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The effects of different irrigation frequencies in morphological responses of *Talinum paniculatum* (Jacq.) Gaertn.

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INFO

Keywords
growth
water availability
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ABSTRACT

Water is essential for plant survival and understanding plant acclimatization to irrigation variations is necessary considering global climate change. However, few studies relate plant responses to variations in irrigation frequency. Therefore, we tested the influence of four irrigation treatments in Talinum paniculatum (Jacq.) Gaertn, an edible tropical plant: constant (C), predictable variable (PV), unpredictable variable (UV) and extremely variable (EV), keeping the same number of irrigation events for all treatments at the end of the experiment. Root and shoot length, root/shoot ratio, root, shoot and leaf fresh and dry mass, leaf number, stomatal density, stomatal guard cells length and stomatal area index were measured. T. paniculatum plants that received higher irrigation frequencies (C and PV treatments) showed greater growth. Plants in the EV treatment exhibited reduced growth, with shorter shoot length, lower fresh and dry weight of shoots, and a lower number of leaves, compared to the C and PV treatments. However, plants in the EV treatment had a higher root/shoot ratio, indicating greater biomass allocation to the root system, suggesting a strategy to increase water uptake efficiency and increase survival rates under drought stress. Some traits did not differ between treatments, such as root length, guard cell length, and stomatal density, which may be because T. paniculatum is a facultative CAM plant. Thus, T. paniculatum responds to changes in irrigation frequency and evaluating the responses of tropical plants to different precipitation frequencies can favor our prediction of vegetation responses considering current precipitation changes.

Palavras-chaves
crescimento
disponibilidade de água
estômatos
frequencia de irrigação

RESUMO

Efeitos de diferentes frequências de irrigação nas respostas morfológicas de Talinum paniculatum (Jacq.) Gaertn.

A água é essencial para a sobrevivência das plantas e a compreensão sobre a aclimatação das plantas às variações de irrigação é necessária considerando as mudanças climáticas globais, no entanto, poucos estudos relacionam as respostas das plantas a variações da freqüência de irrigação. Assim, testamos a influência de quatro tratamentos de irrigação em Talinum paniculatum (Jacq.) Gaertn, uma planta tropical comestível: constante (C), variável previsível (PV), variável imprevisível (UV) e variável extrema (EV), mantendo o mesmo número de eventos de irrigação ao final do experimento. Foiavaliado o comprimento de raiz e parte aérea, relação raiz/parte aérea, massa fresca e seca de raiz, parte aérea e folha, número de folhas, densidade estomática, comprimento das células guarda dos estômatos e índice de área estomática. Plantas de T. paniculatum que receberam maior freqüência de irrigação (tratamentos C e PV) apresentaram maior crescimento. Plantas mantidas no tratamento EV exibiram redução do crescimento, com menor comprimento da parte aérea, menor massa fresca e seca da parte aérea e menor número de folhas, comparado aos tratamentos C e PV. Entretanto, plantas do tratamento EV tiveram maior taxa raiz/parte aérea, indicando maior alocação de biomassa para o sistema de raiz, sugerindo estratégia para aumentar a eficiência na absorção de água e aumentar a taxa de sobrevivência sob estresse por seca. Algumas características não diferiram entre os tratamentos, como comprimento da raiz, comprimento das celula-guarda e densidade estomática, o que pode ser devido T. paniculatum ser uma planta CAM facultativa. Assim, T. paniculatum responde a mudanças na frequência de irrigação e avaliar as respostas de plantas tropicais a diferentes frequências de precipitação pode favorecer nossa previsão de respostas da vegetação em vista das mudanças atuais de precipitação.

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INTRODUCTION

Climate change is a global public and political problem that leads to extensive debates and experimental efforts to understand impacts on species using simulations focusing on plant-environment interactions (Moler et al., 2021; Varol et al., 2021; Varol et al., 2022).In the last few decades, plants natural environment has been extensively changed by human activities, thus modifying the quantity, distribution and quality of resources available.Soil water content is one of the most important factors for plant survival and colonization (Riederer and Schreiber, 2001; Shao et al., 2008) and its availability may induce several morphological variations (Valladares, 2017).

