Leaf anatomy of maize inoculated with plant growth-promoting bacteria under different water conditions

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Abstract

Adopting plant growth-promoting bacteria configures a new technology with sustainable potential for maize production. Maize anatomy with this type of interaction is used as a tool to understand the structural mechanisms of plants, especially when planted under water stress conditions. This study sought to evaluate the leaf anatomy of maize plants inoculated with plant growth-promoting bacteria under different water stress conditions. Experiments were conducted in randomized blocks using a factorial scheme of five (inoculation with *A. brasilense*, inoculation with *B. aryabhattai*, combination of *A. brasilense* + *B. aryabhattai*, positive control and negative control) x three irrigation levels (water depths of 25 %, 50 % and 75 % of field capacity), totaling 15 treatments. Evaluations were carried out after the plants reached the V 6 stage of development. Leaf sections were performed to measure epidermis thickness and leaf mesophyll, and to quantify and measure the thickness of stomatal structures. Significant differences in the thickness of the upper and lower epidermis, in the mesophyll, and in the stomatal characteristics according to treatments were found. While *A. brasilense* promoted greater thickness of the upper epidermis under low water availability, *B. aryabhattai* had a greater effect on the lower epidermis at 75 % irrigation level of the field capacity. Number and stomatal diameters also varied according to treatment. Overall, plant growth-promoting bacteria influence the leaf anatomy of maize plants under different irrigation levels, evincing their potential in developing plants under water stress.

Keywords: Bioinputs. Water availability. Anatomical sections. *Zea mays.*

Introduction

Maize (*Zea mays* L.) constitutes one of the most economically significant agricultural crops in Brazil, cultivated in all regions and widely used in human and animal food and in the agribusiness sector. In recent years, maize production has faced challenges related to the need for sustainable systems capable of reducing environmental impact while maintaining high productivity levels. Notable among the most limiting and important environmental factors for crop performance is water availability, considered one of the main factors in maize crop productivity reduction (Bergamaschi *et al.*, 2006; Taiz *et al.*, 2017; Zarei, 2022).

Besides water stress, the high nutritional requirements of maize—especially nitrogen—intensify its dependence on chemical fertilizers, a practice that drives up costs and heightens environmental concerns (Coelho, 2006; Cantarella *et al.*, 2022). Strategies based on bioinputs have garnered attention in this context, since plant growth-promoting microorganisms can favor plant development, improve nutrient use efficiency, and mitigate negative effects of environmental stress. *Azospirillum brasilense* and *Bacillus aryabhattai* stand out among these microorganisms for their potential to act on biological nitrogen fixation, phytohormone production, nutrient solubilization, and increased tolerance to water deficit (Lee, Ka, Song, 2012; Mariano, 2022).

Leaf anatomy analysis represents a relevant tool to understand the responses of plants to environmental conditions and bioinputs application. Structural changes in the epidermis,

mesophyll, and stomata reflect physiological adjustments related to photosynthesis, transpiration, and gas exchange, and are often used to assess adaptations to water stress (Jha, Bohra, 2019; Beebe, Souza, Lopez, 2022; Perosini, 2025).

According to Nascimento *et al.* (2006), Pinheiro and Chaves (2011), and Baliza *et al.* (2012), significant changes in leaf anatomy can occur due to factors such as radiation, temperature, nutrients and water availability. Additionally, plant growth-promoting microorganisms can influence these characteristics, resulting in structural changes that favor the physiological performance of plants under stress conditions (Jesus *et al.*, 2022).

Given this scenario, the effects resulting from inoculating *A. brasilense* and *B. aryabhattai* into maize plants may modify their anatomy; hence, understanding the structural mechanisms associated with water tolerance and plant growth promotion becomes relevant. Thus, this study sought to evaluate the leaf anatomy of maize plants inoculated with plant growth-promoting bacteria under different water stress conditions.

Material and methods

Experiments were conducted in a standard arch-type greenhouse with plastic covering and shade cloth on the sides (50 % shading), at temperatures ranging from 16 to 29 ± 1°C and 70 % relative humidity, at Professor Edson Antônio Velano University (UNIFENAS) in Alfenas, Minas Gerais, Brazil (21°30'26" S, 45°54'51" W, and an elevation of 845 m), which has a mesothermal tropical climate.

