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Mitigating Drought Stress in *Physalis alkekengi*: Synergistic Effects of Foliar Boron and Zinc on Photosynthesis and Metabolite Accumulation

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ABSTRACT

This study investigated the effects of foliar boron (B) and zinc (Zn) on *Physalis alkekengi* under four levels of drought stress (0%, 25%, 50%, and 75% of field capacity). Plants were treated with B at 0, 100, 200, and 400 ml/L and Zn at 0, 1, 2, and 3 g/L. Drought stress significantly reduced fruit length (3.5–5.2 cm), weight (13.7–22.8 g), and firmness (1.7–3.5 N). The combined foliar application of B (200 ml/L) and Zn (2 g/L) under moderate drought (50% field capacity) produced the best outcomes. Fruit weight increased by 28%, total soluble solids (TSS) reached 11.6%, chlorophyll content rose to 2.1 mg/g FW, and photosystem II efficiency (Fv/Fm) improved to 0.78. Total phenolics (7.2 mg/g FW), flavonoids (32.3 mg/g FW), and proline (38.5 mg/g FW) also peaked under this treatment, indicating enhanced antioxidant metabolism and osmotic adjustment. Strong correlations were observed between proline and total phenolics (r = 0.90), and between flavonoids and total phenolics (r = 0.86), suggesting coordinated stress-response mechanisms. Principal component analysis (PCA) revealed clear clustering of treatments, separating those with higher fruit quality and metabolite accumulation from treatments with improved photosynthetic efficiency. Overall, foliar B and Zn acted synergistically to alleviate drought stress, stabilize photosynthesis, enhance antioxidant defenses, and improve fruit growth and quality in *P. alkekengi*. These findings demonstrate that integrated micronutrient management can be an effective strategy to improve plant performance under water-limited conditions, benefiting both productivity and the nutritional value of fruits.

Keywords: *Photosynthesis*, Fruit firmness, Total soluble, Antioxidant metabolism, Photosystem II

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INTRODUCTION

One of the most common sources of abiotic stress is drought. Studies have shown that drought can negatively impact crop yield, photosynthetic performance, and the quality characteristics of many agricultural crops [1, 2] because low moisture levels disrupt cellular homeostasis, leading to reduced turgor, increased oxidative stress, and metabolic suppression [3]. Plants respond differently to environmental stresses such as salinity and drought; however, they employ various mechanisms to enhance tolerance to these stresses, including the accumulation of osmolytes, enhanced antioxidant capacity, and modifications of photosynthetic processes [4, 5, 25].

Micronutrients, particularly boron (B) and zinc (Zn), play essential roles in plant growth, development, enzymatic activity, and stress adaptation [6, 26]. Boron contributes to cell wall structural stability, facilitates carbohydrate transport, and maintains membrane integrity, whereas zinc is involved in multiple enzyme systems, regulates auxin metabolism, and supports chloroplast stability [7, 8]. Foliar application of Zn, particularly in the form of Zn nanoparticles, has been reported to enhance plant drought tolerance by stabilizing photosynthetic pigments, regulating osmotic balance, and promoting the scavenging of reactive oxygen species (ROS) [9, 10, 24].

Recent studies have also explored the influence of micronutrients on phenolic synthesis and sugar accumulation under drought and salinity stress conditions, suggesting that boron may promote phenolic compound biosynthesis and enhance soluble sugar levels [11, 12]. Despite these findings, the potential physiological synergy between B and Zn in modulating drought stress responses remains poorly understood, particularly in relation to their interactive effects in *Physalis alkekengi*. This species is valued for its horticultural and medicinal importance due to its rich content of bioactive compounds, including flavonoids, phenolics, vitamins, and other health-related metabolites. However, *P. alkekengi* is highly susceptible to water deficit stress, which can negatively affect plant productivity and fruit quality.

