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Water Stress Effects on Growth, Physiology, and Bioactive Metabolite Accumulation in Javanese Ginseng (*Talinum paniculatum* Gaertn.)

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ABSTRACT

Understanding how *Talinum paniculatum* responds to varying water availability is critical to maximizing its cultivation under climate-induced changes. This study aimed to evaluate the effect of varying water availability on the morphophysiological traits and metabolite profiles of *Talinum paniculatum* grown under seven water levels (50%-110% field capacity (FC)). Key traits evaluated included growth index, leaf area, root length, biomass, physiological parameters (net assimilation rate, chlorophyll content, stomatal density, relative growth rate, and relative leaf water content), and metabolite composition using FT-IR analysis. The results showed that moderate drought (60-70% FC) enhanced root proliferation, photosynthetic efficiency, and bioactive compounds (flavonoids and phenolics), indicated by increased O-H stretch and naringin match scores. Correlation analysis revealed that biomass accumulation was mainly influenced by net assimilation rate, leaf area, and root traits, while stomatal density and relative leaf water content (RLWC) showed weaker associations with growth. Extreme drought and waterlogging reduced growth and metabolite stability, leading to pigment degradation and lower RLWC. FT-IR analysis further indicated significant changes in polysaccharide- and phenolic-related compounds. These findings suggest that mild water stress can promote adaptive plasticity, improving both the yield and medicinal quality of *T. paniculatum.*

Keywords: FT-IR analysis; morphology; physiology; *talinum paniculatum*; water stress

INTRODUCTION

Talinum paniculatum, or Javanese ginseng, is an Indonesian medicinal plant, valued for its young leaves, which are consumed raw or cooked (Lakitan et al., 2021). Its roots contain 16 compounds that serve as antioxidants, antimicrobials, anticancer agents, insecticides, etc. (Susilo et al., 2024). Environmental conditions influence the plant's growth, making its cultivation sensitive to climate variations.

Climate change poses a significant threat to plant survival by exacerbating floods and extreme precipitation, impacting water availability (Renziehausen & Frings, 2024). Plants often experience water stress during dry periods, with evapotranspiration exceeding water absorption and water saturation during the rainy season. These stressors affect plant growth, physiology, and secondary metabolite production (Sato et al., 2024; Zhao et al., 2024).

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Plants have developed various mechanisms to cope with water stress, affecting morphological (shoot growth, root growth, and leaf size), physiological (leaf water content, stomatal conductance, and photosynthetic pigments), and biochemical parameters (increase in secondary metabolites) as seen in various plant species, including herbaceous and woody plants (Nour et al., 2024). For instance, thyme plants adapt to water stress by restricting growth and reallocating carbohydrates to roots to enhance water absorption (Tátrai et al., 2016).

Some plants, like *Ailanthus altissima*, are highly resistant to water stress, as evidenced by their ability to increase leaf mass per area (LMA) under stress (Pepe et al., 2022). Some plants demonstrate remarkable resistance to water stress through morpho-anatomical adaptations that maintain water status and enhance resilience (Zahedi et al., 2025). Medicinal plants grown under water stress tend to accumulate higher quantities of secondary metabolites compared to those grown with ample water. For example, lavender showed significant changes in essential oil composition and secondary metabolites under drought (Hosseini & Heidari, 2025), while *Desmodium styracifolium* exhibited enhanced flavonoid biosynthesis under stress (Gao et al., 2024). *Talinum paniculatum* (Javanese ginseng) also endures prolonged water stress (Nurcahya et al., 2022), likely due to secondary metabolite accumulation, which helps plants withstand harsh conditions. However, previous studies on *T. paniculatum* under water stress have largely focused on basic growth parameters such as growth index, plant height, leaf number, fresh weight, etc. (Nurcahya et al., 2022), without comprehensively examining morphological, physiological, and phytochemical responses. This fragmented approach limits the ability to draw integrated conclusions about how water availability regulates both the agronomic performance and medicinal quality of this species. Therefore, this study aimed to evaluate the effect of varying water availability on the morphophysiological traits and bioactive metabolite profile of *T. paniculatum*.

