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Bactérias promotoras do crescimento de plantas contribuem para a maior persistência das pastagens tropicais em déficit hídrico? - Uma revisão

Do plant-growth promoting bacteria contribute to greater persistence of tropical pastures in water deficit? - A review

¿Bacterias promotoras del crecimiento de plantas contribuyen a una mayor persistencia de las pasturas tropicales en déficit hídrico? - Una revisión

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Resumo

O uso de bactérias promotoras do crescimento de plantas (BPCP) em pastagens é uma alternativa sustentável para incrementar a produção de forragem, além de ser uma tecnologia inovadora capaz de mitigar os efeitos do déficit hídrico (DH) nas pastagens. Atualmente, o DH é um dos principais agentes estressores abióticos responsáveis por impactar negativamente na produção agrícola. O DH permanente ou temporário limita o crescimento e o desenvolvimento das plantas forrageiras mais do que quaisquer outros fatores ambientais. Embora, estudos destinados a melhorar a resistência ao DH e a eficiência no uso da água sejam realizadas há muitos anos, o mecanismo envolvido ainda não está claro. Um maior entendimento das relações planta-água e os mecanismos de tolerância ao DH podem melhorar significativamente a produtividade das pastagens e a qualidade ambiental. Apesar dos mecanismos que permitem as plantas ajustarem-se como resposta ao DH, contudo, a depender da severidade e duração, essas plantas sozinhas não são capazes de sobreviverem ao estresse. Por isso, o uso de tecnologias como as BPCP pode conferir às plantas tolerância ao DH, sem prejudicar o seu desenvolvimento e produtividade. Existem estudos mostrando efeito positivo das BPCP em gramíneas em DH. Nesta revisão, é apresentada uma breve ideia sobre as causas, efeitos e respostas da inoculação de BPCP em gramíneas em déficit hídrico.

Palavras-chave: BPCP; Estresse hídrico; Gramínea; Resistência ao estresse hídrico; Seca; Tolerância ao estresse.

Abstract

The use of plant-growth promoting bacteria (PGPB) in pastures is a sustainable alternative to increment forage production. Besides, it is an innovative technology that can mitigate the effects of water deficit (WD) in pastures. Currently, WD is one of the main abiotic stressor agents responsible for a negative impact on agricultural production. Permanent or temporary WD imposes limitations on the growth and development of forage plants more than any other environmental factors. Although there have been studies for many years to improve resistance to WD and efficiency in water usage, the mechanism involved in the process is still not clear. A better understanding of the relations between plant and water and the mechanisms of tolerance to WD can significantly improve pastures productivity and environmental quality. Despite the mechanisms that allow plants to adjust as a response to WD, depending on its severity and duration plants are not capable to survive the stress by themselves. For that reason, the use of technologies such as PGPB can make them more resistant to WD without jeopardizing their development and productivity. There are studies that show the positive effects of PGPB in grasses during WD. In this review, we are going to present an overview of the causes, effects and responses of the inoculation of PGPB in grasses exposed to water deficit.

Keywords: Drought; Grass; PGPB; Resistance to drought stress; Tolerance to stress; Water deficit.

Resumen

El uso de bacterias promotoras del crecimiento de plantas (BPCP) en pasturas es una alternativa sostenible para aumentar la producción de forraje, además de ser una tecnología innovadora capaz de mitigar los efectos del déficit hídrico (DH) en las pasturas. Actualmente, el DH es uno de los principales estresores abióticos responsables de afectar negativamente la producción agrícola. El DH permanente o temporal, limita el crecimiento y el desarrollo de pastos forrajeros más que cualquier otro factor ambiental. Aunque los estudios destinados a mejorar la resistencia al DH y la eficiencia del uso del agua se han llevado a cabo durante muchos años, el mecanismo involucrado aún no está claro. Una mayor comprensión de las relaciones planta-agua y los mecanismos de tolerancia al DH pueden mejorar significativamente la productividad del pasto y la calidad ambiental. Aunque los mecanismos que permiten que las plantas se ajusten en respuesta al DH, sin embargo, dependiendo de la gravedad y la duración, estas plantas por sí solas no pueden sobrevivir al estrés. Por lo tanto, el uso de tecnologías como PGPB puede conferir tolerancia de plantas al DH, sin dañar su desarrollo y productividad. Hay informes que muestran efectos positivos de PGPB en pastos bajo DH. En esta revisión, se presenta una breve idea sobre las causas, los efectos y las respuestas de la inoculación de PGPB en pastos en DH.

Palabras clave: BPCP; Estrés hídrico; Resistencia al estrés hídrico; Sequía; Tolerancia al estrés.

1. Introduction

Plants' growth and development in agriculture are influenced by some environmental stresses and, depending on their severity and incidence, production systems may be seriously restricted, which leads to a poor performance.

Water stress, be it due to lack or excess of water, is one of the main stressor agents responsible for a negative impact on agricultural production (Dar et al., 2018). It causes hormonal imbalance, followed by physiological disorders with consequent senescence, abscission of parts of the plant's organs and increased susceptibility to diseases (Nadeem et al., 2010).

Water deficit (WD) can modify the operation and morphology of plants. It can even cause irreversible alterations (Staniak & Kocoń, 2015) in case of long and high-intensity exposure that exceeds the plant's predetermined genetic resistance, which can, in extreme cases, cause its death (Chaves & Oliveira, 2004).

Moderate WD reduces the growth and speed of foliar cell division due to the decrease in water content. As for longer WD, there can be metabolic changes, especially regarding the photosynthetic machinery of the plant, reducing its activity, possibly due to an increase in stomatal conductance and activities of the RuBisCo enzyme (Hura et al., 2007).