Experiment design used plastic pots with a 8 dm^3 capacity filled with sieved soil consisting predominantly of red latosol, composed of ravine soil collected from a depth of 10–20 cm Soil chemical analysis yielded the following results: pH (5.3); organic matter content (5 g dm^{-3}); phosphorus (1 mg dm^{-3}) and potassium (14 mg dm^{-3}). Exchangeable calcium and magnesium exhibited values of 1.2 and 0.6 cmolc dm^{-3}, respectively. No exchangeable aluminum was detected. Potential acidity (H+Al) was 1.9 cmolc dm^{-3}, resulting in a base sum of 1.8 cmolc dm^{-3} and total cation exchange capacity of 3.7 cmolc dm^{-3}, with base saturation of 49 %. Residual phosphorus (P-rem) concentration was 5 mg L^{-1}.

Dolomitic limestone with an 85 % PRNT was used to adjust the pH, raising soil V% to 70 %, resulting in an application rate of 2 t ha^{-1}. Corrective phosphorus fertilization was performed using the base saturation method, considering the specific needs of the crop in question. As phosphorus (P) source, the experiment used SS super-simple mineral fertilizer (18 % P_2O_5) at a rate of 1,800 kg ha^{-1}, as recommended for this crop (Coelho, 2006), incorporated into the soil at a rate of 25.3 g pot^{-1}. After the pots were placed in the greenhouse, 1.7 liters of water were added to each pot for limestone activation. All pots remained in the greenhouse for 40 days, with 200 mL of water applied daily.

Experimental design used randomized blocks, in a factorial scheme of five (inoculation with *A. brasilense*, inoculation with *B. aryabhattai*, combination of *A. brasilense* + *B. aryabhattai*, positive control and negative control) x three irrigation levels (water depths of 25 %, 50 % and 75 % of field capacity), totaling 15 treatments with four replications and three plants per pot. Negative control consisted of growing maize without inoculation and no addition of mineral nitrogen. Positive control adopted topdressing fertilization, applied as per crop recommendations (Cantarella *et al.*, 2022) without inoculant.

Subsequently, the inoculants were prepared at the UNIFENAS Soil Microbiology Laboratory. Strains were cultured in Petri dishes containing culture medium 79 for *A. brasilense* (AbV5) from the Embrapa Soja collection and nutrient agar for

B. aryabhattai (CMAA1363), for 48 hours. The colonies were then transferred to the corresponding liquid culture media and cultured for the same period – long enough to reach the log phase – with a concentration of approximately 10^8 cells/mL. Concentration was estimated by counting the cells in the culture medium, expressed in colony-forming units per milliliter (CFU). For inoculation, the seeds were homogenized and completely coated in Petri dishes, following the recommendations for commercial products that use the bacterial strains employed here, at a rate of 4 mL kg^{-1} of seed.

After inoculating the maize seeds (*Zea mays* L.), they were manually sown at a rate of six seeds per pot. Fifteen days after planting, the seedlings were thinned, leaving three plants per pot. When the plants reached phenological stage V 4, topdressing was applied as per crop recommendations, using mineral nitrogen in the form of urea (227.27 kg ha^{-1}) and potassium chloride (51.72 kg ha^{-1}).

Before sowing, the soil in the pots was saturated with water to raise the moisture content to maximum field capacity. Immediately afterward, the pots were weighed to determine the initial mass (Mi) at full field capacity. Irrigation was performed every two days, when the pots were weighed to determine the daily mass (M_d). The subtracted value ($M_i - M_d$) was multiplied by the crop coefficient used (0.6) to then calculate the fraction of water to be replenished according to the requirement established for each treatment (25, 50, and 75 %) (Bonfim-Silva *et al.*, 2011; Passos, 2024).

$$V = (M_i - M_d) * K_c$$

In which: V = volume to be replaced (mL); M_i = initial mass of full field capacity (kg); M_d = daily mass (kg); K_c = crop coefficient.

When the plants reached phenological stage V 6, the leaves were cut flush with the sheath and preserved in 70 % alcohol at the UNIFENAS Plant Biotechnology Laboratory. Leaf sections were cut freehand.

