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Research article

Enhanced drought tolerance in seedlings of Neotropical tree species inoculated with plant growth-promoting bacteria

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ABSTRACT

The inoculation of tree species with plant growth-promoting bacteria (PGPB) has emerged as an important strategy for the acclimation of seedlings by improving plant tolerance to biotic and abiotic stresses. This study aimed to evaluate the effects of inoculation with bacterial species (*Azospirillum brasilense* - Ab-V5, *Bacillus* sp., *Azomonas* sp. and *Azorhizophillus* sp.) on the growth and physiology of the Neotropical tree species *Trema micrantha* and *Cariniana estrellensis* under drought conditions. When associated with Ab-V5 and *Azomonas* sp., *T. micrantha* showed increased protein in the leaves, starch in the leaves and roots, photosynthesis, instantaneous carboxylation efficiency and root and shoot dry mass. Moreover, there were reductions in hydrogen peroxide, lipid peroxidation, water potential and proline. In *C. estrellensis* associated with Ab-V5, higher values of photosynthesis and instantaneous carboxylation efficiency were observed, in addition to higher starch content in the leaves and roots and higher protein content in the leaves; lower hydrogen peroxide and lipid peroxidation contents were also observed. The associations of *T. micrantha* with Ab-V5 and *Azomonas* sp. and *C. estrellensis* with Ab-V5 favored the activation of metabolic processes under drought, leading to greater drought tolerance. This work demonstrates the effects of compatible associations of Neotropical tree and PGPB species and suggests that the identification of compatible PGPB strains can result in tree seedlings with increased tolerance to abiotic stresses, such as drought.

1. Introduction

The use of Neotropical tree species for the reforestation and restoration of degraded areas and reforestation is a requirement of Brazilian legislation with an aim to reduce the environmental impact caused by the human exploitation of natural landscapes and to contribute to biodiversity conservation (Keller et al., 2009). The costs of recovery programs for degraded areas are high. This is due to the high mortality rates of these seedlings in the field, since they are often exposed to environmental conditions to which they are not properly acclimated (Carvalho-Filho et al., 2003).

Environmental changes induced by vegetation degradation can influence the soil-plant system, and associated responses to tolerate the new conditions can therefore be observed (Ortiz et al., 2015). Among the abiotic stress factors that most affect the development of seedlings in the field are drought, high light intensities, high salt levels and the deficiency of mineral nutrients, such as nitrogen (Yang et al., 2009; Franzini et al., 2010; Kraiser et al., 2011). Drought events have increased in recent decades in association with climate change caused by global warming (Stokstad, 2004). Forecasts indicate that weather extremes will tend to increase, such as more frequent and prolonged droughts, which makes it desirable to use plants that are more tolerant to drought in ecological restoration (Mendonça, 2006).

Alternatives for improving seed germination and seedling growth and minimizing the damage caused by abiotic stresses after transplanting, such as restrictions in water availability, are of fundamental importance to produce tree seedlings with a higher ability to resist prolonged stresses and survive following outplanting, consequently reducing the costs of reforestation programs. In this sense, attempts to better understand the natural ecological relationships between soil microbes and Neotropical tree species and how these relationships can influence plant metabolism under stressful conditions can result in

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Abbreviations

Ψ_w	water potential
A	net photosynthetic rate
Ab-V5	*Azospirillum brasilense* Ab-V5 strain
C_i	intercellular CO_2 concentration
FC	field capacity
GH	gravimetric humidity
gs	stomatal conductance
IAA	indol-3-acetic acid
IBR	integrated multiple biomarker response
k	instantaneous carboxylation efficiency
MCW	methanol:chlorophorm:water solution
MD	moderate drought
MDA	malondialdehyde
PGPB	plant growth-promoting bacteria
ROS	reactive oxygen species
RuBisCO	ribulose 1,5-bisphosphate carboxylase/oxygenase enzyme
TBARS	thiobarbituric acid reactive substances
TCA	trichloroacetic acid
TSS	total soluble sugars
UEL	State University of Londrina

innovative nursery practices focused on attaining tree seedlings of superior physiological quality. The influence of the plant microbiome on plant fitness is well described in the literature and is thought to modulate developmental and physiological characteristics that can be exploited in the production of high-quality seedlings at low economic and environmental costs (Kusano et al., 2011; Ortiz et al., 2015; Pieterse et al., 2016).

Among the organisms described as part of plant microbiomes, a group of beneficial bacteria arouses interest because of their potential to develop direct and indirect mechanisms that have been demonstrated to be related to the promotion of the growth, development and metabolism of plants and can hence be used as an input in extensive crops (Vejan et al., 2016). These bacteria are generically defined as plant growth-promoting bacteria (PGPB) and are a diverse group of phylogenetically non-related genera that share common ecological and physiological characteristics with positive impacts on plant development. The mechanisms of PGPB that led to an increase in plant tolerance against biotic and abiotic stresses may be the provisioning and/or facilitation of nutrient acquisition, the modulation hormone levels and the activation of defense mechanisms (Bulgarelli et al., 2013; Ortíz-Castro et al., 2009). PGPB strains are used to inoculate seeds and plants, where they express their growth-promotion effects after the establishment of an associative interaction as determined by the colonization of the plant rhizosphere and even the internal plant tissues. Therefore, the identification of a PGPB strain showing a compatible interaction with a given plant species is a valuable strategy that can be used to develop biological inputs, such as microbial inoculants, that can be applied to produce seedlings with higher adaptive and developmental potential (Finkel et al., 2017).