Adverse environmental conditions result in a great impact on the production and performance of grasses, which are highly responsive to good hydric conditions of the soil.

Plants have a mechanism of tolerance to WD. Yet, it varies according to each species (Lisar et al., 2012). Therefore, it is evidently necessary to carry out studies with technologies that are capable of making plants more resistant to WD in a way that does not hinder their development and productivity. The use of technologies, such as the inoculation of plant-growth promoting bacteria (PGPB) can enhance the development of grasses under stressful conditions.

PGPB are microorganisms commonly found in rhizospheric environments with little or no stress. However, in hostile environments, some PGPB strains are not able to survive and compete for resources (Dar et al., 2018). Some others are not only efficient in resisting WD, but also capable of promoting the growth of host plants from mechanisms such as the biosynthesis of phytohormones (Upadhyay et al., 2011), mineralization and decomposition of organic matter, and enhancement of bioavailability of minerals, such as phosphorus (Kumar & Verma, 2018).

In the literature, there have been positive responses regarding the interaction between grasses and PGPB, proving the capacity of such organisms to alter the physiology of plants and make them more resistant to abiotic stressor agents. The inoculation of PGPB can lead to morphophysiological and productive improvements in *Urochloa* sp. (syn. *Brachiaria*).

Several studies have demonstrated to be inconclusive in their results, which points to the need for more research. Thus, in this review, we are presenting an overview of the causes, effects and responses of the inoculation of PGPB in grasses exposed to water deficit.

2. Physiological Mechanisms in Response to Water Deficit

The systems of livestock production are constantly subjected to several types of environmental stress throughout their productive cycles. They are exposed to toxicity by elements in the soil, high salinity of the soil, extreme temperatures and water deficit.

These systems have been facing frequent and long drought periods, especially due to the incidence of dry periods during the rainy season, which, depending on the region, can happen in different periods of the year, regardless of the season. The occurrence of WD in areas of animal production has been affecting its system and, consequently, its productivity.

WD is defined as an external factor capable of promoting some type of disadvantageous influence over plant species, leading to responses such as the capacity to tolerate stress, which simply is the ability to face different conditions of WD through a higher performance in the use of water resources available (Taiz & Zeiger, 2009). Maintenance of the hydrated plant cells and efficiency in water usage are mechanisms that plants use to survive (Odokonyero et al., 2017).

WD has been occurring in a faster way due to climate changes, and it has been affecting many regions in the world causing severe damage to primary production sectors, especially those related to farming. By 2050, a great part of the arable land on the planet will have been affected by WD with negative impacts on plants' growth and development (Kasim et al., 2012), considerable losses in cultures performance (Kaushal & Wani, 2016) and seasonality in production (Bonfim-Silva et al., 2011), as it is the case of some grasses. Drought is one of the main stressor agents that compromise productivity of pastures and cultures, especially in arid and semiarid regions (Odokonyero et al., 2017).

The stress caused by WD jeopardizes the relations plant-water, and unleashes a series of morphophysiological and biochemical responses in plants (Rahdari & Hoseini, 2012). Plants subject to WD have their germination and seeds vigor compromised, a reduction of the stomatal opening as a mechanism to avoid tissues dehydration through transpiration, and reduction of the enzymatic and photosynthetic activity (Lisar et al., 2012). Other mechanisms used by plants are leafroll, accumulation of solutes, delayed flowering and some hormonal signals (Hadiarto & Tran, 2011), besides other physiologic and metabolic processes.

When exposed to WD, plants have an immediate response by reducing their osmotic potential inside the cells (Zafari et al., 2017) and their roots' water potential. This happens in order to keep a positive water balance, ensuring water absorption from the soil or a decrease in transpiration (Guimarães et al., 2011).

In plants under stress, there is the inhibition of leaf elongation (Farooq et al., 2009), a decrease in the emission of new tissues (Borrell et al., 2000a) and a reduction of cell division and growth (Anjum et al., 2011) due to a loss of turgidity of the wall cell (Kaushal e Wani, 2016), and a reduction of tillering, compromising the structure of the canopy, not to mention the acceleration of leaf senescence (Inman-Bamber, 2004). That contributes to a smaller leaf area, with direct impact on light interception (Zafari et al., 2017), degradation of photosynthetic pigments (Streit et al., 2005) and a decrease in photosynthesis efficiency (Zafari et al., 2017).

In case of WD, the concentration of chlorophyll pigments and carotenoids can be used as an indicator for evaluating the sanity and integrity of the photosynthetic apparatus (Rong-Hua et al., 2006), thus, indicating if the plant is tolerant to WD (Jabeen et al., 2008).