Global precipitation patterns have undergone many changes (Allan and Soden, 2008; Felton et al., 2021).Recent data have shown that climate change impacts hydrological cycles by leading to extremes of wet and dry years and causes longer and moreintense dry periods (Trenberth et al., 2014; Knapp et al., 2015; Sun et al., 2022). The spatial precipitation pattern has also been affected, with regions subjected to strong or weak alterations and a strong contrast between wet and dry regions of the globe (Trenberth et al., 2014; Sun et al., 2022). However, more than water quantity, changes in predictability and heterogeneity of precipitation distribution have become frequent, with variations within and between years (Knapp et al., 2015; Felton et al., 2021).

The ultimate result of these precipitation changes is variation in soil water content and thus in water resources available for plant use (Zeppel et al., 2014). Those changes have a profound impact on communities that use these environmental signals to synchronize their life cycle stages (Memmott et al., 2007; Mondoni et al., 2012; Kupler and Kotowska, 2021). Decreased and increased water soil content may represent a stress condition for terrestrial plants, and plants face this in many different ways, including anatomical, morphological and altered resource allocation, which may improve their survival and reproduction in modified environments (Riederer and Schreiber, 2001).

Plant sensitivity to global change varies among species, developmental stage (Moler et al., 2021), functional traits (Anderegg, 2015; Bjorkman et al., 2018) and plant life form (Broennimann et al., 2006).The effects of decreased water availability and the responses of plants have been extensively investigated and contributed to important information on acclimatization mechanisms and their possible consequences (Osakabe et al., 2014; Prince et al., 2017). To deal with effects unrelated to the amount of water, studies with different irrigation frequencies, including predictability, heterogeneity and intensity of watering frequencies may provide additional support for understanding this different type of plant-environment interaction. This information may contribute to predicting and modeling plants responses to global changes (Zeppel et al., 2014). It can also improve simulations that deal with crop tolerance, given the effects of unpredictable environmental alterations on crop production and the importance of phenotypic plasticity to yield-optimized crops and thus to maintenance of global food security(Dalal et al., 2017).

Plant development depends on cell division, expansion and differentiationbetween organs, processes that are affected by water availability (Correia et al., 2001). Perennial plants are believed to be more sensitive than annuals to climate alterations (Broennimann et al., 2006),and thusmay produce enlightening results of simulations based on these changes.

Talinum paniculatum (Jacq.) Gaertn., popularly known as “major-gomes”or “beldroegão” or “Maria-gorda”, is a CAM facultative perennial herb (Güerere et al., 1996; Herrera, 2009) widely distributed, recorded as invasive in some locations (Wang et al., 2016). This weed has broad morphological variation and economic and medicinal importance (Thanamool et al., 2013). In Brazil, *T. paniculatum* is considered an unconventional food plant (Kinupp and Lorenzi, 2014; Biondo et al., 2018; Moura et al., 2021) that grows spontaneously in different environments. For consumption, it is generally harvested 60 days after planting to use its sautéed leaves in the preparation of various foods (Castro and Devide, 2016). This plant has large morphological plasticity (Thanamool et al. 2013). *T. paniculatum* is hermaphrodite, presenting a high degree of inbreeding and populations highly adapted to the local conditions (Valerio and Ramírez, 2003) pollinated by bees (Taura et al., 2007).

Here, we used simulated water frequencies, including intensity, heterogeneity and predictability of irrigation patterns, and we tested their influence on morphology and allocation responses of *T. paniculatum*. The objectives of this paper included: (1) To simulate different irrigation frequencies based on precipitation changes that are already occurring. (2) To evaluate morphological, allocational and anatomical responses of *T. paniculatum* to different water frequencies. (3) To compare these variations and determine which irrigation frequency results in lower plant development, linking this to other works about the effects of global climate change.