All cross-sections were clarified with 5 % sodium hypochlorite for 10 minutes, rehydrated for 10 minutes, stained with astrablau (a solution of safranin and astra blue in a 7.5:2.5 ratio), and mounted on slides with 50 % glycerin. The paraderms were also clarified with 5 % sodium hypochlorite for 10 minutes, rehydrated for 10 minutes, stained with 2 % safranin, and mounted on slides with 50 % glycerin (Kraus, Arduim, 1997).

Tissue thickness measurements were taken in the middle third using a micrometer eyepiece. Parameters measured in the cross-sections consisted of adaxial epidermis, leaf mesophyll, and abaxial epidermis. Parameters measured in the paradermal sections on the abaxial surface covered polar and equatorial stomatal diameters. Stomatal density was determined by counting the number of stomata and then adjusted for the correction factor. Photomicrographs were taken using an OLYMPUS BX-60 photomicroscope.

Results obtained from the measurements and counts were subjected to analysis of variance using the SISVAR 5.3 statistical software program (Ferreira, 2019). Plant growth-promoting bacteria effects and the different treatment conditions were evaluated by F-test; when significant, the means were grouped using the Scott-Knott test ($P < 0.05$).

Results and discussion

All treatments and different irrigation levels exhibited significant interaction for all characteristics evaluated in the vertical sections: thickness of the upper and lower epidermis, mesophyll, and total thickness (Table 1).

Plants treated with *Azospirillum brasilense* inoculation in combination with 25 % of field capacity developed a thicker upper epidermis

Table 1. Upper epidermis thickness (UET), lower epidermis thickness (LET), mesophyll thickness (MT) and total thickness (TT) of maize plants inoculated with plant growth-promoting bacteria under different irrigation levels.

Treatment	Irrigation levels (%)		
	25	50	75
		---UET (μm)----	
A. brasilense	25,00 Aa	11,00 Bb	10,66 Ab
B. aryabhattai	16,66 Ba	15,00 Aa	12,66 Ab
A. brasilense + *B. aryabhattai*	11,66 Ca	13,00 Aa	10,00 Aa
Positive control	13,50 Ca	11,50 Ab	10,00 Aa
Negative Control	12,50 Ca	9,00 Bb	11,50 Aa
		---LET (μm)----	
A. brasilense	15,50 Aa	10,50 Ab	10,50 Cb
B. aryabhattai	16,50 Ab	13,50 Ab	34,50 Aa
A. brasilense + *B. aryabhattai*	12,66 Ab	9,50 Ab	17,50 Ba
Positive control	13,00 Ab	13,00 Ab	18,50 Ba
Negative Control	11,33 Aa	11,33 Aa	15,00 Ba
		---MT (μm)----	
A. brasilense	420,00 Cc	600,00 Ab	720,00 Ba
B. aryabhattai	536,66 Ba	533,33 Ba	413,33 Cb
A. brasilense + *B. aryabhattai*	616,66 Ab	355,00 Dc	810,00 Aa
Positive control	373,33 Ca	450,00 Ca	395,00 Ca
Negative Control	383,33 Ca	420,00 Ca	360,00 Ca
		----TT (μm)---	
A. brasilense	460,50 Cc	621,50 Ab	741,16 Ba
B. aryabhattai	569,83 Ba	561,83 Aa	460,50 Cb
A. brasilense + *B. aryabhattai*	641,00 Ab	377,50 Cc	837,50 Aa
Positive control	399,83 Ca	474,50 Ba	423,50 Ca
Negative Control	407,16 Ca	440,33 Ba	386,50 Ca

Identical letters – uppercase in the column and lowercase in the row – do not differ from one another as per Scott-Knott test at 5 % level within each analyzed variable. Significant effect when $P < 0.05$ by F-test. *A. brasilense* = *Azospirillum brasilense*; *B. aryabhattai* = *Bacillus aryabhattai.*

Source: authors (2025).

(UET) compared with the other irrigation levels. Plants inoculated with *Bacillus aryabhattai* at 25 and 50 % field capacity yielded the greatest results in these conditions. Greater UET was observed in plants grown in the positive control and negative control treatments at 25 and 75 % field capacity, respectively. At 50 % field capacity, plants inoculated with *B. aryabhattai, A. brasilense* + *B. aryabhattai* and the positive control obtained greater UET.