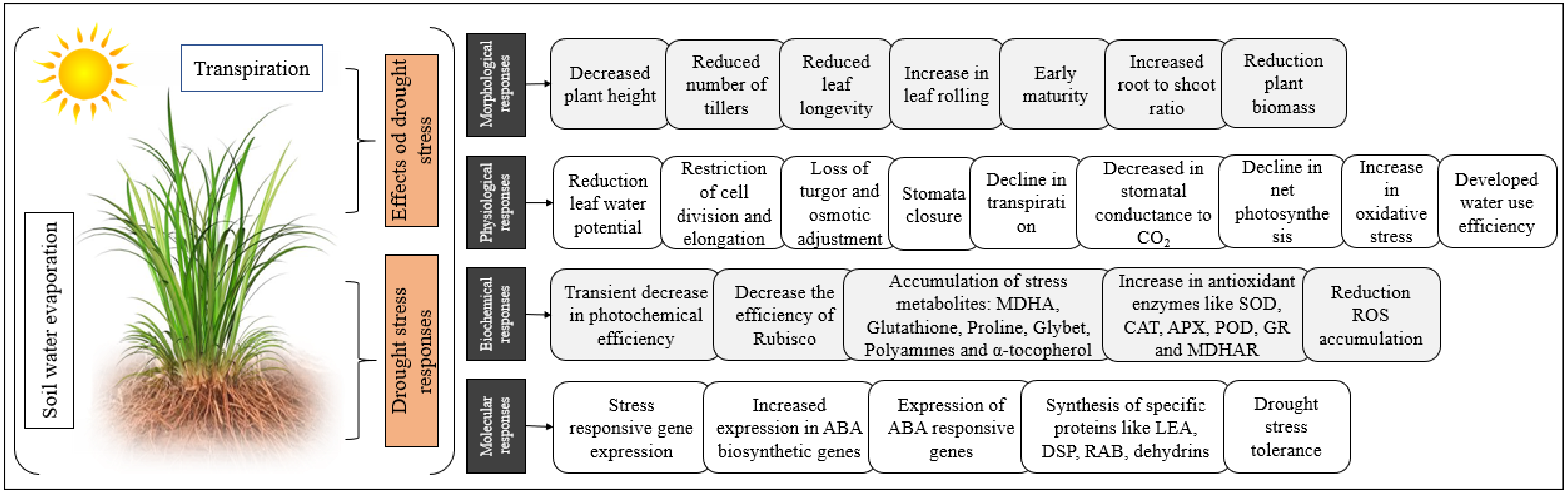
In order to protect themselves from WD, plants activate mechanisms of osmotic adjustment (Kaushal & Wani, 2016) and accumulate metabolites called osmoprotectors or compatible solutes such as proline (Staniak & Kocón, 2015), glycine (Souza et al., 2013) trehalose (Rodríguez-Salazar et al., 2009), glucose, sucrose and fructose (Urano et al., 2010).

Proline, for instance, is found in small amounts in plants, and one of its functions is to help with the osmotic adjustment of plants under drought stress, converting them into cells that are osmoprotected from the deleterious effects of dehydration caused by the constant loss of water through transpiration. It also prevents the denaturation of proteins, preserves the structure of the enzymes and acts like a buffer to stabilize the cellular redox potential. For that reason, this amino acid is considered an important parameter for selecting plants that are tolerant to WD (Nogueira et al., 2001).

In studies with sorghum (*Sorghum bicolor* L.), low availability of water in the soil gradually reduced leaf expansion and the emission of new tissues, with an impact on the production of biomass (Borrell et al., 2000a; 2000b). In sugarcane (*Saccharum officinarum* L.), there was the emission of new tillers and an increase in leaf senescence, thus compromising the canopy structure (Inman-Bamber, 2004).

The literature has shown several problems related to WD which result in stress, thus, jeopardizing grass species such as corn (*Zea mays* L.; Almeida et al., 2017), barley (*Hordeum vulgare* L.; Sanches et al., 2015), wheat (*Triticum aestivum* L.; Raheem et al., 2017), rice (*Oryza sativa* L.; Wei et al., 2017) and *Urochloa* sp. (Odokonyero et al., 2017).

As previously stated, plants make use of several mechanisms to ensure their survival. Figure 1 presents a summary of some effects of WD on plants and their consequences.



Carbon dioxide (CO_2), monodehydroascorbate (MDHA), monodehydroascorbate reductase (MDHAR), superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), peroxidases (POD), glutathione reductase (GR), reactive oxygen species (ROS), abscisic acid (ABA), late embryogenesis abundant (LEA) and dual-specificity phosphatase (DSP).

Figure 1. Morphological, physiological, biochemical and molecular responses of tolerance to water deficit stress in plants. Adapted from Shao et al. (2008), Ullah et al. (2017) and Oladosu et al. (2019).

When plants are exposed to WD conditions, they make use of tolerance mechanisms such as morphological, physiological and metabolic adjustments that allow them to overcome the stressor agent. However, depending on severity and duration, plants are not able to survive the external environmental stress by themselves, even if they make use of the aforementioned mechanisms.

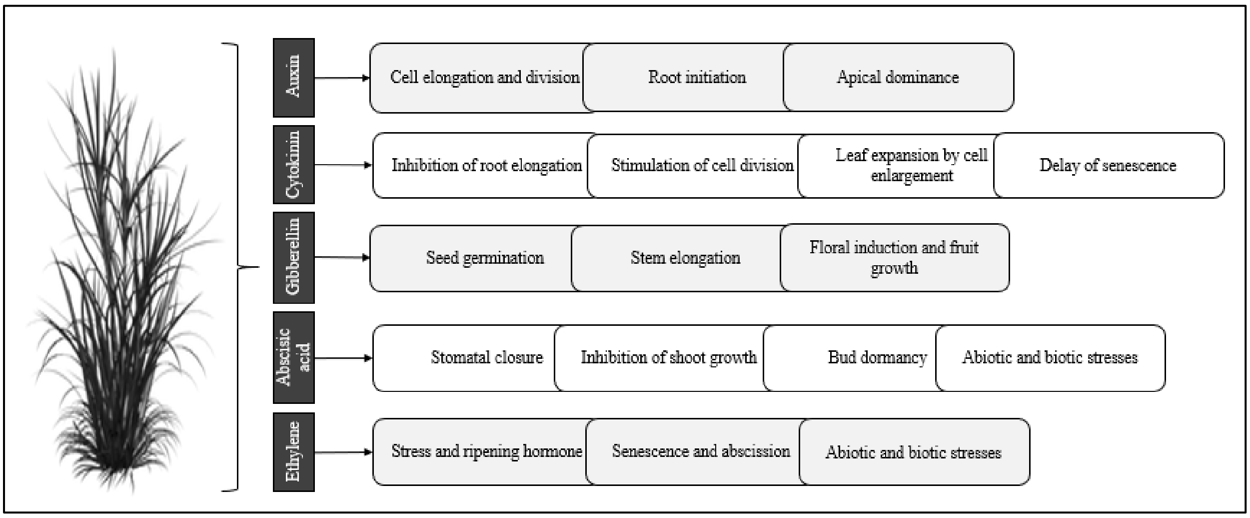
Therefore, it is clearly necessary to carry out studies with new technologies that are capable of making forage species more resistant to WD, in a way that does not jeopardize their development and productivity.

