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Morphophysiological changes in *Bauhinia cheilantha* (Bong.) Steud. (Fabaceae) caused by water deficit

Corresponding author
Rafael Silva Freitas
Universidade Federal de Sergipe
rafaelfreitasse@hotmail.com

José Laurindo dos Santos Júnior
Universidade Federal de Sergipe

Elizamar Círiaco da Silva
Universidade Federal de Sergipe

Abstract. Drought-induced alterations often result in plant acclimation responses, though the extent to which these traits adjust, and their true significance remain species-specific and subject to debate. In order to discern which traits exhibit plasticity and essentiality for the species' survival, we studied the morpho-physiological responses of *Bauhinia cheilantha* seedlings subjected to varying water regimes. We examined modifications in growth patterns, resource allocation and partitioning, morphological traits, organic solute synthesis, relative water content in leaves and roots, and the plasticity index for each trait under different water supply levels. Several traits linked to plant growth were reduced under stress, but those changes were not considered to be plastic. The concentration of organic solutes increased under stress and exhibited a reversible behavior by reducing their levels after re-irrigation. These alterations underscored the significance of such compounds for survival during water deficit periods and the high degree of adaptability. *B. cheilantha* exhibits morpho-physiological plasticity, as demonstrated by alternating high levels of plasticity in physiological and morphological features, which are associated with moderate drought stress. The study discusses how these changes affect the growth and survival of the species.

Keywords: Growth changes, pata-de-vaca, phenotypical plasticity, seedling growth.

Introduction

Water scarcity is one of the most critical environmental stresses that plants can encounter during their growth and development (Turner, 2019; Feng et al., 2021). Restricting water leads to reduced growth rates and interruptions in photosynthesis. These impairments are associated with physiological responses in the entire plant (Turner, 2019; Hashem & Mohamed, 2020). However, plants in drylands have innate survival strategies to cope with water scarcity (Hashem & Mohamed, 2020). These include rigid stomatal control (Silva et al., 2009), increased water-use efficiency (WUE) (Santos et al., 2021), robust root systems (Silva et al., 2009), and osmoregulatory capacity (Silva et al., 2004). As a result, these adjustments increase the likelihood of plant survival in stressful conditions commonly found in drylands.

While it is undeniable that organisms' ability to cope with these challenges is the result of adaptations over millions of years, other factors have also been examined. It has been suggested that achieving survival under stress in heterogeneous environments may be facilitated by the high levels of phenotypic plasticity (Via et al., 1995; Lázaro-Nogal et al., 2015; Murren et al., 2015; Gao et al., 2018).

However, the plasticity of certain traits and their significance in stress survival remains a matter of debate. Our study aims to address two questions: 1) Are drought-induced changes more commonly expressed in physiological or morphological traits? And 2) Which of these changes is more strongly correlated to plant survival under stressful conditions? This study does not focus on theoretical discussions or advancements in phenotypic plasticity under stressful conditions (Valladares et al., 2007; Chevin & Hoffmann, 2017). Phenotypic plasticity is used as a tool to comprehend how stress survival traits are altered by environmental conditions.

However, which traits are plastic and the significance of these changes during stress survival is still under debate. Here, we aimed to answer two questions: 1) do drought-caused changes tend to be expressed more in physiological or morphological traits? And 2) which of these changes is more linked to plant survival under stressful conditions? This is not a study focused on theoretical discussions and advances in phenotypical plasticity in stressful conditions (Valladares et al., 2007; Chevin & Hoffmann, 2017). Phenotypic plasticity here was just a tool used to understand how traits linked to stress survival are altered due to environmental conditions.