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MATERIALS AND METHODS

Seed collection

The seeds were collected in Paraná state, Southern Brazil, from 40 populations separated by 3 to 450 km, covering the municipalities of Ponta Grossa (25° 05′ 42″ S, 50° 09′ 43″ W, Porto Rico (22º46'20" S, 53º16'01" W), Flórida (23º05'13" S, 51º57'14" W), Maringá (23°25′30″ S, 51°56′20″W), and Santa Fé (23°02'16" S, 51°48'18" W). The climate covering the cities of Flórida, Maringá, Porto Rico, and Santa Fé is classified as Cfa, with an average temperature of 21.4 to 22.9°C and an average annual precipitation of 1200 to 1400 mm. Ponta Grossa's climate is classified as Cfb, with an average temperature of 16.5 to 17.5°C and an average annual precipitation of 1400 to 1550 mm (Aparecido et al., 2016). Based on information from other works with *T. paniculatum*, which indicate a high degree of inbreeding and populations highly adapted to local conditions (Valério and Ramirez, 2003), the seeds were sampled from 40 populations separated by distances between 3 km and 450 km to ensure that results can reflect a realistic species acclimatization response. About 100 seeds per population were collected, 4000 seeds at all.

Experimental design

Seeds of *T. paniculatum* were germinated in 200 seedling bags 18x30x20 cm, 50 per treatment. The plants were kept for 15 days under daily irrigation to ensure their germination and emergence and then distributed among the treatments for 150 days. The substrate used was standardized for all treatments, using 2:1 of washed sand and commercial substrate Genesolo (GenfértilLtda EPP, Mogi Mirim, SP, Brazil). The substrate is a Class B Organic Fertilizer, rich in organic matter, composed of sugarcane bagasse, coffee straw, and peat. The substrate contains 15% organic carbon, a pH of 6.0, and a carbon-to-nitrogen ratio of 20 (C/N) (Information obtained from the manufacturer.)

The experiment was conducted in the greenhouse of the State University of Maringá, where experimental plots was divided into four sectors. The experimental plot was located in a sunny site covered by a plastic roof to ensure that place was protected against rain. To investigate the effects unrelated to the amount of water, an automatic irrigation system provided by a digital water timer (Melnor Electronic Aqua Timer, Melnor, Winchester, VA) was used to create different precipitation patterns, using four independent outputs with specific programming.

The irrigation system was made with wooden frames measuring 1.5 m in height, in which a garden hose was installed with Model MA-50 micro-sprinklers with screw base, Agrojet, for irrigation. Thus, eight sprinklers were placed on the installed hoses, two for each treatment. The irrigation area of each micro-sprinklers was verified toensure that plants received a similar water quantity in each experimental group, about 100 mL of water in each irrigation event.

The following irrigation frequencies were tested according to the methodology described by Scheiner (2002), being four treatments with different irrigation were used: constant (C), predictable variable (PV), unpredictable variable (UV) and extremely variable (EV). At the end of the experiment, the same number of irrigation events occurred in all treatments.

Constant (C) - The irrigation was regular, programmed every 48 hours during the whole experiment.

PredictableVariable (PV) - Irrigation was alternated cyclically between different periods. Thus the plants were watered every 24 h for five days, every 72 h for nine days, every 48 h for 10 days and every 72 h for six days. This cycle was repeated five times during the experiment, that is, every 30 days.

UnpredictableVariable (UV) - Irrigation was randomly and non-cyclically alternated between the same irrigation periods as the unpredictable Variable treatment.

Extremely Variable (EV) - Irrigation was performed every 12 hours for five days, without irrigation for nine days, every 48 hours for 10 days and without irrigation for six days, repeating the cycle five times during the experiment, in order to avoid interaction of the factors unpredictability and intensity.

Thus, for all treatments, the number of irrigation events was the same at the end of the experiment (75 irrigation events), differing in the heterogeneity, predictability and severity of this distribution. The irrigation depth is 5.085 mm per irrigation event (5 minutes per event).

