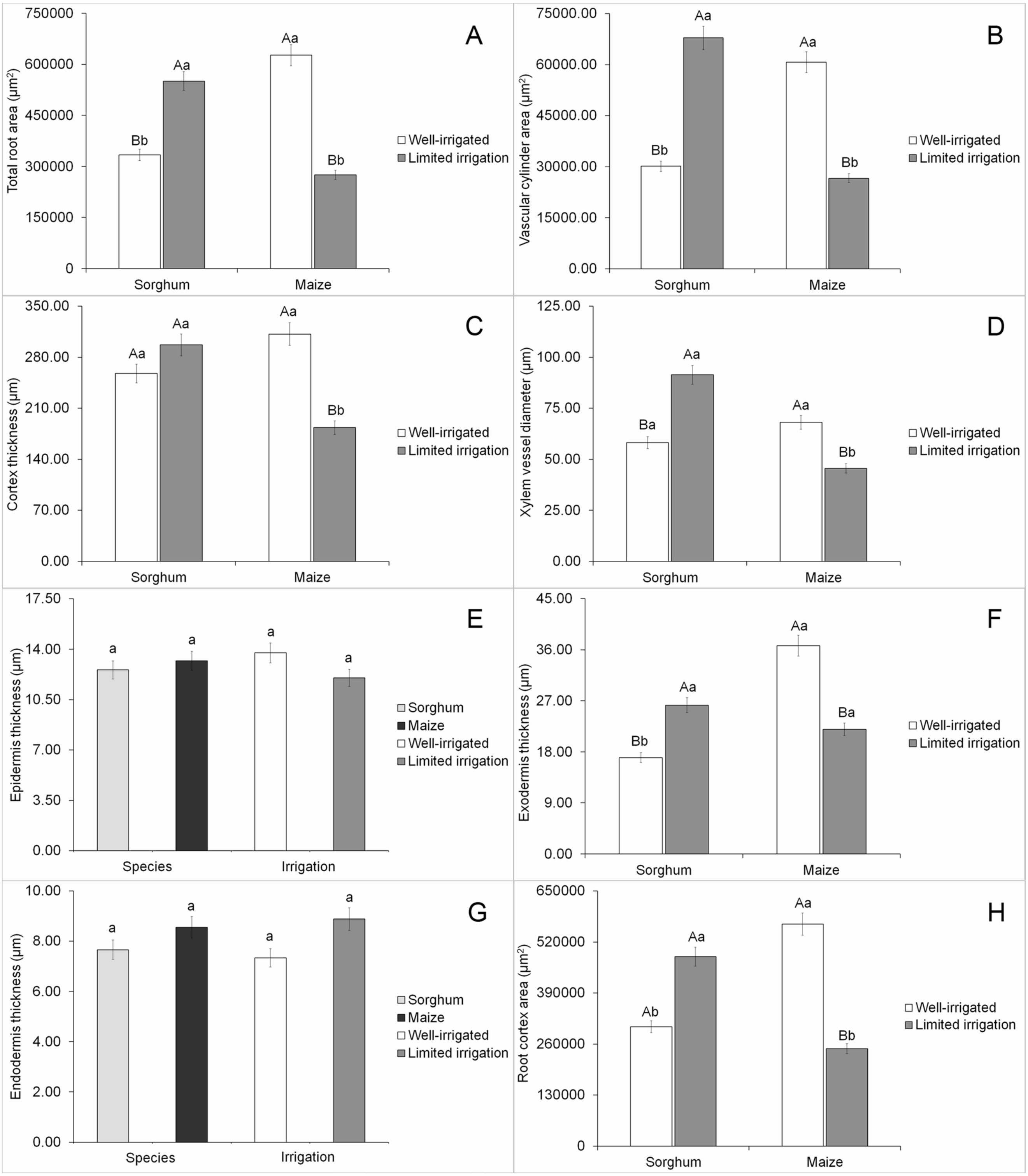

Fig. 7 Root anatomical parameters from the piliferous region of *Sorghum bicolor* and *Zea mays* under different irrigation conditions. Interaction between plant species and irrigation was significant ($p < 0.05$) for the total root area (**A**), vascular cylinder area (**B**), cortex thickness (**C**), xylem vessel diameter (**D**), exodermis thickness (**F**), and root cortex area (**H**); however, no significant interaction was observed for the epidermis thickness (**E**) and endodermis thickness (**G**). The lowercase letters compare plant species, and the uppercase ones compare water conditions for panels A, B, C, D, F, and H, while for panels E and G, lowercase letters compare means within each factor. The same letter shows no significant differences according to the Scott-Knott test at $p < 0.05$. Bars = standard errors