To help us answer these questions, we evaluated the performance of *Bauhinia cheilantha* (Bong.) seedlings (popularly known as pata-de-vaca in Brazil) facing varying levels of water restriction. This species has a broad geographic distribution and is also present in landscapes of the Brazilian seasonally dry tropical forest known as the *Caatinga*. *B. cheilantha* colonizes both primary and secondary forest formations with varying degrees of plasticity in various untested attributes in this study (Campos et al., 2020). We hypothesize that physiological traits will have a higher degree of change compared to morphological traits, potentially resulting in phenotypic plasticity. The paper will discuss the species's survival implications resulting from these characteristics.

Material and Methods

Two experiments were conducted to analyze the morphophysiological responses. The first experiment aimed to analyze the physiological responses of *B. cheilantha* seedlings exposed to water shortage by collecting plant material for destructive analysis. A second experiment was conducted to examine *B. cheilantha*'s growth and morphological alterations under water scarcity. Seedlings were cultivated from seeds harvested in a semi-arid terrain in the city of Petrolina, located in the state of Pernambuco, Brazil. After germination in washed sand (n=100), we transferred 20 individuals approximately two months of age to 4.5 kg pots, containing as substrate vegetal soil, washed sand, and bovine manure in a proportion of 3:1:1. v/v supplemented with 50g of potassium chloride and simple superphosphate. Plants were watered daily near field capacity (20%) and soil moisture was monitored using a Falker HFM2010 Hydrofarm moisture sensor during the period prior to the differentiation of the water treatments (approximately 30 days).

Plants were arranged in a completely randomized experimental design, featuring four water treatments. The control group was watered daily while the S7 group received water every seven days. The SR group had water withheld until a loss of turgidity was noticed. Recovery irrigation (RI) consisted solely of plants that reached the SR and were subsequently re-irrigated, and recovery was determined based on the presence of turgor recovery and increased soil moisture in the pots. Twenty seedlings were studied with five replicates per treatment. The procedures utilized during the acclimatization period in the first experiment were also implemented in experiment 2. In the latter experiment, the design was completely randomized, utilizing three different water supplies: daily irrigation as the control group, seven-day intervals between irrigations (S7), and water deficiency until loss of turgescence occurred (SR). The SR treatment involved rewatering plants, then suspending irrigation again, repeating this cycle over the 15-week experimental period. Each treatment had ten replications, and there were 30 seedlings in total.

Plant growth analyses were assessed on a weekly basis for 15 weeks. Plant height was measured using a 50cm ruler, with the criterion being the distance from the base of the plant to the tip of the last fully formed leaf. To measure stem diameter, a digital caliper was used on a region approximately 3 cm from the surface of the pot, marked previously with a permanent marker. Only fully expanded leaves were considered for our weekly counting.

At the conclusion of the experiment, we measured the leaf area (LA) per plant using the leaf contour method and calculated dry matter production (Benincasa, 2003). We harvested the plants, separated them into leaves, stems, and roots, and dried them in paper bags in a forced-air circulation oven at 65ºC until reaching a consistent weight. After drying, we weighed the material on an analytical balance (Shimadzu AUY220) to determine the dry matter weight of leaves (LDM), stem (SDM), roots (RDM), and total dry matter (TDM). We also calculated the leaf area ratio (LAR), specific leaf area (SLA), root-to-shoot ratio (R/S), biomass partitioning to leaves (BPL), stem (BPS), and roots (BPR).

Relative water content (RWC) was estimated every two weeks at noon by measuring leaf blades with an area of approximately 1cm². The fresh weight (FW) was obtained by weighing the cut blades, after which they were hydrated in Petri dishes for 24 hours to determine the turgid weight (TW). Subsequently, the blades were dried in a forced-circulation oven until they reached a constant weight to determine the dry weight (DW). To calculate RWC, the following equation was used (Weatherley, 1950): RWC = (FW - DW) / (TW - DW) x100.

We collected half a gram of fresh leaf tissue (FW) to quantify osmotically active organic solutes. We prepared crude extracts by macerating FW in a mortar containing 5 mL of 0.1M monobasic sodium phosphate buffer, pH 7, and 0.01M EDTA. The mixture was filtered, centrifuged at 4000 x g for 10 minutes, and the resulting supernatant was stored for further analysis.