Plants inoculated with *B. aryabhattai* and grown in pots at 75 % field capacity showed greater lower epidermis thickness (LET) compared with plants in the other treatments. Plants inoculated with *B. aryabhattai*, *A. brasilense* + *B. aryabhattai* and the positive control grown at 75 % field capacity achieved higher LET compared with the other irrigation levels (Table 1).

Plants inoculated with *A. brasilense* and *A. brasilense* + *B. aryabhattai* grown at 75 % field

capacity yielded higher mesophyll thickness (MT) values. Plants grown at 50 % field capacity and inoculated with *A. brasilense*, as well as plants inoculated with *A. brasilense* + *B. aryabhattai* grown at 25 % field capacity, achieved the highest MT in this combination. Plants grown in these treatments exhibited higher MT compared with plants cultivated in the control treatment (Table 1).

Total thickness (TT) results were very similar to MT values. MT was the main contributing factor to the plants' TT, notably for the *A. brasilense* + *B. aryabhattai* at 25 or 75 % field capacity treatment (Table 1).

Epidermis thickness analysis revealed that plants grown at 25 % field capacity and inoculated with *A. brasilense* achieved the greatest thickness, suggesting that this bacterium contributes to structural mechanisms of water stress tolerance. Similar result was reported by Batisttus (2019), who highlights its effect on leaf characteristics, including an increase in leaf blade thickness. The thickening of the epidermis acts as a physical barrier against water loss, reducing the rate of perspiration and increasing resistance (Perosini, 2025). For plants with greater total thickness at 25 or 75 % field capacity in combination with *A. brasilense* + *B. aryabhattai*, the bacteria may have promoted structural changes under conditions of both higher water availability (75 %) and lower water availability (25 %). However, greater soil water availability resulted in greater total leaf thickness (TT) compared with plants grown in an environment with lower water availability (25 %).

Regarding leaf mesophyll thickness, the greatest thickness was achieved by *A. brasilense* + *B. aryabhattai* under 75 or 25 % field capacity, indicating stimulation of photosynthetic tissue development and reflecting a potential synergistic effect between the two bacteria. The leaf mesophyll compaction observed at the other irrigation levels in this treatment may be associated with greater leaf resistance under water-stress conditions, which may help reduce plant dehydration (Beebe, Souza, Lopez, 2022; Perosini, 2025).

These results corroborate those found by Jesus *et al.* (2022), who observed – in native Caatinga plants inoculated with rhizobacteria – significant thickening of leaf tissues, including the mesophyll, epidermis, and palisade and spongy parenchyma. According to the authors, these responses were associated with the influence of microorganisms on physiological mechanisms related to water deficit tolerance, which reinforces the relation between microbial inoculation and beneficial structural changes – a phenomenon observed in plants grown under the *A. brasilense* + *B. aryabhatta*i treatment at 25 % field capacity (Table 1).

All treatments and different irrigation levels exhibited significant interaction for all characteristics evaluated in the paradermal sections: number and diameters of stomata (Table 2).

Regarding the number of stomata (NS), plants inoculated with *Azospirillum brasilense* at 50 % field capacity developed greater stomatal density compared with plants grown in the negative control. Plants grown under negative control at 25 % field capacity exhibited higher NS compared with inoculated plants. Plants grown in pots with 75 % field capacity and positive control treatment achieved higher NS compared with inoculated plants (Table 2).

This finding may indicate an adaptive response by plants to severe water stress, in which the number of stomata increases in an attempt to optimize CO_2 uptake, although this does not always result in greater physiological efficiency. On the other hand, as expected, the essential nutrient nitrogen plays an important role in plant growth and resulted in higher NS compared with plants grown under the other

Table 2. Number of stomata (NS), polar stomatal diameter (PD), and equatorial stomatal diameter (ED) of maize plants inoculated with plant-growth-promoting bacteria under different irrigation levels.