Although the potential of PGPB to benefit their host plants by helping them to overcome environmental and nutritional restrictions to optimal growth, as reported in previous phytoremediation and reforestation studies (Bashan et al., 2012; Kong and Glick, 2017; Thijs et al., 2016), information about the effects of PGPB use in native Brazilian tree species is scarce in the literature.

Most of the studies that address associations with PGPB were carried out on agricultural crops or with non-native Atlantic Forest biome species. In addition, the rates of growth promotion by the PGPB are closely related to the needs of the plant under stress. Thus, suboptimal amounts of hormone, nitrogen, phosphorus, iron or water, for example, will direct how much plant-bacteria interaction will be beneficial to the plant (Glick, 2012).

Here, we aimed to evaluate the effects of inoculation with four bacterial species (*Azospirillum brasilense* - Ab-V5, *Bacillus* sp., *Azomonas* sp. and *Azorhizophillus* sp.) on the growth and metabolism of seeds of the Neotropical tree species *Trema micrantha* (L.) Blume (pioneer or shade-intolerant) and *Cariniana estrellensis* (Raddi) Kuntze (non-pioneer or shade-tolerant) under drought conditions. We hypothesized that Neotropical tree species seedlings inoculated with a compatible PGPB would present more drought tolerance due to a positive influence of the inoculated bacteria on plant metabolism.

2. Material and methods

2.1. Biological material and experimental design

The bacterial species used are part of the Plant Growth-Promoting Bacteria Collection of the State University of Londrina (UEL). The *Azospirillum brasilense* (diazotrophic - Ab-V5 strain) is registered at the Ministry of Agriculture of Brazil for use in commercial inoculants (Hungria et al., 2010). *Bacillus* sp. (potential diazotrophic) was characterized as a PGPB species by Goes et al. (2012). *Azomonas* sp. (diazotrophic) and *Azorhizophillus* sp. (diazotrophic) were characterized as PGPB by Costa (2013).

The inoculants were prepared according to Oliveira et al. (2017). The PGPB species were initially cultured in 5 mL of liquid DYGS medium in test tubes kept under orbital shaking (180 rpm) at 28 ± 2 °C for 24 h for the preparation of the preinoculum. The inoculants were prepared from 1 mL of the preinoculum inoculated into 50 mL of FORM15 culture medium placed in Erlenmeyer flasks and kept under orbital shaking (180 rpm) at 28 ± 2 °C for 48 h. After the growth period, the cultures were normalized by dilution with sterile FORM15 culture medium to a final density of 1×10^6 cells mL^{-1}, constituting the inoculants used in the assays.

Two native tree species from seasonal semideciduous forest (a phytophysiognomy of Brazilian Atlantic Forest) were chosen for this study: *Trema micrantha* (L.) Blume (Cannabaceae), pioneer or shade-intolerant species, and *Cariniana estrellensis* (Raddi) Kuntze (Lecythidaceae), which is a non-pioneer or shade-tolerant species. The seeds were kindly provided by the Laboratory of Biodiversity and Ecosystem Restoration (LABRE) of the UEL. The *T. micrantha* seeds were treated to break dormancy before sowing by immersion in concentrated sulfuric acid for 20 min and then washed in running water.

In a greenhouse at the UEL, the seeds were inoculated by applying 800 mL of the inoculant at a concentration of 1×10^6 cells mL^{-1} in plastic trays (1 L) containing an inert substrate of low fertility, which was obtained by heating sieved sand at 100 °C in a heating chamber for 8 h. After germination, seedlings with a completely expanded pair of leaves were transferred to plastic bags (2 L, 10.5 cm high, 9.5 cm lower diameter, 14 cm upper diameter) containing fertile soil (pH 5.8; CEC 4.4 cmolc/dm^3; NO_3^- 47.23 ppm; NH_4^+ 3.28 ppm) characterized as Eutrophic Red Latosol (EMBRAPA, 1999) and the inert substrate in a ratio of 1:1. At the time of transplanting and after 30 days, each plastic bag received an additional inoculation by the application of 50 mL of inoculum of each PGPB strain prepared as described above. The plants were kept under greenhouse conditions for two months (for acclimation and to moderate stress) under natural light, relative humidity and temperature conditions. The experiments were carried out from September to October 2015 for *T. micrantha* (winter-spring) and from February to March 2016 for *C. estrellensis* (summer). The average daily values and standard deviations of temperature, relative humidity, and accumulated global solar radiation were 23.1 ± 3.1 °C, 80.2 ± 15.3%, and 15.7 ± 5.5 MJ m^{-2}, respectively (data kindly provided by the Laboratory of Agrometeorology, Embrapa Soja,

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