The concentration of total soluble sugars (TSS) was determined in micromoles per gram of fresh weight ($\mu mol.g^{-1}$ FW) using the phenol sulfuric acid method (Dubois et al., 1956). The concentration of free proline (FP) was measured in micromoles per gram of fresh weight ($\mu mol.g^{-1}$ FW) using ninhydrin as a specific reagent and pure proline as a standard (Bates et al., 1973). Additionally, we measured total soluble proteins (TSP) using the dye-binding method and expressed the results in milligrams per gram of fresh weight (mg.g^{-1} FW), with pure bovine serum albumin as the standard (Bradford, 1976). We also quantified the organic solutes that are osmotically active in both leaves and roots.

The plasticity index (PI) indicates the phenotypic distance expressed when exposed to varying environmental conditions, ranging from 0 (no plasticity) to 1 (maximum plasticity). The IP value is calculated by dividing the difference between the highest (HM) and lowest mean (LM) value between treatments, by the highest average value (HM). A greater IP value reflects greater plasticity of the analyzed variable (Valladares et al., 2007).

The study data was analyzed using descriptive statistics. Afterwards, they underwent analysis of variance (ANOVA) and means were compared using the Tukey test (P<0.05). Graphs and tables were created using SigmaPlot 11.0 (SigmaPlot, La Jolla, CA).

Results and discussion

The severe water restriction (SR) resulted in a 25% decrease in SD, a 45% reduction in the production of new leaves (LN), and a 62% reduction in leaf area (LA). Consequently, dry matter production was reduced by 47% in the leaves, 42% in the stem, and 77% in the roots, leading to a 60% reduction in total dry matter production. In contrast, severe water restriction did not have an impact on plant height, SLA, and LAR (Table 1).

Table 1. Effects of intermittent drought on vegetative growth, dry matter accumulation and biomass partition in *Bauhinia cheilantha* seedlings. Values are means (n=10). Height (H) (cm), stem diameter (SD) (mm), leaf number (LN), leaf dry matter (LDM) (g), stem dry matter (SDM) (g), root dry matter (RDM) (g), total dry matter (TDM) (g), leaf area (LA) (cm²), specific leaf area (SLA) (cm^2.mg^{-1}), leaf area ratio (LAR), biomass partition to leaves (BPL) (%) biomass partition stem (BPS) (%), biomass partition to roots (BPR) (%) and root/shoot ratio (R/S). Equal letters do not differ by Tukey's test (P<0.05).

Plant growth				Carbon allocation			
	C	S7	SR		C	S7	SR
H	56.1 a	57.2 a	56.1 a	LDM	3.57 a	3.5 ab	1.92 b
SD	5.4 a	4.7 b	4.0 c	SDM	3.6 a	2.7 b	2.1 b
LN	12.6 a	11.8 a	7.1 b	RDM	9.0 a	3.6 b	2.2 b
				TDM	16.2 a	9.8 b	6.2 c
Leaf development				Biomass partition			
	C	S7	SR		C	S7	SR
LA	297.9 a	218.4 b	112.6 c	BPL	22.2 c	35.8 a	30.2 b
SLA	83.9 a	62.8 a	61.9 a	BPS	22.3 c	26.9 b	34.5 a
LAR	18.6 a	22.5 a	18.1 a	BPR	55.4 a	37.1 b	35.1 b
				R/S	1.25 a	0.59 b	0.54 b

Regarding biomass partition, no clear patterns were identified. BPL was higher under moderate water restriction (S7), BPS increased under severe stress (SR), and BPR reduced in both moderate and severe stress. This dynamicity was reflected in the root/shoot ratio which showed a reduction of 47% and 57% in S7 and SR stressed plants, when compared to the control, respectively (Table 1).