MATERIALS AND METHODS

The plants used in this study were from a previous experiment (Nurcahya et al., 2022). The experiment was arranged in a Randomized Complete Block Design (RCBD) with a single treatment factor consisting of seven soil moisture levels based on field capacity (FC): 50% (A), 60% (A), 70% (C), 80% (D), 90% (E), 100% (F), and 110% (G) FC, with four replications (blocks) yielding 28 experimental units in total. Water treatments were initiated when plants reached 10-15 cm in height and maintained until harvest at seven months of age. Field capacity was determined gravimetrically prior to the experiment by saturating the growing medium and allowing it to drain for 48 hours. The actual volume of water applied per pot was calculated based on the target FC level and the weight of the growing medium. Soil moisture was monitored and adjusted daily throughout the experiment. At harvest, three plants per experimental unit were sampled for morphological and physiological measurements, while root material from all plants within a unit was pooled for phytochemical analysis.

Measurement of Plant Morphology

Plant morphology was measured at the end of the experiment, including leaf area, root biomass, root length, and growth index (GI). Root biomass was determined after carefully uprooting each plant

from the growing medium. Roots were separated from shoots by cutting at the crown using a sharp blade, and any adhering soil or debris was gently removed. Root fresh weight was then recorded using an analytical balance. The GI was calculated using Irmak et al. (Irmak et al., 2004):

$$GI = H + ((WEW + WNS)/2)/2 \quad (1)$$

where:
H: Plant height (cm)
WEW: the canopy width in the east-west direction (cm)
WNS: the canopy width in the north-south direction (cm)

Measurement of Plant Physiological Parameters

Chlorophyll content

Chlorophyll content was measured non-destructively using a Force Dualex Optical Leaf Clip Meter. The third fully expanded leaf from the apex was selected per experimental unit as the sampling unit. The leaf was inserted into the sensor clip of the instrument, and the reading was recorded directly from the device display. Measurements were taken once at the end of the experiment, and the value recorded for each experimental unit represented a single reading from the designated sampling leaf.

Net assimilation rate (NAR)

Plant dry biomass was recorded at two time points: the first measurement (W_1) was taken at the beginning of the treatment period (t_1), and the second measurement (W_2) was taken at the end of the experiment (t_2). At each sampling time, the corresponding leaf area (LA_1 and LA_2) was also measured using a leaf area meter. Plants were oven-dried at 70°C for 48 hours prior to weighing to obtain dry biomass values. NAR was then calculated according to (Díaz-López et al., 2020):

$$NAR = \left(\frac{W2-W1}{t2-t1}\right)\left(\frac{\ln LA2-\ln IA1}{LA2-LA1}\right) \quad (2)$$

Where:
NAR: Net assimilation rate
W1, W2: dry biomass weights of the plant at the respective times t2 and t1
LA1, LA2: the respective leaf areas corresponding to the times t2 and t1

Relative growth rate (RGR)

Relative growth rate was calculated using the formula (Hoffmann & Poorter, 2002). Plant dry biomass was recorded at two consecutive time points (the beginning and the end of the treatment period), and the data were then used to calculate RGR using the following formula:

$$RGR = \frac{(\ln W2 - \ln W1)}{(t2 - t1)} \quad (3)$$

Where:
W1 & W2: plant dry weight at times t1 and t2

Relative Leaf Water Content (RLWC)

Leaf disc samples were collected from the third fully expanded leaf from the apex and immediately weighed to obtain fresh weight (FW). Discs were then floated on distilled water in Petri dishes for 4-5 hours under dim light at room temperature to allow full rehydration, after which turgid weight (TW) was recorded. The leaf discs were then oven-dried at about 80 – 85°C for 24 h for dry weight (DW). RLWC was calculated according to (Smart & Bingham, 1974).

$$\text{RLWC (\%)} = [(\text{FW-DW}) / (\text{TW-DW})] \times 100 \quad (4)$$

Stomatal density

Stomatal density was measured with a formula according to (Paul et al., 2017). Leaf samples were collected from the abaxial surface of the third fully expanded leaf, gently washed with distilled water, and allowed to air-dry. Transparent nail polish was applied as a replica fluid to the abaxial leaf surface and left to dry completely before being peeled off carefully with adhesive tape. The nail polish replica was then mounted on a glass slide and observed under a light microscope (400× magnification). Three fields of view per sample were photographed, and stomatal counts were made in a defined area (mm^2).