3. Production of Phytohormones in Response to Drought Stress and its Effects on Plants

Hormones are substances produced by plants and microorganisms. They act by modifying the way specific cells function, and are responsible for promoting their growth and development.

The literature presents a huge amount of research describing the main classes of hormones produced by PGPB, such as auxins, cytokinins, gibberellins, abscisic acid (ABA) and ethylene, as shown in Figure 2.

Figure 2. Descriptive summary of the main classes of phytohormones produced by plants growth promoting bacteria and its effects on the plant.



Source: Adapted from Spaepen (2015, p. 249).

Bacteria use hormones to interact with plants, stimulating them and, thus, starting the colonization process avoiding the activation of basal defense mechanisms of the plant (Pérez-

Montaño et al., 2014).

Bacteria used in studies up to now have demonstrated specificity of results regarding the interaction between PGPB and grasses. Therefore, it is necessary to better understand the mechanisms used by plants under WD conditions.

Although it is not clear how growth stimulus occurs in plants associated with PGPB, it is known that the responses are different due to the distinct compounds (and their concentrations) produced by the microorganisms (Dimkpa et al., 2009), and this set of mechanisms promotes stress relief (Rolli et al., 2014).

Studies have evidenced that indole-3-acetic acid (IAA) is the main auxin produced by plants and PGPB (Kavamura et al., 2013a). The synthesizing of IAA can stimulate the proliferation and/or elongation of plant cells, due to the loosening of the plant's wall cell (Glick, 2014), besides promoting root growth and stimulating the differentiation of meristematic tissues (Souza et al., 2017).

The auxin produced by most bacteria has brought benefits to the growth of plants associated with PGPB, especially with an increment of roots production, due to the greater development of the secondary branching zone and the piliferous zone (Long et al., 2008). That way, there is an increase in the capacity of absorbing water (Kasim et al., 2012) and nutrients (Dimkpa et al., 2009), and greater extension of root exudation (Glick, 2014).

Many species of bacteria are recognized as synthesizers of IAA, such as the species *Azospirillum* sp., *Pantoea* sp. and *Pseudomonas* sp, used in the study of Mamédio (2020). In studies involving *Urochloa* sp., it was observed that 91% of the 81 inoculated strains synthetized IAA (Figueiredo et al., 2010). The synthesis of IAA by *Azospirillum* is one of the most relevant advantages for the growth of grasses (Fukami et al., 2017), and it ensures that the plant will be more tolerant to WD (Dimkpa et al., 2009). Similar responses were also found in the association between *Azospirillum-T. aestivum* L. (Arzanesh et al., 2011; Pereyra et al., 2012).

With the inoculation of *Pseudomonas* sp., researchers have observed that the production of IAA led to higher tolerance to WD, with the best survival index of the plants (Marulanda et al., 2009). In studies with the isolation of bacterial species associated with Cactaceae from the Brazilian semiarid region, it was observed that *Pantoea* sp. was one of the species that synthesized the greatest amount of IAA (Kavamura et al., 2013a).

Another mechanism that is beneficial to plants affected by WD, which is inherent in a group of bacteria, is the deaminase activity and the regulation of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) (Saleem et al., 2007). PGPB that contain the ACC deaminase enzyme can cause a decrease in the level of ethylene of the plant (Long et al., 2008), thus, reducing stress, since ACC is the precursor of this hormone (Saleem et al., 2007). It favors an increase in growth of the root and the aerial part (Glick, 2014).

The synthesis of ethylene is increased as a response to the stressor agent (Glick, 2005). This hormone acts as an important modulator of plant tissues growth and the normal development of the plant because, when its synthesis occurs at high levels, it unleashes the initial processes of chlorosis, senescence and leaf abscission (Glick, 2014). That is why the interaction between PGPB-grasses are important.

In bacteria that contain ACC deaminase, there is a reduction of the WD effect on the growth of roots and the aerial part (Dimkpa et al., 2009). In studies with *T. aestivum* L. cultivated in semiarid climate conditions and inoculated with bacteria that synthesize this enzyme, there was an increase in length, number and root mass when compared to the control treatment. That favored greater absorption of water and nutrients, resulting in a better growth and productivity, even under WD conditions (Shakir et al., 2012).

Another hormone that can be synthesized in response to cellular dehydration due to water deficiency in the soil is the abscisic acid (ABA) (Kaushal e Wani, 2015). It is an important compound synthesized by the root system in WD (Perlikowski et al., 2019). This acid is responsible for inducing stomatal closure, thus, avoiding loss of water by the cell, inhibition of seed germination and leaf senescence. It also stimulates the transcription of genes involved in the protection against dehydration and osmotic stress, with consequent production of proteins of osmotic stabilization and detox enzymes of ROS, such as CAT, SOD and the ascorbate-glutathione cycle (Prakash et al., 2019).

Studies with the inoculation of *A. lipoferum* in *Z. mays* L. evidenced a positive effect of this association for the mitigation of WD negative impacts, and attributed this result to the production of ABA (Cohen et al., 2009). The synthesis of this this phytohormone by the *A. brasilense* strain was also observed. It was found that its biosynthesis can hinder the cytokinins levels of the plant. Besides, under WD conditions, it can relieve the negative effects of stress (Spaepen, 2015).