Postharvest measures

Aerial part length, root length, root/aerial part ratio, plant fresh mass, plant dry mass and leaf number were measured in 20 plants per treatment. Stomatal density, guard cell length and stomatal area index were also analyzed from leaves of 5 plants per treatment. Root and shoot lengths were measured with a ruler. To obtain fresh mass, plants were separated by treatment and removed from the substrate, separated into shoots, roots, and leaves, and weighed on a precision analytical balance (BEL Mark M164Ai, Bel Equipamentos Analíticos LTDA, Piracicaba, SP, Brazil). The plant material

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was then placed in an oven at 60°C for one week. Dry mass was then obtained using a precision balance. The number of leaves was counted manually.

Leaves for anatomical analyses were randomly chosen, being removed from the third node in the base apex direction. The freshly collected leaves were cut free-hand and the samples were placed in hypochlorite solution (%) and then stained with Safrablau solution. Afterwards, these stained epidermal fragments were placed on slides, glycerin was added and covered with a coverslip. Five sections were taken per leaf, which were photographed in a digital camera (Leica ICC50, Leica Microsystems, Wetzlar, Germany) coupled to a microscope (Leica DM500, Leica Microsystems, Wetzlar, Germany). Stomatal, epidermal cell, and guard cell length counts were performed manually using Image Pro Plus 4.5 software (Media Cybernetics, Rockville, MD, USA). Stomatal density (SD) was calculated using the formula SD = *N*S/*A*S, where NS indicates the number of stomata and AS (mm^2) the area where the stomata are located. Stomatal area index (SAI) was calculated using the formula SAI = [(NS/(NE+NS)], where NE indicates the number of epidermal cells.

Data analysis

The experimental design was completely randomized. The effect of the different irrigation frequencies on plant length, mass, leaf number and stomatal traits was analyzed with one-way ANOVA. Tukey multiple comparisons were used to compare means. In all cases, a significance of 5% was used. In addition, to verify if the different irrigation frequencies may change the allocation pattern, a Covariance Analysis (ANCOVA) was performed. These statistical analyses were performed in software R version 3.0 (R Development Core Team 2012).

RESULTS AND DISCUSSION

The different irrigation frequencies changed morphological traits and allocation patterns in *T. paniculatum*. These changes occurred even though plants received the same amount of water at the end of the experiment. The four irrigation treatments induced changes in some of the evaluated traits, and these differences were greater in EV irrigation treatment. Thus, as water availability may influence many plant traits (Bjorkman et al., 2018), our study shows that plants can interact with water conditions that may vary in natural environments, but not only in relation to quantity.

Plant growth

In general, plant growth was higher in plants developed under C simulation. The same occurs with plants grown under PV irrigation, which were similar to those in C treatment for the majority of the evaluated traits. This greater growth t in C and PV treatments probably results from water availability, which is favorable to maintaining plant growth. This occurs because plant growth is mediated by cell division, expansion and differentiation, which are affected by water availability (Correia et al., 2001; Davatgar et al., 2009). Adequate water availability supports cell turgidity, which promotes cell expansion and growth, and maintains plant structure (Kim et al., 2024). Thus, the longer irrigation periods promoted by the C and PV treatments led to greater growth of *T. paniculatum* plants, with similar responses for most of the parameters analyzed. In contrast, a decrease in plant growth occurs under EV irrigation, and fresh and dry mass was 50% less when compared to C and PV simulations (Figure 1).

The intermediate values observed for the plant length and mass in the UV treatment are probably due to the randomization of the water program in repeated cycles of lower or greater water availability, generating conditions that are unfavorable to plant growth. This response probably results from different turgor pressures necessary to cell expansion; since turgor pressure is mediated by water conditions that may be greater than cell wall resistance to promoting plant growth (Shao et al., 2008; Husen et al., 2017).