Measurement of Plant Phytochemical Parameters

Plant Extract Preparation

The extraction was carried out using the maceration technique. Separated roots were dried at 50 degrees Celsius for four days. After the samples were dried, they were ground, followed by the addition of 200 grams of simplicia powder and 96 percent ethanol to a light-protected maceration vessel for three cycles of 24 hours with intermittent stirring. The extract of viscous liquid was concentrated using a rotary evaporator.

FT-IR analysis

The FTIR analysis was conducted at the Integrated Laboratory of Universitas Islam Indonesia using a Perkin Elmer Spectrum Two System L160000A equipped with an Attenuated Total Reflectance (ATR) accessory. For each sample, approximately 5 mL of the extract was applied directly onto the ATR crystal surface. Spectral data were recorded in the mid-infrared region (4000–450 cm^{-1}).

Data Analysis

All statistical analyses were conducted using RStudio (version 4.4.1) to evaluate the effects of water volume treatments on plant growth and physiological parameters. Prior to the analysis of variance (ANOVA), the homogeneity of variances was tested using Bartlett's test, and the additivity of the model was assessed using Tukey's test for non-additivity. A two-way ANOVA was then applied to assess the effects of treatment and replication (block effect) on each parameter. Post-hoc comparisons, if required, were conducted using Tukey's HSD test to identify differences among treatment groups. Significance was determined at a 95% confidence level ($p < 0.05$).

RESULTS AND DISCUSSION

Morphological Plasticity of *Talinum paniculatum* Under Water Stress

The most critical finding from the morphological analysis was that moderate water deficit at 60% FC significantly enhanced root elongation and biomass while maintaining acceptable shoot growth, demonstrating that *T. paniculatum* strategically prioritizes root development under mild drought as an adaptive water-foraging mechanism. Although the growth index (GI) at 60% FC was numerically highest, it did not differ significantly from other treatments (Figure 1a), indicating that overall canopy architecture was relatively plastic across moisture levels. In contrast, leaf area, root length, and root biomass were significantly influenced ($p < 0.05$), confirming that underground growth responses were the primary adaptive output of mild water stress (Figures 1b-d). This pattern suggests that *T. paniculatum* employs a plastic growth strategy, where mild drought triggers compensatory growth mechanisms that enhance resource allocation to both shoots and roots. Similar compensatory growth responses have been observed in grasslands where mild drought promotes accelerated recovery or overcompensation when water is available again (Zhou et al.,

