



Research article

Different mechanisms drive the performance of native and invasive woody species in response to leaf phosphorus supply during periods of drought stress and recovery



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ARTICLE INFO

Article history:

Received 31 March 2014

Accepted 13 May 2014

Available online 22 May 2014

Keywords:

Chlorophyll fluorescence

Climate change

Drought tolerance

Gas exchange

Water deficit

ABSTRACT

The effects of drought stress and leaf phosphorus (P_i) supply on photosynthetic metabolism in woody tropical species are not known, and given the recent global environmental change models that forecast lower precipitation rates and periods of prolonged drought in tropical areas, this type of study is increasingly important. The effects of controlled drought stress and P_i supply on potted young plants of two woody species, *Anadenanthera colubrina* (native) and *Prosopis juliflora* (invasive), were determined by analyzing leaf photosynthetic metabolism, biochemical properties and water potential. In the maximum stress, both species showed higher leaf water potential (Ψ_l) in the treatment drought + P_i when compared with the respective control – P_i . The native species showed higher gas exchange under drought + P_i than under drought – P_i conditions, while the invasive species showed the same values between drought + P_i and – P_i . Drought affected the photochemical part of photosynthetic machinery more in the invasive species than in the native species. The invasive species showed higher leaf amino acid content and a lower leaf total protein content in both P_i treatments with drought. The two species showed different responses to the leaf P_i supply under water stress for several variables measured. In addition, the strong resilience of leaf gas exchange in the invasive species compared to the native species during the recovery period may be the result of higher efficiency of P_i use. The implications of this behavior for the success of this invasive species in semiarid environments are discussed.

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1. Introduction

Water shortages are already a threat around the world and are particularly critical in tropical environments (Donohue et al., 2013). Despite the importance of P_i , few studies have been published on the effects of a limited supply of P_i , and even fewer studies examine

interactions with other factors, such as water stress (Santos et al., 2006), high atmospheric CO_2 (Campbell and Sage, 2006; Fleisher et al., 2012; Singh et al., 2013), the availability of other nutrients (Naeem and Khan, 2009) and biodiversity (Chazal and Rounsevell, 2009).

A water deficit can reduce the flow of P_i into plant shoots (Santos et al., 2004) due to the low mobility of this element underground (Miguel et al., 2013). This compromises the export of photo-assimilates, the rate of leaf growth and the net assimilation of CO_2 (Santos et al., 2004, 2006).

Water stress substantially alters plant metabolism, decreasing the rate of gas exchange (Tezara et al., 1999; Santos et al., 2004) and affecting water potential and cell turgor (Tezara et al., 1999; Garg et al., 2004; Santos et al., 2004), proteins, photosynthetic pigments and starch (Garg et al., 2004). Changes in plants' photosynthetic metabolism can also be verified by chlorophyll fluorescence, with reduced photochemical quenching and increased non-photochemical quenching (Tezara et al., 1999). Such changes promote imbalance in the antioxidant system, with the increased production of reactive oxygen species (ROS) triggering antioxidant

Abbreviations: A, CO_2 assimilation; AA, Amino acids; APX, Ascorbate peroxidase; ATP, Adenosine triphosphate; CAT, Catalase; Chl a, Chlorophyll a; Chl b, Chlorophyll b; Car, Carotenoids; E, Transpiration; ETR, Electron transport rate; F_0 , Minimum chlorophyll fluorescence; F_m , Maximum chlorophyll fluorescence (dark-adapted); F_v , Fluorescence emission at steady state; F'_m , Maximum chlorophyll fluorescence (light-adapted); F_v/F_m , Maximum quantum efficiency of photosystem II; F'_v/F'_m , Maximum efficiency of photosystem II; g_s , Stomatal conductance; H_2O_2 , Hydrogen peroxide; MDA, Malondialdehyde; NPQ, Non-photochemical quenching; P_i , Inorganic phosphorus; PPF, Photosynthetic photon flux density; qP, Coefficient of photochemical quenching; ROS, Reactive oxygen species; SC, Soluble carbohydrates; SOD, Superoxide dismutase; TP, Protein total; VPD, Vapor pressure deficit; WUE, Water use efficiency; Ψ_l , Water potential.

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enzymatic and non-enzymatic mechanisms (Keunen et al., 2013) to counterbalance the production of ROS. Damage to cell membranes is observed with the corresponding increase in malondialdehyde (MDA).

Various effects of global environmental change on plants have been studied, including increased photosynthetic rates under high atmospheric CO₂ concentrations and the relationship between climate change and availability of phosphorus nutrition (Campbell and Sage, 2006; Fleisher et al., 2012; Singh et al., 2013). However, few studies have focused on woody species under arid or semiarid environmental conditions (Donohue et al., 2013). Furthermore, few studies have examined the relationship between phosphorus and drought in woody species, with the exception of a study on shrub species in which high CO₂ and P_i supply increased gas exchange, chlorophyll fluorescence parameters and rubisco carboxylase activity (Singh et al., 2013).

In Brazil, the word Caatinga is used to designate tropical dry forests that occur in markedly seasonal areas in which the limited rainfall (500–750 mm year⁻¹) is concentrated during a period of 3–5 months (Cramer et al., 2011). The resilience of exotic species, which may become invasive, has been attributed both to human-related mechanical disturbance and to elevated soil nutrient levels.