We observed a decrease in RWC with an increase in drought stress. RWC was reduced by approximately 52% in SR-stressed plants. Upon re-irrigation, plants exhibited an increase in their RWC, indicating recovery. No significant changes were detected in RWC among control, S7, and recovery plants (Figure 1D).

Soluble sugar accumulation fluctuated over time (see Figure 1A). The concentration of these compounds decreased over time, and comparable values were observed among the water treatments, indicating a greater movement of solutes to other plant organs as the plant develops. Total soluble sugar concentrations ranged from 67.2 to 724.7 µg/gFW (see Figure 1A). In contrast to carbohydrates, the concentration of soluble proteins in the leaves increased over time under stress (see Figure 1B). Notably, there were no significant changes identified between the control, S7, and RW treatments. The concentration of soluble proteins ranged from 6.9 to 49.9 mg/gFW, as shown in Figure 1B. No significant changes were observed in soluble protein concentrations in the roots, as depicted in Figure 1E. Proline concentration in the leaves increased under severe stress, indicating a peak at the end of the experiment. A similar trend was observed in the roots, albeit to a lesser extent, as illustrated in Figure 1C. Proline values ranged from 4.56 to 180.5 µmol/gFW, increasing approximately 30-fold. These unique responses in solute accumulation confirm their dynamic nature, which will be discussed to some extent in the present study (see Figure 1C, D).

Finally, we calculated the plasticity index (PI) of the analyzed attributes to determine which traits exhibit greater plasticity. Our objective was not to compare the plasticity values between morphological and physiological traits, given that biochemical changes can occur within minutes, whereas morphological alterations require a prolonged period of acclimation and the formation of a new organ under the present circumstances. We aimed to assess the extent of trait variation within treatments rather than hastily comparing variables, to comprehend the significance of these fluctuations within the current context.

Thus, *B. cheilantha* exhibited plastic biochemical traits with values exceeding 0.8 in the plasticity index (Figure 2). Notably, the most plastic variable observed was free proline in leaves (FPL), followed by total soluble carbohydrates (SCL) and total soluble proteins (SPL), all in leaves. Additionally, free proline in roots (FPR) was found to be a plastic attribute in alignment with root dry matter. Variables such as Relative Water Content (RWC), Stem Diameter (SD), Specific Leaf Area (SLA), Total Soluble Proteins in Roots (SPR), and Leaf Area Ratio (LAR) exhibited stable values across diverse water deficit regimes and failed to exhibit any plastic behavior. The specific leaf area (SLA) and leaf dry matter content (LDMC) did not exhibit plastic responses to varying water deficit treatments, maintaining consistent values across moisture regimes. The implications of these findings will be further examined in the subsequent discussion.