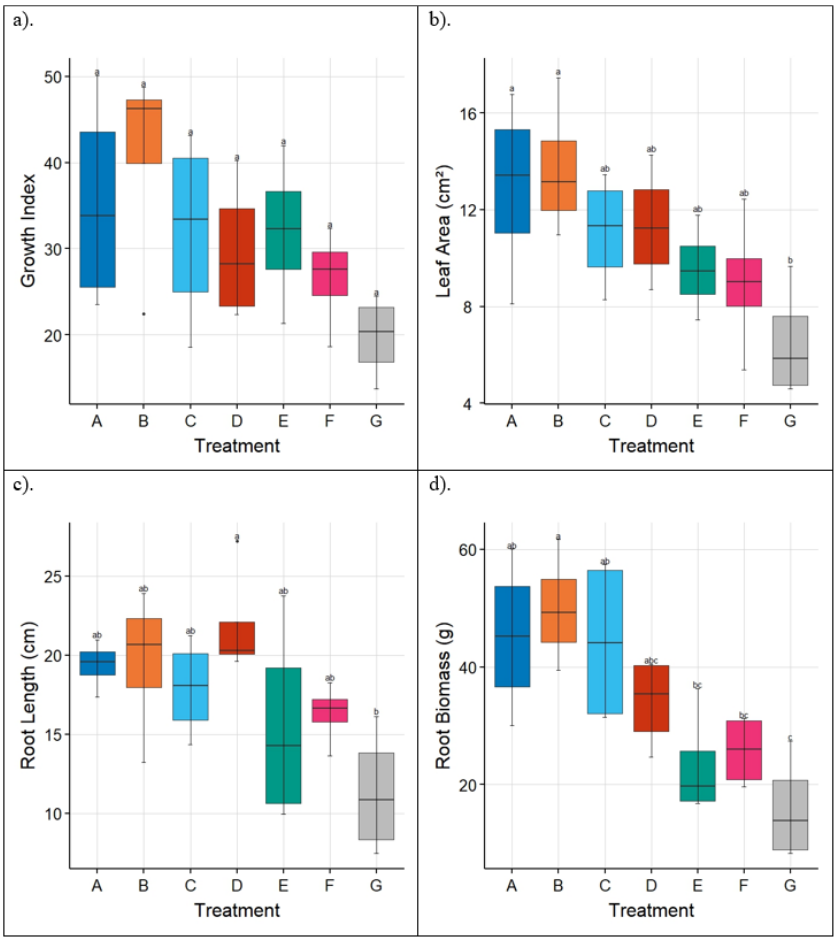

Figure 1. Morphological responses of *Talinum paniculatum* under seven levels of water availability: (a) growth index, (b) leaf area (cm²), (c) root length (cm), and (d) root biomass (g). Treatments represent percentages of field capacity: A (50%), B (60%), C (70%), D (80%), E (90%), F (100%), and G (110%). Different letters above the boxes indicate significant differences among treatments according to Tukey's HSD test at $p < 0.05$

2022). Moreover, recent evidence from woody shrub species reinforces this interpretation. Other research demonstrated that *Crataegus monogyna* saplings subjected to repeated mild summer drought exhibited a 24% increase in height increment in the following year, compared to well-watered controls, despite showing no immediate drought symptoms (Mijnsbrugge et al., 2024).

Overwatering (100%-110% FC) led to suppressed growth across all morphological traits, consistent with hypoxia-induced reduction in root metabolic activity (Figures 1a-d). The mechanism aligns with studies indicating that hypoxic conditions induced by flooding impair root metabolic activity and alter hormonal signaling (Aslam et al., 2023; Renziehausen & Frings, 2024). Flooding triggers a rapid rise in ethylene concentration within waterlogged tissues, which promotes aerenchyma formation but simultaneously suppresses lateral root development and overall biomass accumulation (Voesenek & Bailey-serres, 2015). The absence of such structural adaptation in *T. paniculatum*, as reflected by its root biomass decline at 110% FC, suggests that this succulent herb lacks robust aerenchyma-forming capacity and is therefore particularly susceptible to waterlogging injury. This interpretation is consistent with its ecological origin as a plant of well-drained, seasonally dry tropical environments rather than flood-prone habitats (Lakitan et al., 2021).

Physiological Plasticity of *Talinum paniculatum* Under Water Stress

From a physiological perspective, both relative growth rate (RGR) (Figure 2a) and net assimilation rate (NAR) (Figure 2b) in *Talinum paniculatum* peaked under drought conditions (50% FC), indicating that water limitation may enhance carbon assimilation and growth efficiency. In response to drought, *Talinum paniculatum* likely switches to Crassulacean Acid Metabolism (CAM) (Guerere et al., 1996). This process helps conserve water, maintain photosynthetic function, and sustain quantum yield. The capacity for CAM induction in T. paniculatum places it within a broader group of facultative-CAM succulent herbs that maintain a positive carbon balance under water deficit through metabolic flexibility. Consistent with this drought-responsive plasticity, long-lived leaves of the perennial facultative-CAM arborescent species *Clusia pratensis* has been shown to repeatedly shift between C3 and CAM across successive wet-dry-wet cycles (Winter & Holtum, 2024); moreover, *Pereskia aculeta* showed inducing facultative CAM and recovery under drought stress for 60 days (Cenciareli et al., 2025).

Talinum paniculatum maintained stable cellular hydration across moderate drought and normal hydration conditions, as evidenced by the relatively consistent RLWC values from 50–90% FC (Figure 2c). This homeostatic water status regulation is ecologically significant because it implies that *T. paniculatum* actively adjusts its osmotic potential to prevent dehydration, likely through accumulation of compatible solutes such as proline and glycine betaine rather than relying passively on soil water availability. This active osmotic adjustment decouples leaf water status from soil moisture over a broad range, granting the plant a wide ecological amplitude. Only at 110% FC did RLWC decline significantly, indicating that the osmotic adjustment capacity is overwhelmed under prolonged waterlogging. The role of osmoprotectants such as glycine betaine in maintaining turgor under water stress is well-established, and their accumulation is consistent with broader patterns observed in stress-tolerant herbaceous species (Jarin et al., 2024).