Cytokinins, in their turn, are the phytohormones involved in cell division and the differentiation of the meristematic tissues of the aerial part and the roots of a plant (Spaepen, 2015), also in organs formation, leaf expansion and senescence delay (Davies, 2010). Bacterial cytokinins are noticed by the plant’s receptors and, for that reason, the presence of PGPB manages to potentialize the synthesis of this compound by the plant (Spaepen, 2015).

PGPB, according to the specificities of each genre, also have the capacity of both stimulating and inhibiting alterations in the architecture of roots. They promote the plant's development through the synthesizing of gibberellins (GAs) (Martínez et al., 2016; Nelson & Steber, 2016) and stimulate important processes, such as seed germination, stem elongation, and the reproductive part of the plant, such as inflorescence (Zaidi et al., 2015), can also improve photosynthetic performance and chlorophyll pigments (You et al., 2012; Khan et al., 2015).

There is not much genetic evidence of the efficiency of PGPB when it comes to synthesizing GAs (Spaepen, 2015). Yet, based on more detailed analyses of the *A. lipoferum* strain, it is possible to characterize the biosynthesis of different GAs (Cassán et al., 2014), as observed in studies carried out by Cohen et al. (2009) involving corn (*Z. mays* L.).

4. Effects of PGPB on Grasses Subjected to Water Deficit Stress

The association PGPB-grasses can result in several benefits, such as a contribution to the sustainability of productive systems, with lower probability of pastures degradation (Hungria et al., 2016) through the possibility of contributing to part of the nitrogen (N) supply required by grasses (Marques et al., 2017) and, finally, mitigation of the negative effects of WD (Vurukonda et al., 2016).

The presence of PGPB can initiate a greater production of genes related to WD and, that way, enable tolerance to stress conditions (Kasim et al., 2012). However, little is known about the effects of PGPB on grasses from tropical climates, such as Urochloa sp. (Acuña et al., 2016), especially because most studies evaluated only the effects on plants growth (Dimkpa et al., 2009).

Studies carried out in the Brazilian semiarid region have shown that the use of xerotolerant microorganisms associated with vegetable crops may represent an alternative for cultivation in areas affected by WD (Kavamura et al., 2013b). Such microorganisms develop mechanisms to survive dry environments, such as the production of exopolysaccharides (Nocker et al., 2012), the formation of biofilms (Chang et al., 2007) and the production of osmolytes to avoid loss of cell water (McNeil et al., 1999).

These microorganisms are also capable of protecting the plant against desiccation by promoting a humid environment that favors the development of the root system. They also provide nutrients and some hormones that promote the plant's growth (Kavamura et al., 2013a). The exopolysaccharides synthesized by these microorganisms are hydrated compounds with around 97% of water, and they are responsible for keeping the roots hydrated for longer, thus, avoiding dehydration.

In case of low water availability in the soil, plants depend on microorganisms that enable them to increase their metabolic activity in order to resist WD (Sandhya et al., 2017).

Studies with the inoculation of *P. fluorescens* AKM-P6 and *P. putida* AKM-P7 in sorghum (*S. bicolor* L.) and wheat (*T. aestivum* L.) show that there was an increase in tolerance to stress due to the synthesis of proteins of high molecular weight and an improvement in the levels of cellular metabolites (Ali et al., 2009 e 2011).

In the association between *Azospirillum*-wheat (*T. aestivum* L.) under WD conditions, there was a greater content of leaf water and an increase in root growth, thus allowing an increase in the absorption of water and nutrients (Arzanesh et al., 2011). Other studies using the same species of PGPB and grasses have evidenced an increment in grain production and an adjustment of the volumetric cell wall of the grain, which improved its water status (Creus et al., 2004), and greater survival of the plants after a few days under WD (Kasim et al., 2012).

The inoculation of *Pantoea* sp. in corn (*Z. mays* L.) under WD resulted in greater leaf area and stem length, and an increment in dry biomass (Kavamura et al., 2013a). The inoculation of *A. lipoferum* led to better corn growth rates, besides a greater accumulation of free amino acids and soluble sugars (Qudsaia et al., 2013). As for the association *A. brasilense*-corn, there were increments of 7.9 and 4.3% in the accumulation of dry biomass of the aerial part and number of grains, respectively, at harvest (Cassán e Diaz-Zorita, 2016). Another study presented an increment of 16% in root dry matter mass (Coelho et al., 2017).

The application of *P. ananatis* AMG 501 in *U. brizantha* pasture, via leaf and root, led to an increase in production of biomass of 10 to 60% (Megías et al., 2017). The inoculation of *A. brasilense* Ab-V5 and Ab-V6 led to an increment of 27% in root mass, 28% in the number of tillers, and reduced the daily accumulation of forage mass to only 7% in comparison with the 17% of the control treatment (Leite et al., 2018).

Taking into account the examples aforementioned, it is clear that PGPB play a relevant role in the mitigation of WD effects, ensuring the survival of grasses. It is also clear that the use of this technology not only allows us to understand the action of these bacteria in the biological responses of plants, but also helps us when it comes to decision-making along with efforts to modernize agricultural production systems and make them more profitable and efficient from the perspective of sustainability.

4.1 The use of PGPB in Urochloa sp. under water deficit stress

Mamédio (2020) developed an experiment in plastic vases (12 dm^3 of capacity), in an agricultural greenhouse at the State University of Maringá (UEM), Maringá, Paraná, Brazil (23°24'S, 51°56'W, and 542 m.a.s.l.), between 2017 and 2019.