Therefore, it is of considerable agronomic interest to evaluate nutritional pathways to improve drought tolerance and the biochemical profile of *P. alkekengi.* With this objective in mind, the present study aimed to evaluate the effects of foliar-applied boron (B) and zinc (Zn) on the nutritional, physiological, and biochemical traits of *P. alkekengi* under drought stress conditions. We hypothesized that combined foliar application of B and Zn would mitigate the negative impacts of drought by enhancing photosynthetic efficiency, stimulating antioxidant metabolism, and improving fruit quality parameters.

MATERIALS AND METHODS

Plant Materials and Experimental

The experiment was conducted in the Research Greenhouse at the University of Al-Qadisiyah, Iraq, during the 2023–2024 growing season. In this study, single-stemmed and identically sized *Physalis* plants were prepared and transferred to pots measuring 17 × 15 cm. Each pot contained two plants, and the experiment was conducted with three replicates. The culture medium consisted of perlite and cocopeat at a 1:1 (v/v) ratio. The plants were maintained under natural light conditions, with day/night temperatures of 19.27 ± 5°C and a relative humidity of 50 ± 10%. From the beginning of planting in the pots, the plants were irrigated three times a week. Drought stress was applied at four levels of field capacity (control, 25%, 50%, and 75% FC), boron at four concentrations (0, 100, 200, and 400 mL/L), and zinc at four concentrations (0, 1, 2, and 3 g/L). The characteristics of ZnO (zinc oxide) nanoparticles used in current research are given in Table 1.

Table 1 Structural properties of zinc nanoparticles

Structural properties of zinc nanoparticles	Zinc nanoparticles
Thermogravimetric analysis (TGA)	3.1 ± 0.02
Inductively coupled plasma (ICP)	2.5 ± 0.06
size	18 - 29
Purity percentage	95
Active surface (g/m^2)	55 - 137

Measurement of Yield and Nutritional Traits

Fruit Length and Fruit Weight

A digital balance was utilized to measure the fruit weight at the end of the experiment. Fruit length was also measured using a Mitutoyo digital caliper (precision of 0.01 mm).

Fruit Firmness

Using a TA-XT Plus, a texture analyzer from Stable Micro Systems (Surrey, UK), fruit firmness (FF) was assessed as a texture indicator.

TSS (Total Solid Soluble)

A refractometer (model CETI, Belgium) was used to measure the TSS (Total Soluble Solids) content in the fruit juice. The TSS value was reported as % Brix.

Titratable Acidity (TA)

Juice was taken from each of the three samples, with 10 mL from each sample measured into an Erlenmeyer flask. Afterward, 4 drops of the 1% Phenolphthalein solution (prepared by dissolving 0.5 g of Phenolphthalein in 70 mL of ethyl alcohol, then diluting to 100 mL with distilled water) were added to the juice [13]. The data collected will be displayed through data analysis by the use of the formula:

Titratable Acidity (%) = V×N×EqW×100\W

(V = Volume of NaOH used for titration (in mL), N = Normality of the NaOH solution, EqW = Equivalent weight of the predominant acid, W = Weight of the sample (in grams))

Total Chlorophyll Content

Fresh leaves (0.5 g) were collected to determine the concentrations of photosynthetic pigments, including chlorophyll a and chlorophyll b. Pigment extraction was performed by grinding the samples and extracting the pigments using 80% acetone solution. The absorbance of the extracts was measured at wavelengths of 663 nm and 646 nm using a spectrophotometer. Photosynthetic pigment concentrations were calculated as a function of absorbance values at these wavelengths using the equations described by Gulen et al. [14]. The results were expressed as milligrams per gram of fresh weight (mg/g FW).

Chla (mg/ml) =12.25A663-2.79A646
Chlb (mg/ml) =21.50A646-5.10A663
TChl=Chla + CHlb

Total Phenol Content (TPC) and Flavonoid Content (FC)

TPC was determined following the method described by Luo et al. [15]. The FC was measured based on the method described by Liu et al. [16]. For each sample, 3 g of fruit tissue was ground in liquid nitrogen and extracted with 10 mL of 80% acetone. The mixture was allowed to macerate at room temperature for 1 hour, with gentle shaking every 10 minutes. Finally, the absorbance was measured at 415 nm using a spectrophotometer.