In general, tropical soils have shown low concentrations of phosphate, and soil phosphate is expected to be exhausted in the upcoming decades (Miguel et al., 2013). The application of P_i fertilizer can improve plant growth under drought conditions (Sawwan et al., 2000; Garg et al., 2004; Santos et al., 2004; Campbell and Sage, 2006). The ability of P_i to increase plant tolerance to abiotic stress has been attributed to increased control of stomatal conductance (Brück et al., 2000; Naeem and Khan, 2009), increased photosynthesis (Santos et al., 2004, 2006; Singh et al., 2013), increased cell-membrane stability and improved water use efficiency (Sawwan et al., 2000; Faustino et al., 2013).

Several species respond to P_i supply with a positive response in biomass and photosynthetic leaf metabolism (Brück et al., 2000; Santos et al., 2004, 2006; Naeem and Khan, 2009) when P_i is limiting (Campos et al., 2013). In this study, we hypothesized that the superior performance of the invasive species was due in part to its ability to survive under conditions of low P_i and water availability. Our hypothesis was that the species with higher P_i utilization efficiency (*Prosopis juliflora*) would not respond to the foliar application of phosphorus, while the less efficient species (*Anadenanthera colubrina*) would benefit from the application of phosphorus during the drought and recovery periods. To test our hypothesis, we measured the foliar P_i content, leaf water potential, gas exchange, chlorophyll fluorescence and several parameters of primary photosynthetic metabolism and anti-oxidative stress in a greenhouse experiment.

2. Materials and methods

2.1. Plant materials and growth conditions

We selected two Fabaceae woody species for our study, an invasive tree (*Prosopis juliflora* (Sw.) DC.) and a native tree (*Anadenanthera colubrina* (Vell.) Brenan). Fabaceae is the most common family of invasive species in Caatinga, and both of our study species exhibit the most frequently observed attributes of invading exotics in the region (Almeida, 2009). The two species are hermaphrodite, perennial, phanerophytes, legume fruit and reproduce by seed. *Prosopis juliflora* is native to Central America, northern South America and the Caribbean Islands and was introduced in Brazil as a supplementary food for grazing animals. *Prosopis* invasion profoundly impacts Caatinga forest biodiversity, dramatically decreasing the richness of native trees and shrubs, and

compromises the ability of native vegetation to regenerate. The native species *Anadenanthera colubrina* is a tree that was formerly dominant in the region, where it had economic importance for timber, charcoal production and traditional medicine. Due to environmental degradation, including competition with invasive species, its population has declined significantly, and the tree is currently considered threatened.

Seeds of *Anadenanthera colubrina* (Vell.) Brenan and *Prosopis juliflora* (Sw.) DC. were collected in Serra Talhada, Pernambuco, Brazil (7°54'35"S, 38°17'59"W). The germination of *P. juliflora* was promoted through scarification with sulfuric acid for 5 min in seeds without the endocarp to stimulate better synchrony and speed of germination. The seeds of both species were placed in petri dishes with moistened filter paper (5 mL) and maintained at 25 °C with a 12 h photoperiod. The germinated seeds were transferred to pots of 3.5 kg of silt loam soil collected from the same location as the seeds, with one individual planted per pot. The soil texture was 3% clay, 71% silt and 26% sand, and the soil properties were as follows: pH (H₂O) = 6.70; P = >40 mg dm⁻³; K = 0.16 cmolc dm⁻³; Al = 0.00 cmolc dm⁻³; Ca = 6.60 cmolc dm⁻³ and Mg = 1.45 cmolc dm⁻³. Air temperature ranged from 36 °C (maximum) to 22 °C (minimum) during the experimental period.

The experiment used a factorial design of phosphorus application (with (+P_i) or without (-P_i)) and water regimes (control or drought). Prior to transplanting, a dose of 450 mg kg⁻¹ P_i (superphosphate) was applied to each pot. Two days before the water treatments were begun, the phosphorus treatment was applied as a foliar spray with a dose of 20 g P_i L⁻¹ ammonium phosphate. For the treatments without phosphorus, a dose of 5.28 g N L⁻¹ urea was applied as a foliar spray to compensate for the addition of nitrogen (Santos et al., 2006). For the water regime treatments, the well-watered treatment group received 150 mL of water, which represented the total water-holding capacity of the pot, and the water deficit treatment group received 10% of the pot's water-holding capacity. Water restriction began at 212 days after germination with 10 repetitions per treatment, analyzed five plants exclusive biomass and five for the other parameters. Maximum water stress occurred seven days after the start of the drought treatment, and the plants were subsequently rehydrated over 8 days.

2.2. Water status and soil moisture

The tension of water in the xylem (Ψ_i) was measured with a Scholander pressure chamber (Soilmoisture Equipment Corp., Santa Barbara, CA, USA) on a branch with the leaves fully expanded but not senescent. Measurements were performed at 6:00 h. Soil moisture was measured with a soil moisture meter (HFM2010-HidroFarm).

2.3. Biomass

On the day of maximum stress (day 7), a count was performed of the number of leaves on each plant. At the end of the experiment (day 15), measurements of length, dry biomass and stem diameter were obtained for an analysis of plant growth.

2.4. Gas exchange

Values for gas exchange and chlorophyll *a* fluorescence were obtained with an infrared gas analyzer (IRGA, LI-COR, model LI-6400XT, Lincoln, NE, U.S.) with a leaf chamber fluorescence (6400-40) with an area of 2 cm² and a gas flow of 400 μmol s⁻¹. Photosynthetic photon flux density (PPFD) remained consistent at 2000 μmol m⁻² s⁻¹ day to day, and on the last day of recovery, the PPFD was 1000 μmol m⁻² s⁻¹. Fig. 1 shows the vapor pressure

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