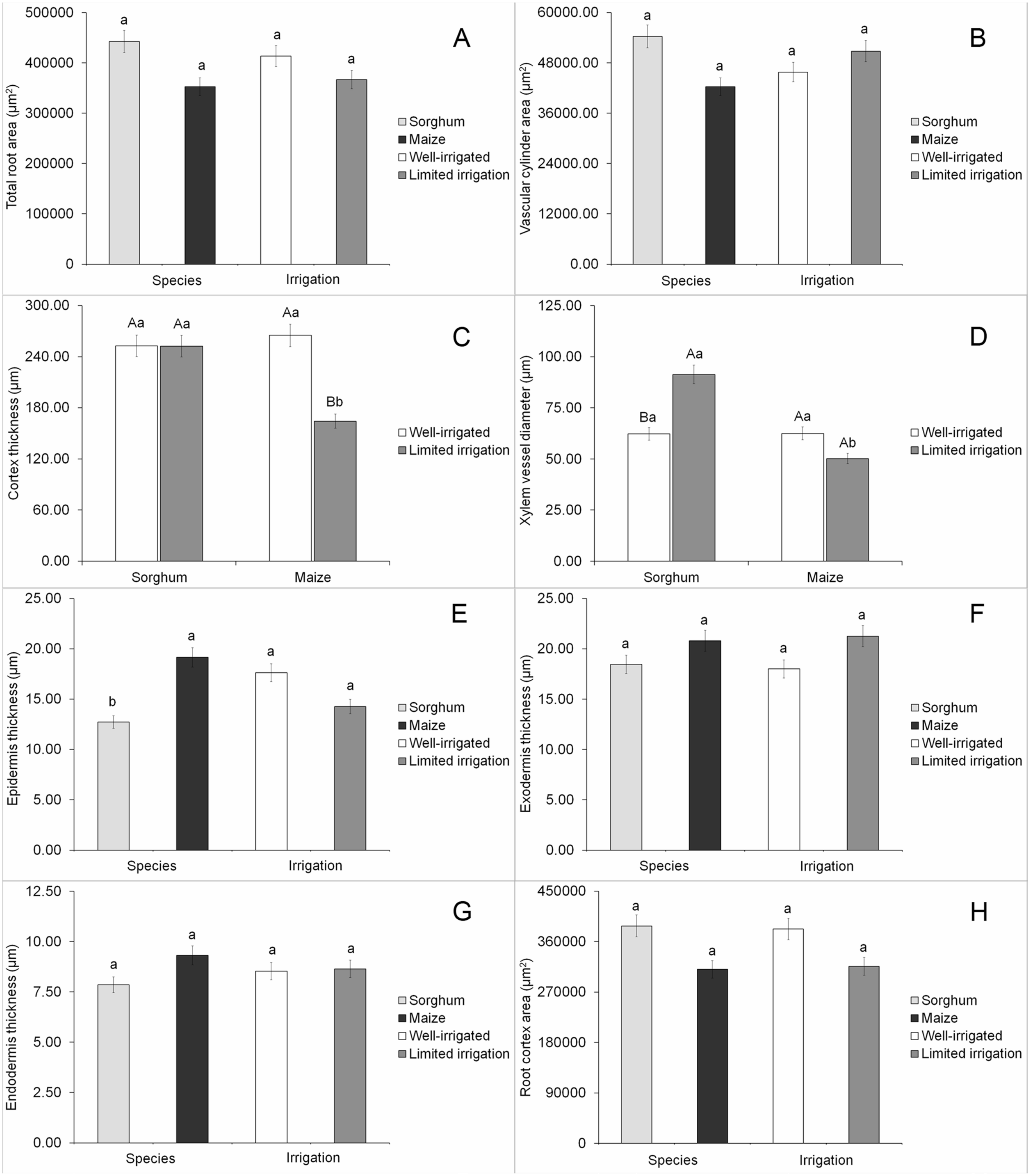

Fig. 8 Root anatomical traits from the maturation region of *Sorghum bicolor* and *Zea mays* under different irrigation conditions. Interaction between plant species and irrigation was significant ($p<0.05$) for the cortex thickness (**C**) and xylem vessel diameter (**D**); however, no significant interaction was observed for the total root area (**A**), vascular cylinder area (**B**), epidermis thickness (**E**), exodermis thickness (**F**), endodermis thickness (**G**), and root cortex area (**H**). The lowercase letters compare plant species, and the uppercase ones compare water conditions for panels C and D, while for panels A, B, E, F, G, and H, lowercase letters compare means within each factor. The same letter shows no significant differences according to the Scott-Knott test at $p<0.05$. Bars = standard errors

and nutrient acquisition favored photosynthesis in sorghum, maintaining its dry mass production, even under drought, unlike maize. Thus, results suggest that higher root volume is a relevant tolerance mechanism in sorghum for limited water availability, and since maize showed smaller roots, it limited its water and nutrient uptake.

The improved nutrient content in sorghum and better Mo and Fe acquisition under limited irrigation are key parameters for its improved photosynthesis and growth under limited irrigation. Sorghum showed higher N, Mg, Ca, Zn, Cu, Mo, and Fe compared to maize. It is important to note that N and Mg