Proline Content

The proline concentration in the leaf samples was assessed using the colorimetric method by Renzetti et al. [17]. The absorbance was measured at 520 nm using a UV/Visible spectrophotometer (UV-1800, Shimadzu Corporation, Japan).

Fluorescence Parameters (Fo, Fm) and (Fv/Fm)

Before measurement, leaves were dark-adapted for 30 minutes to ensure proper stabilization of the photosynthetic apparatus. The minimum fluorescence (Fo) and the maximum fluorescence (Fm) were recorded. Each treatment was replicated three times. The maximum photochemical efficiency of photosystem II (PSII) was calculated using the following formula [18]:

$Fv/Fm = (Fm - Fo) / Fm$

RESULT AND DISCUSSION

Fruit (length, weight, firmness)

Drought stress, as well as boron and zinc treatments, significantly affected fruit length ($P < 0.01$) at the 75% field capacity level. The lowest fruit length (3.50 cm) was observed under the combined treatment of 100 ml/L boron and 1 g/L zinc, which was comparable to the control (Fig. 1). The minimum fruit weight was recorded under 25% drought stress combined with 200 ml/L boron and 2 g/L zinc. Similarly, the lowest fruit firmness (1.72 N) under the interaction of drought stress and nano-zinc was observed at 25% drought stress combined with 1 g/L nano-zinc (Fig. 1).

TSS. Brix and TA and TS

The highest total soluble solids (TSS) were observed with the combined application of 200 ml/L B and 2 g/L Zn, reaching 25%. In contrast, the lowest TSS (2.03%) occurred in drought-stressed plants treated with 100 ml/L B + 1 g/L nano Zn (Fig. 1). The minimum titratable acidity (TA) (0.8%) was recorded with 100 ml/L B + 3 g/L Zn under 75% drought stress (Fig. 1). In addition, the maximum total sugar content (1.137 g/g FW) was obtained from fruits subjected to mild drought (75%) and treated with 400 ml/L B + 2 g/L nano Zn (Fig. 1).

Total Chlorophyll Content

The experiments showed that total chlorophyll content was highest (1.137 g/g FW) in 75% mild drought-stressed fruit that received a combination of 400 ml/L B and 2 g/L nano Zn.

TPC and TFC and Proline Content

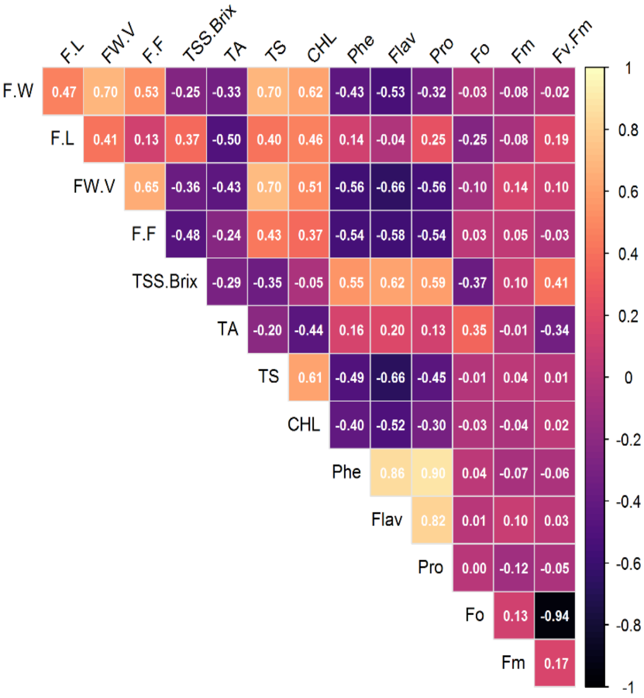
The highest total phenolic content (7.20 mg/g FW) and total flavonoid content (32.33 mg/g FW) were recorded under 50% drought stress combined with 200 ml/L B and minimal Zn (Fig. 1). The maximum proline concentration (38.5 mg/g FW) occurred under 75% drought stress with the lowest B and nano-Zn levels, whereas the minimum proline (15.46 mg/g FW) was observed in the control treatment (Fig. 1).