Plants growing under abundant watering tend to prioritize aboveground growth (Moler et al., 2021). In *T. paniculatum,* the length of the aerial part was negatively affected by EV irrigation, while in all other treatments these values were similar (Figure 1a). However, the different water frequencies did not influence root development, which was similar among analyzed plants (Figure1b).The root traits directly affect plant ability to absorb soil water (Anderegg, 2015; Prince et al., 2017). In plants under EV irrigation, a similar root length, together with a decreased shoot length, can increase water capture and is, therefore, an efficient acclimatization strategy for environments with low or unstable water availability. The root/shoot ratio, contrary to aerial length, was greater in the EV treatment (Figure 1c). Likewise, the increase in root/shoot ratio, evidenced by the distinct correlation, indicates a higher allocation to this organ to the detriment of shoot growth in plants developed under EV irrigation, which is a recognized strategy to facilitate water absorption (Husen et al., 2017). The roots are highly plastic, changing their morphology and growth depending

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on water availability (Yan et al., 2022). These morphological and physiological changes are regulated by phytohormones in response to environmental stress. (Ma et al., 2024). Drought stimulates the production of abscisic acid (ABA), especially in the roots, and signals responses to water stress in the shoots through its transport via the xylem to the leaves, inducing stomatal closure due to drought (Wu et al., 2022). Thus, ABA regulates stomatal closure, reducing transpiration in response to water stress. Like this, reducing shoot biomass relative to the root system promotes water conservation by decreasing transpiring areas. This was observed in this study with *T. paniculatum*, which has the highest root/shoot ratio in the EV treatment.

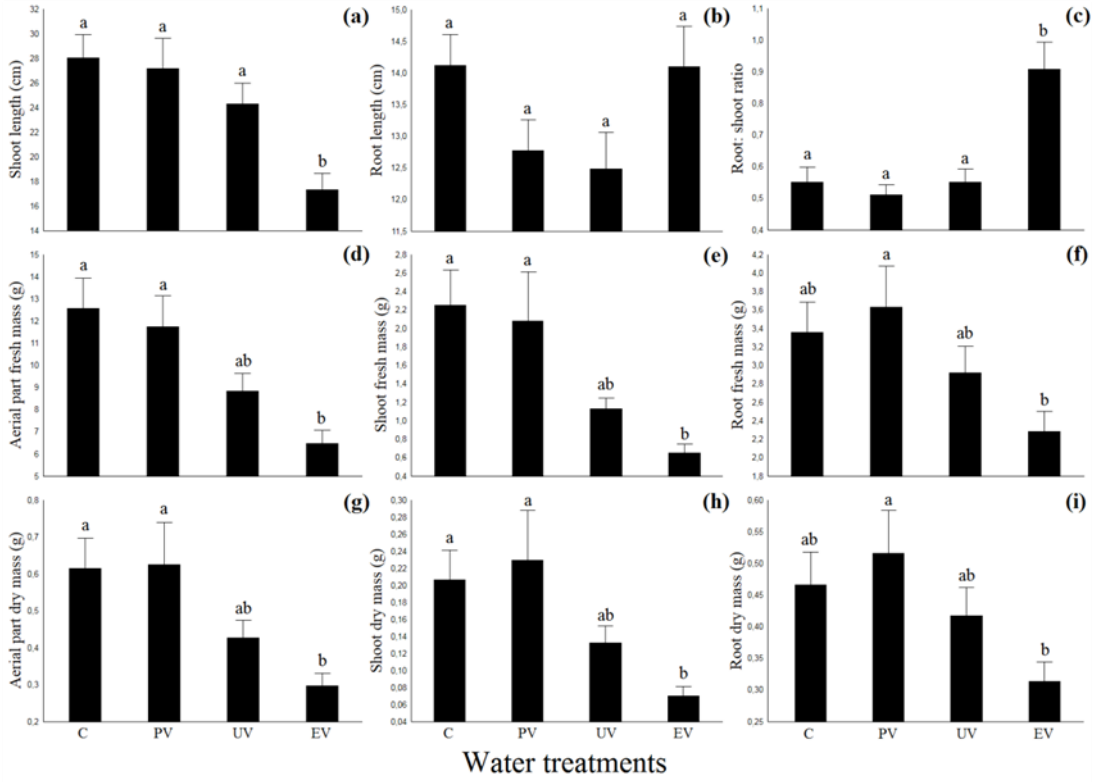

Figure 1 - Trait values measured in *Talinum paniculatum* according to the irrigation condition. Bars with different letters show statistical difference ($p < 0.05$). Mean ± standard error are indicated.