Treatment	Irrigation levels (%)		
	25	50	75
		-----NS-----	
A. brasilense	148,00 Bb	251,60 Aa	155,40 Cb
B. aryabhattai	143,06 Bb	207,16 Ba	214,60 Ba
A. brasilense + *B. aryabhattai*	155,40 Ba	170,20 Ca	155,40 Ca
Positive control	162,80 Bc	229,40 Ab	333,00 Aa
Negative Control	199,80 Aa	148,00 Cb	139,26 Cb
		-----PD (μm)---	
A. brasilense	37,38 Aa	31,69 Aa	35,35 Ba
B. aryabhattai	39,82 Aa	31,69 Aa	34,13 Ba
A. brasilense + *B. aryabhattai*	35,75 Ab	41,45 Ab	53,64 Aa
Positive control	39,01 Aa	31,41 Aa	31,69 Ba
Negative Control	36,57 Ab	31,69 Ab	45,10 Aa
		-----ED (μm)---	
A. brasilense	7,31 Bb	9,75 Aa	7,31 Bb
B. aryabhattai	7,31 Bb	9,75 Aa	8,12 Bb
A. brasilense + *B. aryabhattai*	8,53 Aa	8,93 Aa	8,12 Ba
Positive control	9,75 Aa	8,93 Aa	10,97 Aa
Negative Control	8,53 Aa	8,12 Aa	8,93 Ba

Identical letters – uppercase in the column and lowercase in the row – do not differ from one another as per Scott-Knott test at 5 % level within each analyzed variable. Significant effect when $P < 0.05$ by F-test. *A. brasilense* = *Azospirillum brasilense*; *B. aryabhattai* = *Bacillus aryabhattai.*

Source: authors (2025).

treatments; this higher NS may be related to higher CO_2 uptake rates (Nasab *et al.*, 2014; Bruns, 2016; Oner, 2024).

Greater polar diameter (PD) values were observed in the stomata of plants inoculated with *A. brasilense* + *B. aryabhattai* and those grown in the negative control treatment at 75 % field capacity compared with plants grown at the other irrigation levels (Table 2).

Overall, the greater the difference between the polar diameter (PD) and the equatorial diameter (ED), the more functional the stomata will be since their shape becomes more elliptical (Khan *et al.*, 2003). Plants grown at a 25 % field capacity environment developed a more elliptical stomata when inoculated with *A. brasilense* or *B. aryabhattai*. Similarly, this more elliptical shape was observed in plants inoculated with *A. brasilense* + *B. aryabhattai* grown at 50 or 75 % field capacity (Table 2).

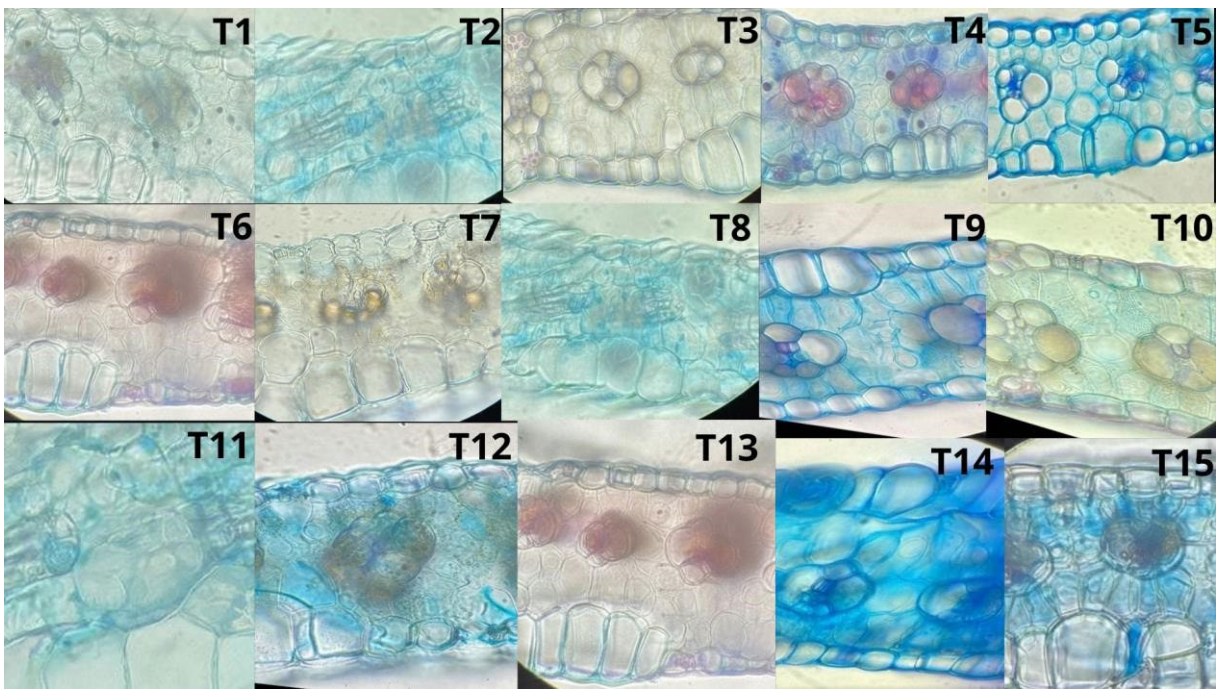
Nutrient availability is associated with stomatal differentiation and development, as noted by Gama *et al.* (2017), who report an increase in the number and diameter of stomata in response to NPK fertilization, emphasizing that mineral nutrition plays a decisive role in this characteristic, which was also observed in plants grown under treatments at 25 % and 50 % field capacity Plants grown in the negative control at 75 % field capacity also exhibited elliptical stomata, which may be related to greater turgidity of the guard cells (Table 2).