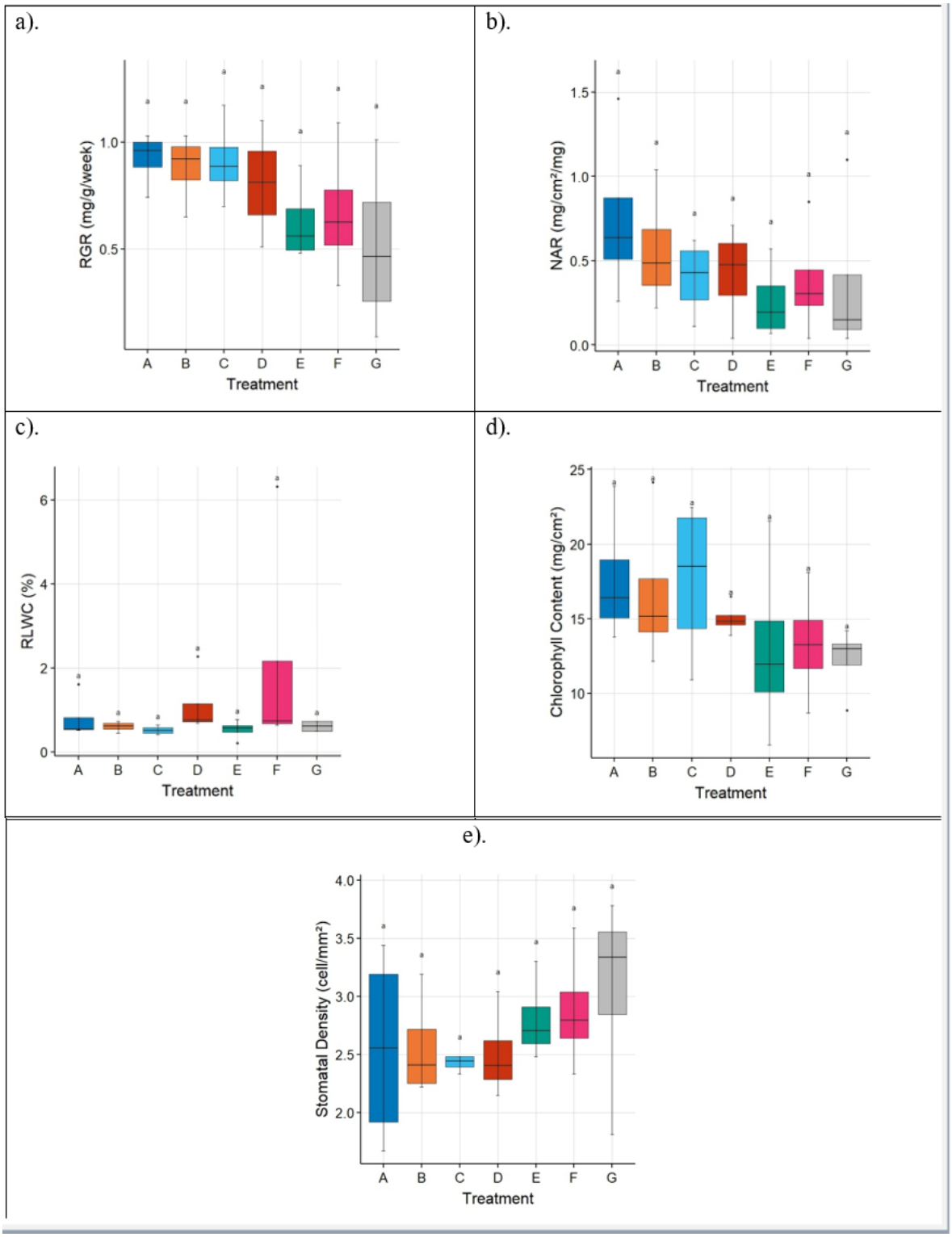

Figure 2. Physiological responses of *Talinum paniculatum* under different water stress treatments: (a) relative growth rate (RGR), (b) net assimilation rate (NAR), (c) relative leaf water content (RLWC), (d) chlorophyll content and (e) stomatal density. Treatments represent field capacity levels: A (50%), B (60%), C (70%), D (80%), E (90%), F (100%), and G (110%). Different letters indicate statistically significant differences among treatments based on Tukey's HSD test at $p < 0.05$