Plant fresh and dry mass was also frequently altered in response to different irrigation conditions (Borrajo et al., 2018). Shoot fresh and dry mass were significantly higher for C and PV irrigation frequencies. Lower values occur for the EV condition, as well as for plant length. Plants exposed to the UV treatment had intermediate values and were similar to all the others (Figure 1d, e). The lower value of these traits for the plants developed in the EV treatment is commonly related to low water conditions, since the increase in plant biomass depends on the maintenance of its physiology and efficient resource allocation (Fang et al., 2017; Liu et al., 2022), both processes that are affected by water stress (Husen et al., 2017).

Although the shoot fresh mass of EV plants was about 70% lower than that of plants growing in constant irrigation, this reduction was only 30% of root fresh mass (Figure 1f) . The same was observed for the dry mass, which for the aerial part and shoot was approximately 65% lower in plants grown under EV compared to plants under constant conditions (Figure 1g, h), while the root dry mass was only 30% lower (Figure 1i).

Thus, for several analyzed traits responses were found that were similar to those caused by water deficit when plants face an extreme change in water availability. These findings indicate that we must pay attention to climate change not only in relation to the volume of precipitation, but also to the way in which this distribution of rainfall occurs. Zhang et al. (2021) report that soil water availability is influenced by both the amount and distribution of rainfall, which can alter plant productivity.

Leaf traits

Leaf number varies according to irrigation frequencies. In the C treatment, plants developed more leaves, while the PV treatment did not differ significantly from Cand from UV. In the EV

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condition, leaves per plant decreased by 60 % when compared to C and were similar to those under UV irrigation (Figure 2a). Leaf fresh and dry mass, similarly to other evaluated traits, was higher in the C and PV irrigation treatments. The lowest values occurred in the EV treatment, and were intermediate in UV (Figure 2b, c). The reduction of leaf growth is also a typical response to low water availability (Borrajo et al., 2018). Together with this, reduced leaf size decreases the evapotranspiration area and thus reduces water loss. This response may, in turn, influence stomatal leaf number, since the stomatal density did not differ between the treatments.

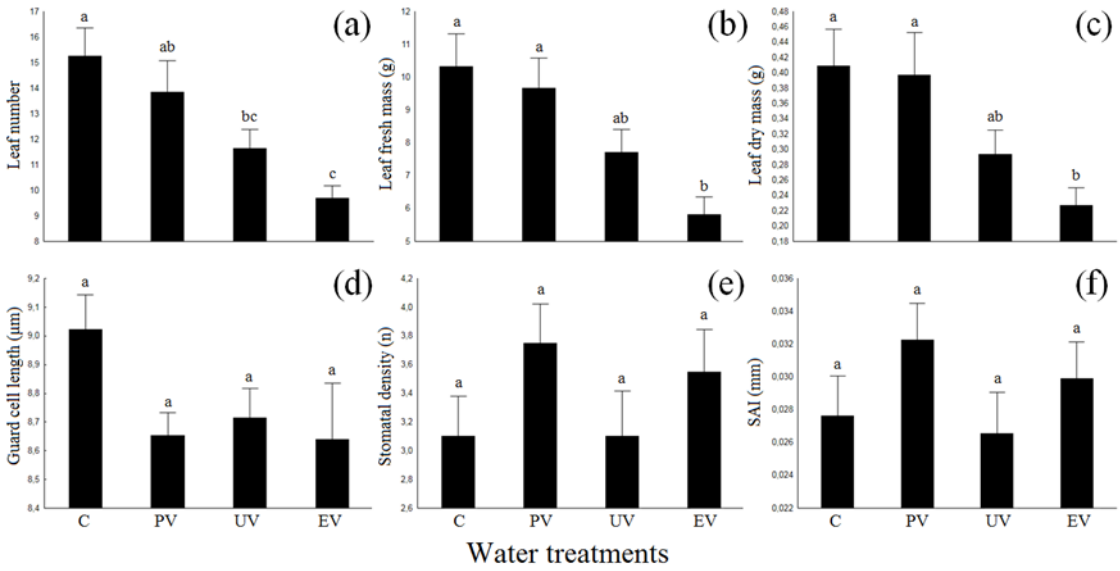

Figure 2 - Foliar traits measured in individuals of Talinum paniculatum according to the irrigation condition. Bars with different letters show statistical difference ($p < 0.05$). Mean ± standard error are indicated.