are structural elements from chlorophyll molecules, being key nutrients for photosynthesis. In addition, N increases the capacity of plants to uptake water in roots and the water conservation in leaves under arid environments (Kumari et al. 2022; Kalra et al. 2024). Drought tolerance is also often associated with Zn (Yavas and Unay 2016; Kalra et al. 2024). In addition, N is part of several proteins related to the photosynthesis complex (Nelson and Ben-Shem 2004). The particular increase in Fe and Mo under limited irrigation in sorghum deserves attention. Iron is a key micronutrient for photosynthesis, present in the iron-sulfur proteins among the electron transport chain in the Z scheme (Nelson and Ben-Shem 2004). The improved Fe uptake in sorghum under drought may have favored its photosynthesis, maintaining the dry mass production. Mo is also an essential element for photosynthesis and growth because this element is a cofactor to key enzymes in the N metabolism, such as the nitrate reductase (Kaiser et al. 2005). In addition, Mo also catalyzes the sulfite oxidase enzyme, which converts sulfite to sulfate, used in the synthesis of amino acids containing sulfur (Kaiser et al. 2005), present in the iron-sulfur proteins from photosynthesis (Nelson and Ben-Shem 2004). Thus, the improved nutrition of sorghum compared to maize and also the higher Mo and Fe acquisition under limited irrigation suggest an important response in sorghum to maintain photosynthesis under limited irrigation.