Chlorophyll content remained stable under mild drought but declined under waterlogging, suggesting oxidative stress and pigment degradation. Supporting this, Hu et al. (2023) proposed that in *Xanthoceras sorbifolium* moderate drought did not significantly affect chlorophyll levels, while severe stress caused marked pigment decline and structural damage to chloroplasts. These findings reinforce that mild water stress may activate protective mechanisms that preserve photosynthetic function, whereas extreme conditions compromise pigment stability and chloroplast integrity. In contrast, drought stress significantly enhanced photosynthetic pigments in stevia (Ahmadzai et al., 2024). The divergent responses to water stress observed across species reinforce that chlorophyll content alone is not a universally reliable indicator of stress tolerance, as its trajectory depends on stress intensity, species-specific antioxidant capacity, and the balance between reactive oxygen species generation and scavenging. In *T. paniculatum*, the maintenance of chlorophyll under mild drought suggests active photoprotection, while the decline under waterlogging reflects oxidative overload that overwhelms the plant's defense mechanisms.

Interestingly, stomatal density at 110% FC (G) exceeded that at 60% (B) (Figure 2e), which can be attributed to the compensatory anatomical response under hypoxic root conditions, a morphological strategy to maximize gas exchange capacity when root oxygen supply is severely limited. Shi et al. (2023) similarly observed that prolonged flooding stress in *Phoebe sheareri* seedlings induced a substantial rise in stomatal density, reaching up to 3467 n/mm², yet it was accompanied by reduced stomatal opening and photosynthetic rate. These findings suggest that while increased stomatal density is a typical stress-induced anatomical adaptation, its functional benefit may be limited when root oxygen supply and carbon assimilation remain constrained (Shi et al., 2023).

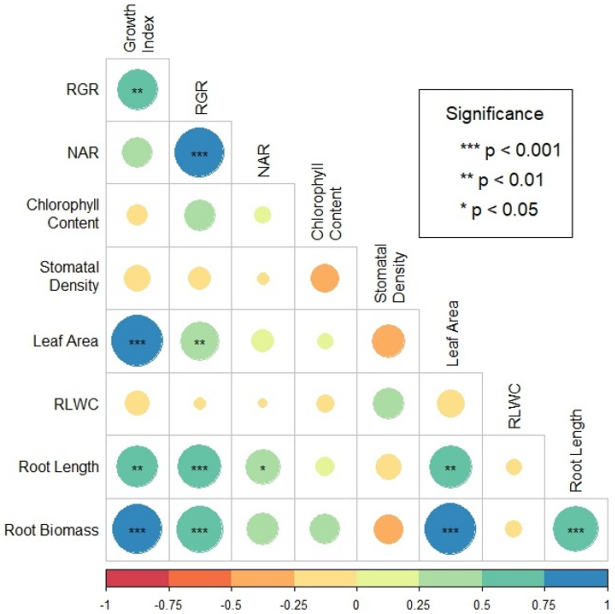

Figure 3. Correlation plot, depicting correlation among traits measured

Correlation analysis (Figure 3) revealed that RGR was strongly associated with NAR, leaf area, root length, and biomass, indicating that carbon assimilation and root development were strongly associated with biomass accumulation under drought stress. Chlorophyll content supported growth but was not the primary factor, while stomatal density and RLWC acted more as stress-buffering

mechanisms rather than contributors to productivity. Similar findings were reported in *Phoebe sheareri* (Shi et al., 2023), where stomatal and water status adjustments understress maintained plant survival but did not necessarily enhance growth efficiency. Overall, these correlation patterns highlight that *T. paniculatum* relies more on carbon assimilation and root development than on water status or stomatal modifications to sustain growth under fluctuating soil moisture.