The epidermal traits of *T. paniculatum* did not change in response to irrigation frequency. The length of the guard cells (Figure 2d), stomatal density (Figure 2e) and stomatal area index were similar for both treatments (Figure 3). As stomata play a key role in plant water use (Bertolino et al., 2019) and the reduction of the stomatal number can also produce a negative effect on plant photosynthesis and thus lead to a decrease in growth (Husen et al., 2017), it was expected that this trait would respond to different irrigation frequencies. Hence, a smaller leaf area will also reduce the stomatal number and consequently the supply of CO_2. Under drought, tomato leaf stomata were predominantly affected, showing lower stomatal density and increased closure, which resulted in reduced photosynthesis and higher leaf temperatures (Jensen et al., 2024).

The responses found in this study could be even greater in plants that do not present a facultative CAM mechanism and are thus less able to tolerate water stress situations. *T.paniculatum* is a CAM facultative plant which may have contributed to the lack of differences in some measured traits.

Plant allocation

The covariance analyses show that treatment effects on plant allocation patterns differed among traits (Fig. 4). Plants developed under EV irrigation have different correlation between some traits when compared to others.Aerial dry mass is positively related to the total dry mass of the plant; however, this relationship differs between treatments ($F = 3{,}355$; $p < 0.05$), and the same occurs for the relationship between root length and total plant length ($F = 4.356$, $p < 0.05$) (Fig. 4A, B). In contrast, the relationship between shoot length and total plant length, although significant, did not vary in response to different irrigation frequencies ($F = 1.150$; $p < 0.33$) (Fig. 4C). Overall, the results showed that different irrigation frequencies affected the morphological traits of *T. paniculatum*. The covariance between traits revealed differences in allocation patterns in more severe or unpredictable irrigation frequencies. The EV treatment negatively affected plant growth and fresh and dry matter production. The changes in growth and plant allocation verified in different irrigation frequencies used in this study may represent a morphological response to increased resource acquisition, which also occurs in plants exposed to different soil water conditions (Liu et al., 2022).

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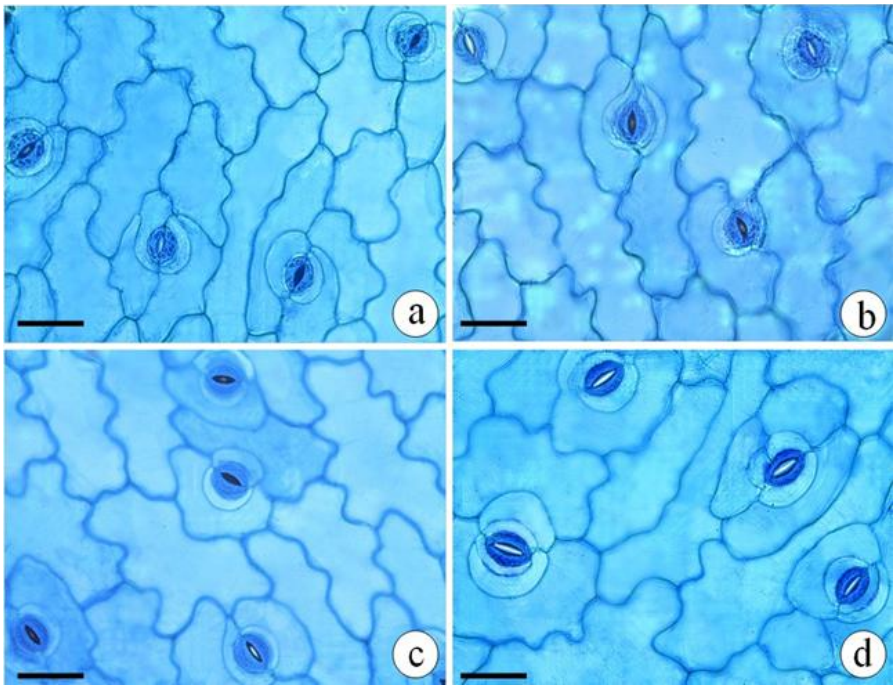