Important anatomical traits in sorghum roots related to improved water and nutrient uptake and transport to leaves were found compared to maize. It is important to note that the vascular system, and particularly the xylem vessels, are key parameters to transport water and nutrients from roots to leaves. The vascular system is modified under drought conditions, and it is one of the main traits of drought tolerance (Kalra et al. 2024). The xylem vessel diameter is important for nutrient acquisition and can be reduced under drought in plants sensitive to water stress, limiting nutrient uptake (Cunha Cruz et al. 2020). Limited nutrient availability can increase the xylem vessel diameter (Scarpa et al. 2022), favoring its transport to shoots. Sorghum showed the capacity to increase the vascular cylinder size and also the xylem vessel diameter under limited irrigation, in contrast to maize, which reduced these parameters in both root regions. Thus, results indicate that the capacity to improve the vascular system under limited irrigation is a key feature of sorghum tolerance to lower water availabilities.

One final adjustment that may have improved root anatomy in sorghum under limited irrigation is its capacity to increase the root diameter, maintaining the cortex thickness under such conditions in both maturation and piliferous regions. Larger roots increase their external surface, favoring water and nutrient uptake, but it is also expected to increase the cortex thickness. Sorghum roots increase their diameter and volume under limited irrigation; however, the cortex thickness remains unaltered. This is only possible because the cortical area geometry is trapezoidal (Pereira et al. 2008). According to Pereira et al. (2008), the cortical area from maize increased in flooding-tolerant maize genotypes while its thickness reduced and claimed that this was possible because the cortex area can be interpreted as this equation: $CA=CT(CIP+CEP)/2$, where CA is the cortex area, CT is the cortex thickness, CIP is the cortex internal perimeter and CEP is the cortex external perimeter. This is similar to the trapezoid area in geometry; it is possible to increase the area when the sum of the cortex perimeters increases, even if its thickness is reduced (Pereira et al. 2008). Results from sorghum under limited irrigation corroborate this model, increasing the total area of the root and maintaining the cortex thickness. This is important to keep the hydraulic conductivity of the root because increased cortex thickness may reduce water and nutrient uptake. This is why many species reduce their cortex thickness under drought, a response found in maize (Figs. 7 and 8). It is also important to note that the cortex is important for aerenchyma formation (Pereira et al. 2008), and by reducing its thickness, aerenchyma development can be compromised, as results also found for maize (Table 1). Drought-tolerant species like sorghum maintain their root circumference under drought (Yang et al. 2024). Thus, sorghum roots seem capable of increasing their size while keeping their conductivity by not modifying the cortex thickness.

Results from this study suggest that maize breeding programs focusing on root aerenchyma development under drought can improve this crop's productivity. Aerenchyma formation in maize breeding programs was important for waterlogging tolerance, as shown by Pereira et al. (2008), but similar investment for drought tolerance is limited. In addition, it is important in future works to test the productivity of maize and sorghum genotypes with higher root aerenchyma formation in field experiments.

5 Conclusion

Sorghum shows a higher capacity to develop aerenchyma compared to maize, and this leads to greater photosynthetic and growth capacity of sorghum compared to maize under limited irrigation. The higher aerenchyma development in sorghum improves root growth, favoring water and nutrient acquisition. Sorghum shows a higher capacity to uptake N, Mg, Ca, Zn, Cu, Mo, and Fe contents compared to maize, and increases Fe and Mo acquisition under limited irrigation. Sorghum shows higher vascular cylinder area and xylem vessel diameter than maize under limited irrigation, which may favor water and nutrient transport to shoots.

Authors' Contributions Each author contributed significantly to the final version of the work. **Jean Paulo Vitor de Oliveira** conducted most of the experiments, data sampling, analysis, and writing of the first draft of the work. **Vinícius Politi Duarte** contributed to the experiment handling, data sampling, and anatomical analysis. **Evaristo Mauro de Castro** contributed to anatomical analysis and critical review. **Paulo César Magalhães** contributed a critical review. **Fabricio José Pereira** was the adviser of the first author, conducted the experimental design, handled the experiments, sampling, analysis, and the writing of the final version of the work.

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Data Availability The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Ethics approval Not applicable.

Consent to Participate Not applicable.

Consent for Publication Not applicable.

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