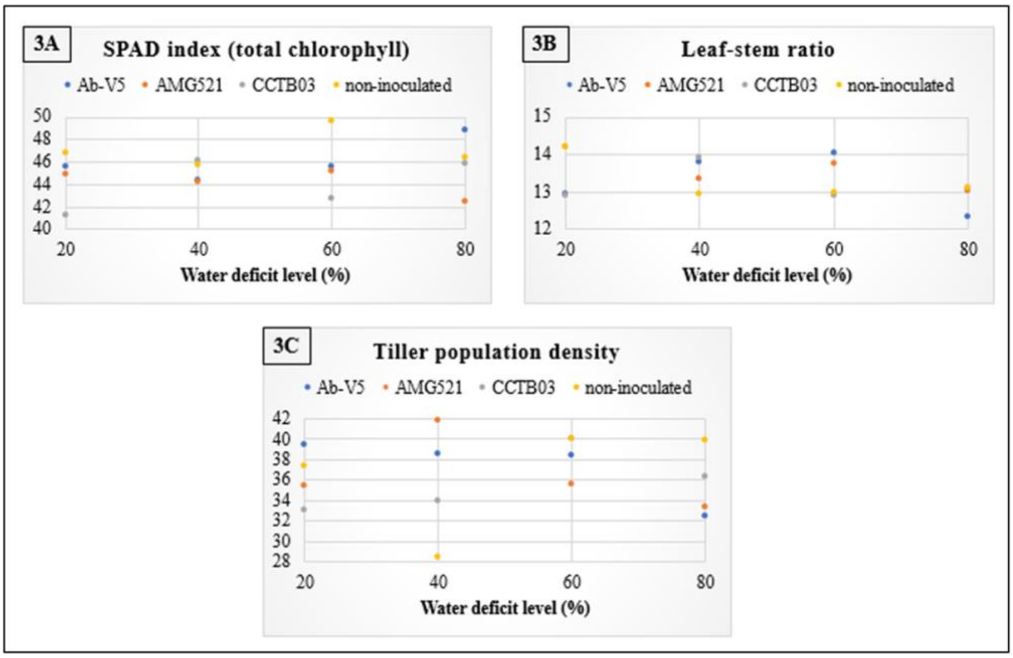
The author tested *A. brasilense* Ab-V5, *P. ananatis* AMG 521 and *P. fluorescens* CCTB03, associated with four levels of WD (80, 60, 40 and 20%). The grass species used in the study were *U. brizantha* cv. BRS Paiaguás and *U. ruziziensis* (Germain and Evrard).

When the plants reached, on average, 35-40 cm in height, shoots were cut to 15 cm. That was determined based on the heights adopted by cattle breeders. All the data were collected according to the harvest periods. The first experimental cycle took place between November 2017 and July 2018, characterizing 5 cuts in Paiaguás grass and 4 cuts in Ruziziensis grass. The second experimental cycle occurred between September 2018 and May 2019, with the same number of cuts of the first cycle.

In the next paragraphs, we will be presenting a brief summary of the results of the experiment (non-published data). They compose part of the authors' doctoral studies in the Postgraduate Program in Animal Science from UEM.

Among the morphological, physiological and productive parameters evaluated in this study, we only observed the interaction between the PGPB and the levels of WD for the SPAD index (cut 1; Figure 3A), leaf:stem ratio (cut 3; Figure 3B) and tillers population density (cut 1; Figure 3C). As for the other parameters, isolated results were observed according to the factors under study.

Figure 3. SPAD index (total chlorophyll) evaluated in cut 1 (3A) and leaf:stem ratio (L:SR) evaluated in cut 3 (3B) of *U. brizantha* cv. BRS Paiaguás and tiller population density (TPD, number of tiller) evaluated in cut 1 (3C) of *U. ruziziensis* under water deficit (WD %).



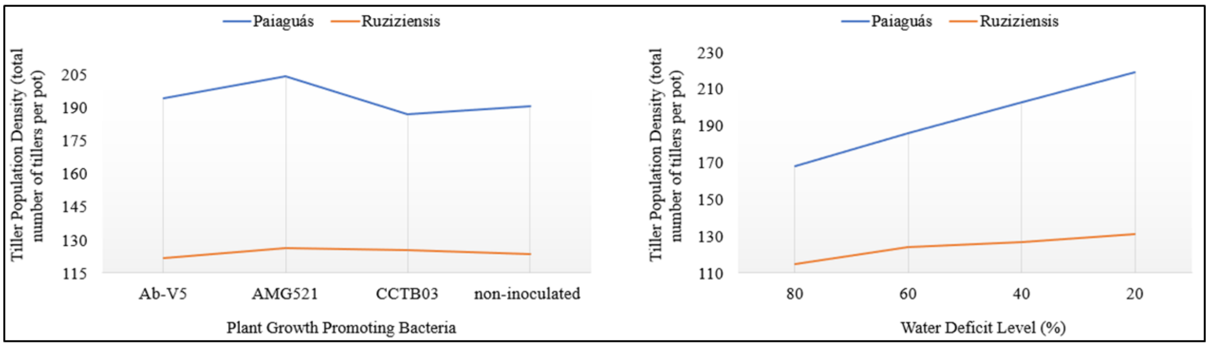
Source: Mamédio (2020).

For the SPAD index in Paiaguás grasses, each strain presented different effects for each of the WD levels. The highest SPAD values were achieved with the inoculation of the strains Ab-V5 in WD 80%, AMG 251 in WD 60%, AMG 521 and CCTB03 in WD 40%, and finally, the non-inoculated treatment in WD 20% (Figure 3A).

For the L:SR of Paiaguás grass, the highest values were achieved by the inoculation of strains CCTB03 in WD 80%, Ab-V5 in WD 60%, CCTB03 in WD 40% and AMG 521 and non-inoculated treatment in WD 20% (Figure 3B). For the TPD of Ruziziensis grass, the highest number of tillers was found in the non-inoculated treatment (WD 80%), strain Ab-V5, AMG 521 and non-inoculated treatment (WD 60%), strain Ab-V5, AMG 521 (WD 40%) and, finally, strain Ab-V5 and non-inoculated treatment (WD 20% (Figure 3C).