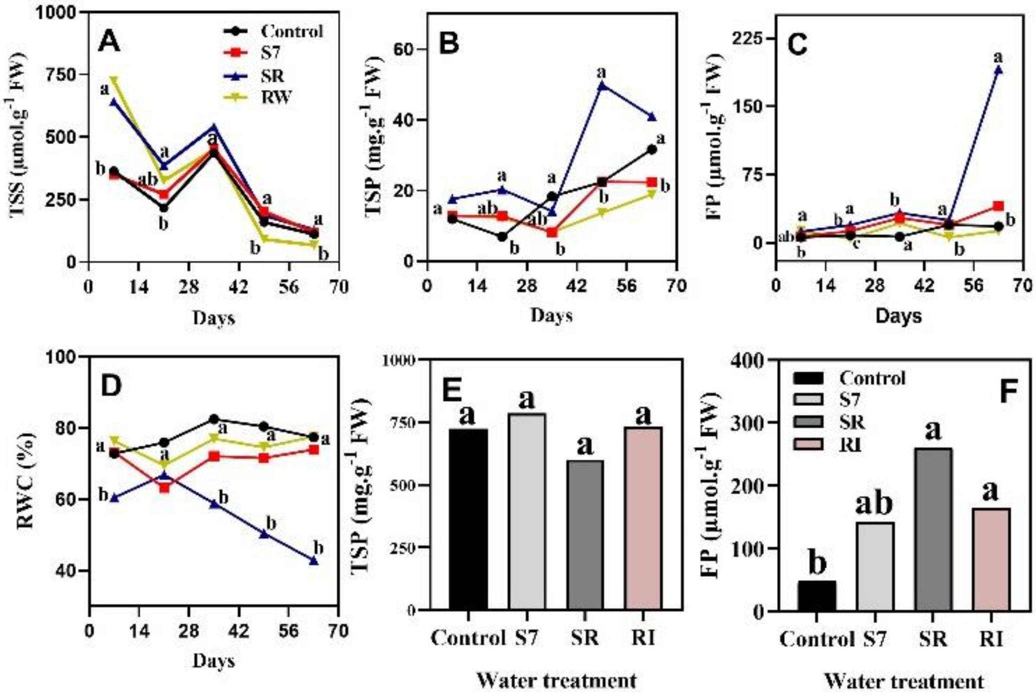

Figure 1. Concentration of osmotically active solutes in leaves and roots, and leaf relative water content of *B. cheilantha* seedlings under intermittent drought. A. Total soluble carbohydrates; soluble proteins (B), free proline (C) and relative water content (D) in leaves at 7, 21, 35, 49 and 63 days of the experimental period, and concentration of soluble proteins (E) and free proline (F) in roots after 63 days of water stress regimes. Mean values ± Control, with daily watering, S7 intervals in irrigation of 7 days, SR intervals in irrigation until they show symptoms of wilting in the leaves and RW 48h after rewatering. Equal letters do not differ by Tukey's test (P<0.05).

In our study, we found that drought resulted in morphological changes in *B. cheilantha* seedlings, generally leading to reduced growth parameters, carbon partition, and accumulation. These effects are widely recognized consequences of drought and were mostly traits exhibiting low levels of plasticity, except for RDM, TDM, and LA, which exhibited plastic behavior. Additionally, various organs displayed differing responses to drought, providing the species with a high level of plasticity in physiological characteristics rather than morphological ones. This indicates a nuanced morpho-physiological plasticity for the species.

Growth reductions resulting from drought occur due to restrictions in turgor pressure required for cell elongation (Anjum et al., 2017). Indeed, our plants displayed reduced traits due to limited water supply, necessary for maintaining growth rhythms (Santos Junior et al., 2020; Oliveira et al., 2021). Nevertheless, *B. cheilantha* seedlings decreased their LA in response to the stress, but we posit that this was a passive response to dehydration rather than a result of morpho-anatomical changes caused by stress. Minor changes occurred in LDM, but there was no response in SLA and LAR, which supports our statement that plasticity changes in LA are linked to reductions in water content and not associated with drought-induced structural changes because SLA and LAR did not display any inter-specific changes or plasticity degree.