The changes observed in stomatal density suggest that the plants are exhibiting an adaptive response, limiting water loss via transpiration without compromising gas exchange. Under water-deficient conditions, the plant reorganizes itself functionally and spatially with regard to its stomata, as evinced in the negative control treatment in plants grown at 25 % field capacity (Jha, Bohra, 2019; Perosini, 2025).

Different responses were observed for the equatorial and polar diameters of the stomata depending on the treatments evaluated. The highest equatorial diameter values recorded in the positive control treatment at 75 % field capacity corroborate the findings of Gama *et al.* (2017), who identified a positive association between NPK fertilizer application rates and increases in stomatal diameters. This characteristic may be related to a greater ability to regulate gas exchange, especially under conditions of greater water availability where plants tend to exhibit higher stomatal turgor. A more elliptical shape of the stomata is related to greater gas exchange control (Khan *et al.*, 2003). Here this can be observed in the treatments involving plants inoculated with *A. brasilense* or *B. aryabhattai* grown at 25 % field capacity, and in plants inoculated with *A. brasilense* + *B. aryabhattai* grown at 50 or 75 % field capacity (Table 2).

The anatomical differences observed in the photomicrographs of the cross-sectional (Figure 1) and paradermal (Figure 2) sections are consistent with the quantitative results obtained. Variations in leaf tissue thickness, arrangement

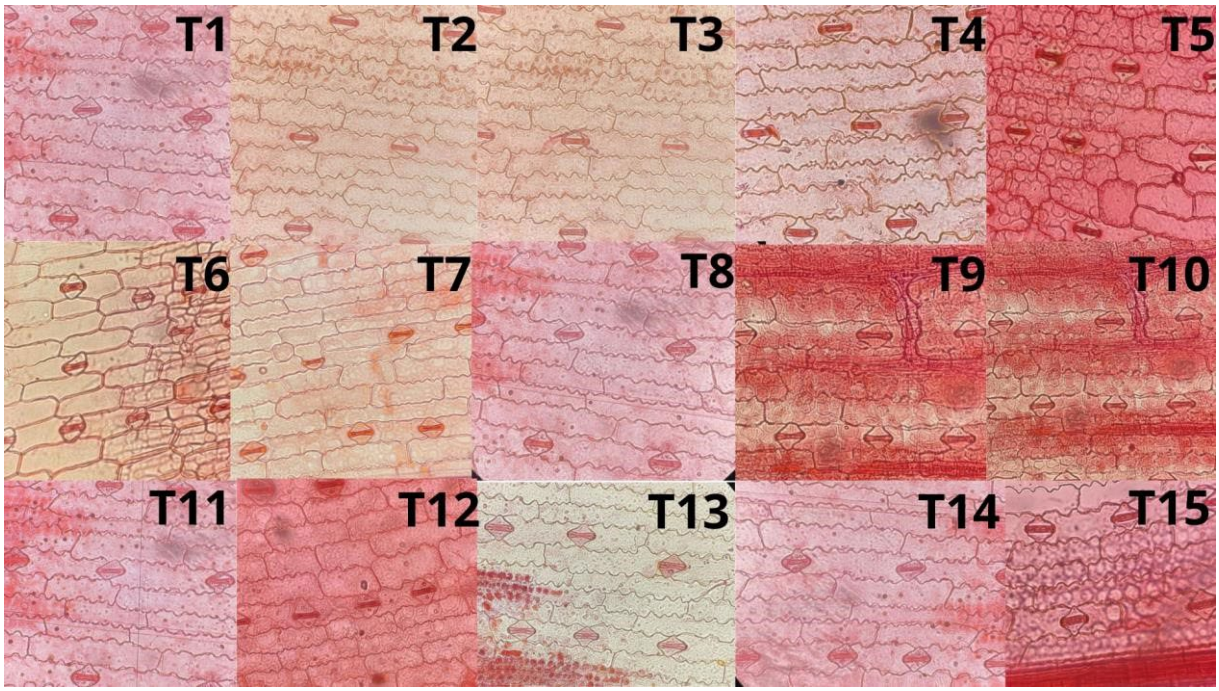
Figure 1. Cross-sections of maize plants inoculated with plant growth-promoting bacteria under different water stress conditions.