The average results of tiller population density (TPD, total number of tillers per pot) of Paiaguás and Ruziziensis grasses are shown in Figure 4.

Figure 4. Tiller population density (TPD, total number of tillers per pot) collected during the experimental period in *U. brizantha* cv. BRS Paiaguás and *U. ruziziensis* under water deficit (WD %).

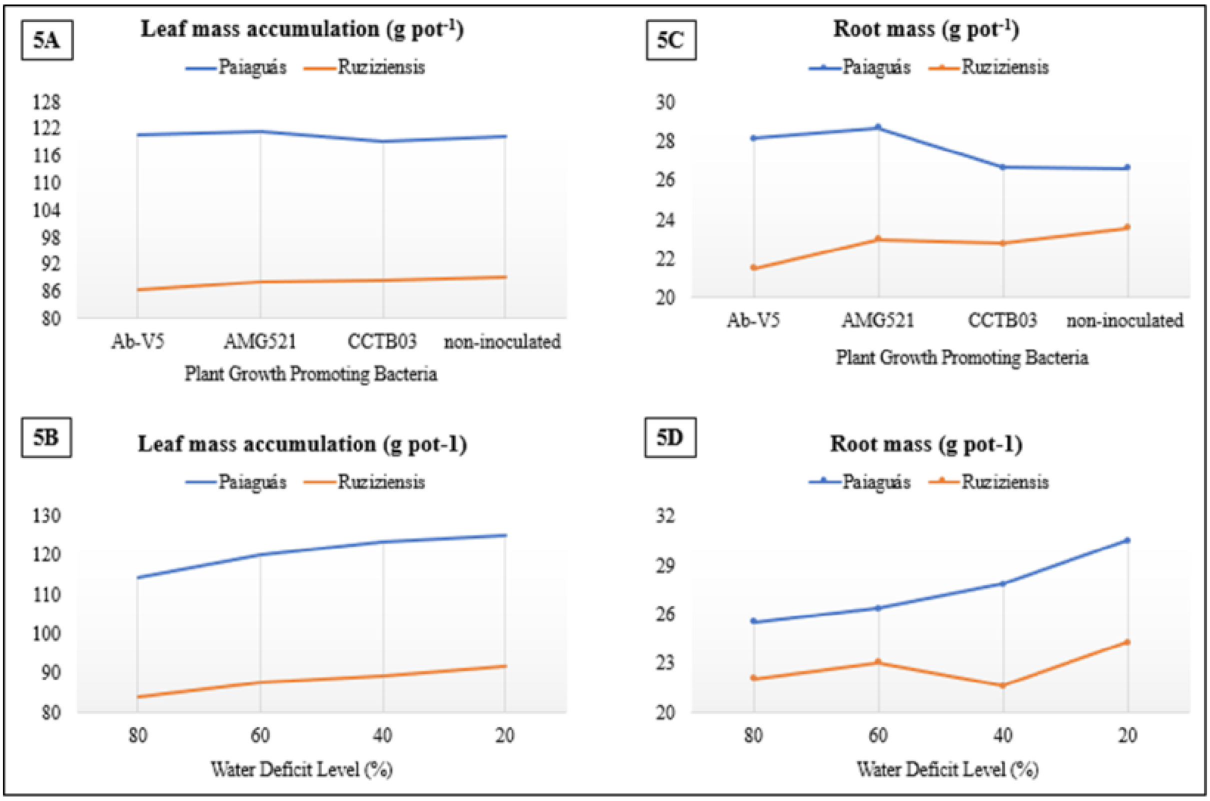


Source: Mamédio (2020).

When taking into account the TPD results referring to the summation of all scores done before each mass cut, there was no effect of the inoculation of PGPB strains. Yet, during WD imposition, there was an increase in the number of tillers as there was more water available to the grasses (Figure 4).

The average results of leaf mass accumulation (LMA, g pot^{-1}) and root mass (RM, g pot^{-1}), of Paiaguás and Ruziziensis grasses are shown in Figure 5.

Figure 5. Leaf mass accumulation (LMA, g pot^{-1}, 5A and 5B) and root mass (RM, g pot^{-1}, 5C and 5D) of *U. brizantha* cv. BRS Paiaguás and *U. ruziziensis* under water deficit (WD %).