Figure 3 - Epidermis in Talinum paniculatum plants developed in different irrigation treatments. A. Constant. B. Predictable variable. C. Unpredictable variable. D. Extremely variable. Bar = 15 µm.

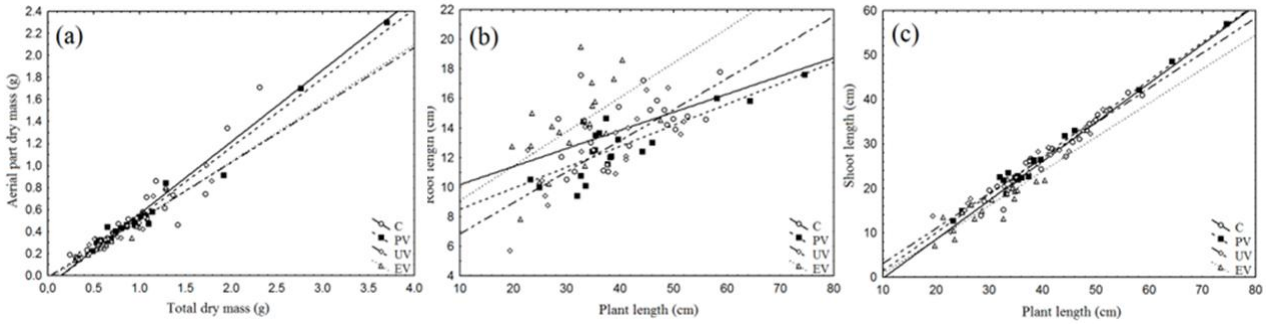

Figure 4 - Covariance of evaluated traits in Talinum paniculatum plants in different irrigation treatments. A. Constant. B. Predictably variable. C. Unpredictably variable. D. Extremely variable.

Plants grown in the EV treatment experienced both periods of abundant and absent irrigation. Thus as increased and decreased water availability in the soil can reduce plant growth (Garcia et al., 2008); these plants have lesser growth when compared to the other irrigation frequencies, which received water in a more regular way. However, plants exposed to abundant watering often increase aboveground growth in relation to belowground growth (Moler et al., 2021), and thus the allocation response observed in the EV treatment was more similar to those observed in plants under water stress. Water stress includes typical reduction of overall plant growth and a high root/shoot ratio (Shao et al., 2008), which tends to improve the acquisition of a limiting resource (Liu et al., 2022).

Considering the influence of irrigation frequency on plant productivity, additional studies are needed to account for the reduction in rainfall distribution due to climate change. Research addressing other physiological aspects, such as photosynthetic capacity, analysis of oxidative stress enzymes, and the accumulation of non-structural carbohydrates, can contribute to a better understanding of plant responses to changes in irrigation frequency.

CONCLUSIONS

T. paniculatum plants that received higher irrigation frequencies (C and PV treatments) showed greater growth. Plants in the EV treatment exhibited reduced growth, with shorter shoot length, lower fresh and dry weight of shoots, and a lower number of leaves, compared to the C and PV treatments. However, plants in the EV treatment had a higher root/shoot ratio, indicating greater biomass allocation to the root system rather than the

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shoot, suggesting a strategy to increase water uptake efficiency and increase survival rates under drought stress. Some traits did not differ between treatments, such as root length, guard cell length, and stomatal density. The lack of differences in some traits may be because *T. paniculatum* is a facultative CAM plant, which makes it capable of tolerating drought stress.

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