Phytochemical Profiles and Functional Associations under Varying Water Conditions

The most analytically significant FTIR finding was the intensity pattern of the O–H stretch band at 3446 cm^{-1}, which serves as a proxy for phenolic and hydroxyl-containing compound accumulation (Figure 4). This band was most prominent at 70% and 80% FC, confirming that moderate water stress is the primary driver of phenolic biosynthesis in *T. paniculatum*. Importantly, the elevation of this band at 110% FC suggests that waterlogging also triggers oxidative-stress-induced phenolic accumulation, albeit via a different mechanistic pathway (hypoxic signaling rather than the drought-induced ABA pathway). Similar increases in phenolic content have been observed in other plants, such as lavender, *Bauhinia ungulata*, and *Solanum lycopersicum* under moderate drought and waterlogging (Borim de Souza et al., 2023; Hosseini & Heidari, 2025; Umićević et al., 2024). These phenolic compounds are known for their antioxidant properties and play a crucial role in protecting plants from oxidative stress induced by water imbalance (Umićević et al., 2024).

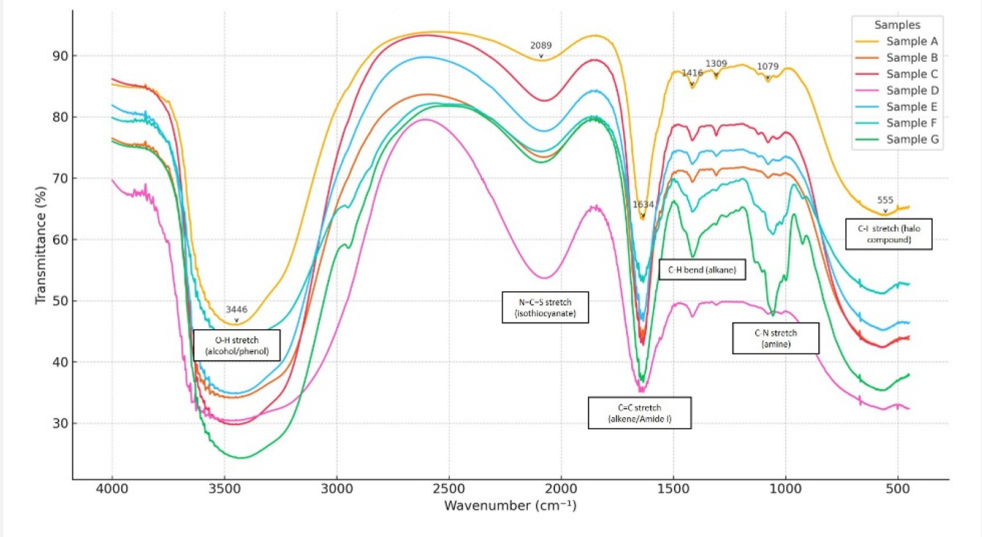

Figure 4. FTIR spectral overlay analysis of *Talinum paniculatum* root extracts under varying soil moisture treatments (Field Capacity, FC). Spectral curves represent absorbance values at major wavenumbers with annotated peaks indicating specific functional groups: 3446 cm^{-1} (O–H stretch, alcohol/phenol), 2089 cm^{-1} (N=C=S stretch, isothiocyanate), 1634 cm^{-1} (C=C stretch, alkene/amide I), 1416 cm^{-1} (C–H bend, alkane), 1079 cm^{-1} (C–N stretch, amine), and 555 cm^{-1} (C–I stretch, halo compound)

The presence of a peak at 2089 cm^{-1} corresponding to the N=C=S stretch (isothiocyanate group) indicates the potential synthesis of sulfur-containing secondary metabolites often linked to plant defense responses. This signal, found more prominent under moderate drought than flooded conditions, could reflect the enhanced biosynthesis of stress-induced compounds in *T. paniculatum*. Under

water stress conditions, isothiocyanates, which are derived from glucosinolates through enzymatic hydrolysis, are known to increase in the Brassica family (Ullah et al., 2025). Under drought conditions, glucosinolate content was detected in broccoli (BR1 accession) with an 85.4% increase and in cauliflower (CV1 accession) with a 72.8% increase in both roots and leaves (Ben Ammar et al., 2023). It must be noted, however, that glucosinolate-derived isothiocyanates are well-characterized in Brassicaceae but have rarely been documented in Portulacaceae, to which *T. paniculatum* belongs. The detection of the N=C=S stretch signal in *T. paniculatu*m roots therefore represents a novel phytochemical observation that warrants further targeted analysis, such as GC-MS or LC-MS/MS, to confirm the chemical identity of this compound class. If confirmed, drought-induced sulfur-containing metabolites in *T. paniculatum* would significantly expand the known pharmacological profile of this species.