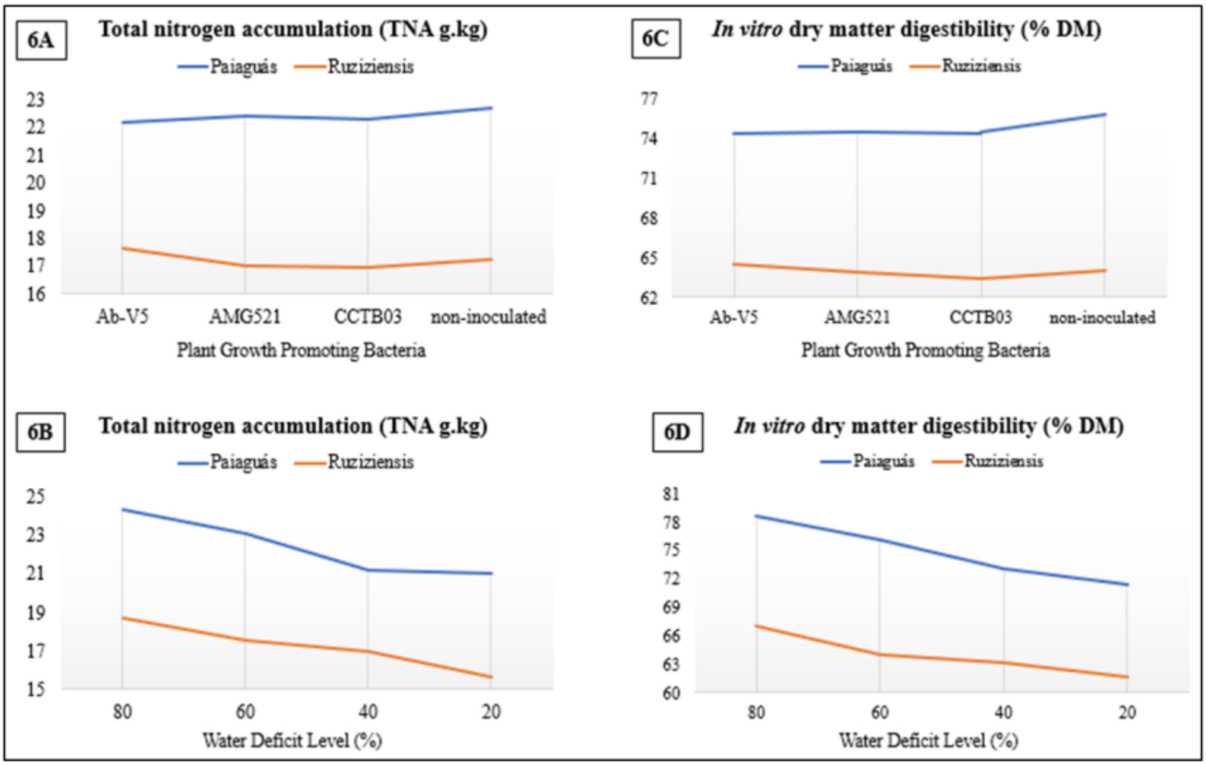
Source: Mamédio (2020).

In this study, we did not observe the effect of the inoculation of the PGPB strains on LMA (Figure 5A) and RM (Figure 5C) of Paiaguás and Ruziziensis grasses. With regard to WD imposition, there were effects on the ALM (Figure 5B) and RM (Figure 5D) of Paiaguás grass and on the LMA of Ruziziensis grass (Figure 5B). The reduction of WD had positive effects on growth, development and grass production.

The average results of total nitrogen accumulation (TNA g kg^{-1}) in aerial part and in vitro dry matter digestibility (IVDMD% DM, dry matter) of Paiaguás and Ruziziensis grasses are shown in Figure 6.

In our study, the use of PGPB did not have influence on the accumulation of total nitrogen (TNA g kg^{-1}; Figure 6A). The concentration of TNA was altered throughout the experiment, with an average decrease in concentration of 45% in Paiaguás grass and 48% in Ruziziensis grass, compared to the first and last cuts. The greatest WD imposition (80%) resulted in a lower TNA in both types of grass (Figure 6B).

Figure 6. Total nitrogen accumulation (TNA g kg^{-1}; 6A and 6B) in aerial part and in vitro dry matter digestibility (IVDMD% DM; 6C and 6D) of *U. brizantha* cv. BRS Paiaguás and *U. ruziziensis* inoculated with plant growth promoting bacteria under water deficit (WD %).



Source: Mamédio (2020).

The inoculation of strains Ab-V5 and AMG 521 led Paiaguás grass, in the fourth cut, to have higher IVDDM percentages (Figure 6C). The greatest WD imposition resulted in higher percentages of IVDDM in Paiaguás and Ruziziensis grasses (Figure 6D).

In this study, the effects of the inoculation of PGPB verified in some parameters are probably due to an increase in the production of phytohormones, such as auxins, cytokinins and gibberellins, which are responsible for inducing the plant's growth with changes in its morphology and physiology, besides inducing it to be more tolerant to environmental stress, such as WD. The effects of these phytohormones have been reported by many studies that attested the inoculation of PGPB in grasses and non-grasses.

The absence of effects in the association between PGPB and grasses can be due to an inadequate combination of them, once not every bacterium is responsive to all grass species. It is also possible that WD is capable of inactivating groups of microorganisms that are more sensitive to such condition.

As a whole, the plant-growth promoting bacteria used in this study were not efficient when it comes to improving the physiological and productive parameters of *U. brizantha* cv.

BRS Paiaguás and *U. ruziziensis* under WD conditions. Conversely, the study was efficient, since it demonstrates the negative effects of WD on the aforementioned grasses.

5. Final Considerations

The use of plant-growth promoting bacteria in tropical grasses is an alternative to the maintenance of pastures growth and development, even when the nutritional profile of the soil does not meet the needs of the grasses and environmental conditions are adverse.

The literature shows conflicting results regarding the effects of the interaction PGPB-grasses. Moreover, there are not many studies testing inoculants in tropical grasses under water deficit conditions. For that reason, we reaffirm the need for studies with the grass species that are mostly explored in animal production, as well as more detailed analyses of the efficiency of such technology, in order to better understand the effects of the interaction between PGPB and grasses in a context of water deficit.

The use of this technology shows great potential to become a reality in the formation and persistence of pastures, due to the great interest by livestock farmers, mainly because it is an advantageous alternative to livestock grazing, soil management and environmental quality, due to its low cost, and also for responding to society's that claims for more sustainable livestock production.

There is still a long way ahead of us regarding research done with the inoculation of tropical grasses, mainly when it comes to field tests in order to verify if the results are as promising as those found in controlled environments, especially if the responses in other grasses also comprise the genus *Urochloa*.

The results found in this type of research, as long as positive, may allow, in the future, the development and trading of products capable of contributing to a greater persistence of pastures in water deficit situations.

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