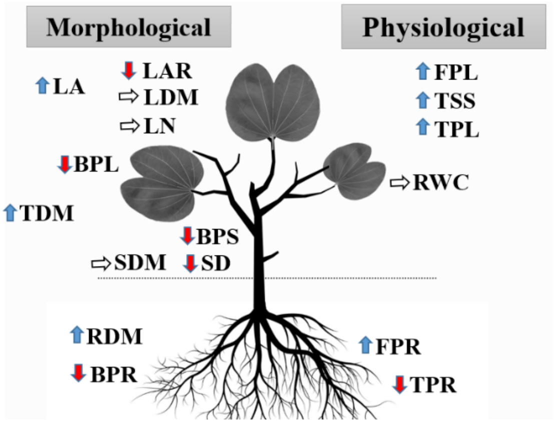

Figure 2. Plasticity index in *B. cheilantha* seedlings under different water regimes. Blue arrows indicate features that expressed high plasticity index values (> 0.8), white arrows indicate intermediate plasticity values (0.5 – 0.4), and red arrows indicate low plasticity index values (< 0.4). The aforementioned traits refer to leaf area (LA), Leaf area ratio (LAR), Leaf dry matter (LDM), Leaf number (LN), Biomass partition to leaves (BPL), total dry matter (TDM), stem dry matter (SDM), Biomass partition to stem (BPS), stem diameter (SD), Root dry matter (RDM), Biomass partition to roots (BPR), Free proline in leaves (FPL), Soluble carbohydrates in leaves (SCL), total proteins in leaves (TPL), Relative water content (RWC), Free proline in roots (FPR) and total proteins in roots (TPR).

Reducing RWC is a passive response associated with impairment in stomatal valves, leading to tissue dehydration. Although we did not assess stomatal responses in our study, *B. cheilanta* increases stomatal resistance under drought (Silva et al., 2004), which aids in conserving water. Furthermore, we observed an accumulation of soluble sugars with osmotic properties. However, our findings indicated a decrease in RWC. Thus, we propose that the presence of these compounds results from cellular dehydration rather than synthesis processes. Additionally, carbohydrate buildup indicates inefficiencies in photoassimilate transport resulting from stress during early developmental stages, causing accumulation in source regions (Klein et al., 2014).

Most of the reductions in morphological traits caused by the drought showed low levels of plasticity (Figure 3). This response may reflect the ecological characteristics of tree species with a slow growth rate, such as *B. cheilantha* (Vaccaro et al., 1999; Vaz & Tozzi, 2003), which tend to express greater stabilization of their growth rates even in heterogeneous environments. This phenomenon was also noted in seedlings of *Hymenaea coubaril L*., a species from the same botanical family and similar ecology. Over the course of 18 months in a *Cerrado* grassland landscape, this species showed the stabilization of various functional traits associated with slow growth rates (Pereira & Rodrigues, 2012).

Proline accumulation can increase by 40 times under stress (Sánchez et al., 1998). However, its contribution to osmoregulation may be around 1% with considerable uncertainties about its efficacy (Fallard et al., 2018). It is observed that proline increases under stress do not necessarily correlate with osmoregulatory properties. This accumulation is believed to relate to the protection and stabilization of biomembranes, macromolecules, and respiratory substrates during stress recovery (Hare & Cress, 1997; Kishor & Sreenivasulu, 2014; Blum, 2017), which has been previously discussed by Silva et al. (2004) and other authors. It is important to note that survival under drought requires several strategies in conjunction. Thus, the accumulation of these compounds alone does not guarantee complete drought tolerance. However, the mechanisms that confer this tolerance utilize the modulatory strategy, as demonstrated by Hasegawa et al. (2000).

Here we demonstrate drought-induced changes in B. cheilantha seedlings and their potential contributions to plant survival (Freitas & Silva, 2018; Silva et al., 2010). Leaves, being sensitive to alterations in water supply, often display a variety of changes. Nevertheless, certain leaf traits exhibited low levels of plasticity whilst some root traits demonstrated plasticity. These modifications showcase the species' adaptability to environmental changes and their probable connection to survival.

Conclusion

The water restriction resulted in the accumulation of organic solutes but did not lead to an increase in relative water content. The imposed stress caused a decrease in several morphological traits, but these changes were not deemed to be plastic. Plasticity was more apparent in physiological attributes than in morphological traits, although some of the latter were also observed to be plastic. Furthermore, the species prioritizes investing in stems over roots, even under stressful conditions. Changes in morphological traits resulting from drought were primarily linked to reduced plant growth, which responds to stress by minimizing transpiring areas and preserving water. It remains uncertain whether this is a strategic adaptation or an outcome of cell dehydration. In contrast, most changes in physiological traits were related to detoxification and shielding from the injurious effects of dehydration after RWC was diminished due to stress.

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