A distinct signal at 1634 cm^{-1} (C=C stretch in alkene or amide I) was found across all samples, suggesting consistent presence of unsaturated bonds or protein-related structures, though its relative intensity was highest in FC 80%. This band is associated with unsaturated C=C bonds in aromatic rings characteristic of flavonoid skeletons, as well as amide I vibrations from stress-response proteins. The highest intensity at 80% FC is analytically consistent with the phenylpropanoid biosynthesis pathway being upregulated under moderate stress. Flavonoid biosynthesis is initiated by phenylalanine ammonia-lyase (PAL), an enzyme whose expression is known to be induced by mild abiotic stress via ABA signaling (Li et al., 2025) In *Cissus rotundifolia*, flavonoid synthase (FLS) was identified as a hub gene tightly linked to ABA signaling, stomatal movement, and transcription factor networks under drought, with nine distinct flavonoid metabolites accumulating under stress (Li et al., 2025). The parallel elevation of the 1634 cm^{-1} band at moderate stress in *T. paniculatum* suggests that a similar ABA-mediated flavonoid induction pathway may be operating. This pattern is also reported in *Lavandula angustifolia* Mill. (Hosseini & Heidari, 2025).

The bending vibration at 1416 cm^{-1} (C–H bend in alkanes) and the stretching vibration at 1079 cm^{-1} (C–N stretch in amines) point toward aliphatic and nitrogenous metabolites, respectively. The differential pattern (C–H intensity peaking at 80% FC while C–N intensity was highest at 110% FC) is analytically informative and suggests two distinct metabolic responses to contrasting moisture regimes. At 80% FC (moderate drought), elevated aliphatic C-H signals are consistent with enhanced membrane lipid remodeling, a known drought adaptation in which plants increase the proportion of unsaturated fatty acids to maintain membrane fluidity under reduced water potential (Henschel et al., 2024). In contrast, the C-N signal dominance at 110% FC (waterlogging) reflects nitrogen-containing compound accumulation, likely free amino acids such as proline and GABA, which are produced as compatible solutes under anaerobic stress to maintain osmotic balance and support mitochondrial metabolism (Komatsu et al., 2024). This mechanistic distinction between the two stress-type responses indicates that *T. paniculatum* deploys fundamentally different biochemical strategies under drought versus waterlogging, which has direct implications for targeted metabolite harvesting under specific cultivation conditions. This finding corroborates the hypothesis of osmoprotectant synthesis and amino compound accumulation under moderate water stress and flooding, as seen in other plants under similar conditions (Henschel et al., 2024; Komatsu et al., 2024). The C–I stretch at 555 cm^{-1},

although less commonly discussed in plant systems, could indicate the presence of trace halogenated bioactives, which serve as antimicrobial agents (Faleye et al., 2024).

CONCLUSION

This study demonstrated that varying water availability significantly influenced the morphophysiological traits and bioactive metabolite profile of Talinum paniculatum. Water availability at 60-80% field capacity optimized both growth and secondary metabolite production in *Talinum paniculatum*, with root elongation and biomass peaking at 60% FC and phenolic and flavonoid accumulation (as indicated by FTIR analysis) most pronounced at 70-80% FC. Severe drought (50% FC) and waterlogging (110% FC) impaired both growth and metabolite stability, confirming the detrimental effects of extreme moisture conditions. Practically, these findings recommend that farmers and cultivation managers maintain soil moisture at 60-80% FC during the growing season to maximize *T. paniculatum* yield and bioactive quality, particularly under climate-induced rainfall variability. Future studies should investigate the specific biochemical pathways linking water deficit to flavonoid and phenolic biosynthesis in this species, validate these findings across different soil types and growing seasons, and employ multivariate approaches such as Principal Component Analysis (PCA) or Path Analysis to better resolve the relative contributions of individual variables to overall plant performance under water stress.

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AUTHORS' CONTRIBUTIONS

VTM and **YS** designed and conceived of the experiments. The experiment was conducted by **SN**. **DI** conducted the statistics analysis. **VTM**, **YS, and SN** contributed to the preparation of samples and interpretation of the results. The manuscript was primarily composed by **VTM**. All authors provided critical feedback and contributed to the development of the research, analysis, and manuscript.

COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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