T1) *A. brasilense* under 25 % field capacity; T2) *B. aryabhattai* under 25 % field capacity; T3) *A. Brasilense* + *B. aryabhattai* under 25 % field capacity; T4) Positive control under 25 % field capacity; T5) Negative control under 25 % field capacity; T6) *A. brasilense* under 50 % field capacity; T7) *B. aryabhattai* under 50 % field capacity; T8) *A. Brasilense* + *B. aryabhattai* under 50 % field capacity; T9) Positive control under 50 % field capacity; T10) Negative control under 50 % field capacity; T11) *A. brasilense* under 75 % field capacity; T12) *B. aryabhattai* under 75 % field capacity; T13) *A. Brasilense* + *B. aryabhattai* under 75 % field capacity; T14) Positive control under 75 % field capacity; T15) Negative control under 75 % field capacity.

Source: authors (2025).

Figure 2. Paradermal sections of maize plants inoculated with plant growth-promoting bacteria under different water stress conditions.



T1) *A. brasilense* under 25 % field capacity; T2) *B. aryabhattai* under 25 % field capacity; T3) *A. Brasilense* + *B. aryabhattai* under 25 % field capacity; T4) Positive control under 25 % field capacity; T5) Negative control under 25 % field capacity; T6) *A. brasilense* under 50 % field capacity; T7) *B. aryabhattai* under 50 % field capacity; T8) *A. Brasilense* + *B. aryabhattai* under 50 % field capacity; T9) Positive control under 50 % field capacity; T10) Negative control under 50 % field capacity; T11) *A. brasilense* under 75 % field capacity; T12) *B. aryabhattai* under 75 % field capacity; T13) *A. Brasilense* + *B. aryabhattai* under 75 % field capacity; T14) Positive control under 75 % field capacity; T15) Negative control under 75 % field capacity.

Source: authors (2025).

of epidermal layers, and morphological characteristics of the stomata were observed among the treatments, suggesting that microbial inoculation and different water availability levels were associated with the anatomical changes observed.

Conclusion

Inoculation with *Azospirillum brasilense* and *Bacillus aryabhattai* promotes relevant leaf anatomical modifications in maize plants, modulated by water availability levels. *A. brasilense* stands out in conditions of greater water stress, increasing upper epidermis thickness, whereas *B. aryabhattai* exerts greater influence in environments with greater water availability, especially in the lower epidermis. Combination treatment of *A. brasilense* + *B. aryabhattai* increases mesophile thickness, suggesting a synergistic effect on the development of photosynthetic tissues. Mineral fertilization directly impacts the number and diameter of stomata, indicating that nutrition significantly influences stomatal differentiation. The potential of plant growth-promoting microorganisms to improve the anatomical responses of maize to

water deficit is therefore evinced, contributing to sustainable and efficient management strategies.

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