Photosystem II Efficiency (Fo, Fm, Fv/Fm)

The highest Fo values were observed under 75% drought stress combined with 400 ml/L B and 3 g/L nano-Zn. Intermediate Fo levels were recorded under osmotic stress and severe drought (75%) in combination with 400 ml/L B + 3 g/L Zn (Fig. 1).

Correlation Analysis

The Pearson correlation analysis of physiological, biochemical, and phytochemical traits (Fig. 2) revealed strong interrelationships among most measured variables. A high positive correlation (r = 0.90) between total phenolic content (TPC) and proline (Pro) suggests a close physiological association, indicating that proline accumulation is likely accompanied by enhanced phenolic synthesis during stress conditions. These findings imply that both proline and phenolic compounds contribute to the plant defense mechanism under stress. Similarly, TPC showed strong positive correlations with total flavonoid content (TFC) (r = 0.86), and TFC was also strongly correlated with Pro (r = 0.82), suggesting a comparable response of these metabolites to environmental stress. Fresh weight (FW) and fruit volume (FWV) exhibited a moderate-to-strong positive correlation (r = 0.65), indicating a significant association between biomass accumulation and fruit volume. Both FW and FWV were also positively correlated with total soluble solids (TSS) (r = 0.70), suggesting that increased biomass accumulation is accompanied by higher soluble carbohydrate content. These results indicate that fruit size and quality, particularly compositional attributes, can be reasonably assessed using either of these traits. In contrast, Fo showed a strong negative correlation with the Fv/Fm ratio (r = −0.94). The Fo parameter represents minimal chlorophyll fluorescence and is often associated with potential damage to photosystem II, whereas the Fv/Fm ratio reflects the maximum quantum efficiency of photosystem II photochemistry. The inverse relationship between these parameters suggests that reductions in Fo are accompanied by improved photosynthetic efficiency, and that both variables respond similarly to environmental stress.



	F.L	FW.V	F.F	TSS.Brix	TA	TS	CHL	Phe	Flav	Pro	Fo	Fm	Fv.Fm
F.W	0.47	0.70	0.53	-0.25	-0.33	0.70	0.62	-0.43	-0.53	-0.32	-0.03	-0.08	-0.02
F.L		0.41	0.13	0.37	-0.50	0.40	0.46	0.14	-0.04	0.25	-0.25	-0.08	0.19
FW.V			0.65	-0.36	-0.43	0.70	0.51	-0.56	-0.66	-0.56	-0.10	0.14	0.10
F.F				-0.48	-0.24	0.43	0.37	-0.54	-0.58	-0.54	0.03	0.05	-0.03
TSS.Brix					-0.29	-0.35	-0.05	0.55	0.62	0.59	-0.37	0.10	0.41
TA						-0.20	-0.44	0.16	0.20	0.13	0.35	-0.01	-0.34
TS							0.61	-0.49	-0.66	-0.45	-0.01	0.04	0.01
CHL								-0.40	-0.52	-0.30	-0.03	-0.04	0.02
Phe									0.86	0.90	0.04	-0.07	-0.06
Flav										0.82	0.01	0.10	0.03
Pro											0.00	-0.12	-0.05
Fo												0.13	-0.94
Fm													0.17

Fig. 2 Correlation heat map of Morphological, Physiological, and Biochemical Traits in *Physalis* under Combined Drought, Nano Zinc, and Brassinosteroid Treatments. The color scale represents correlation coefficients from −1 to +1.

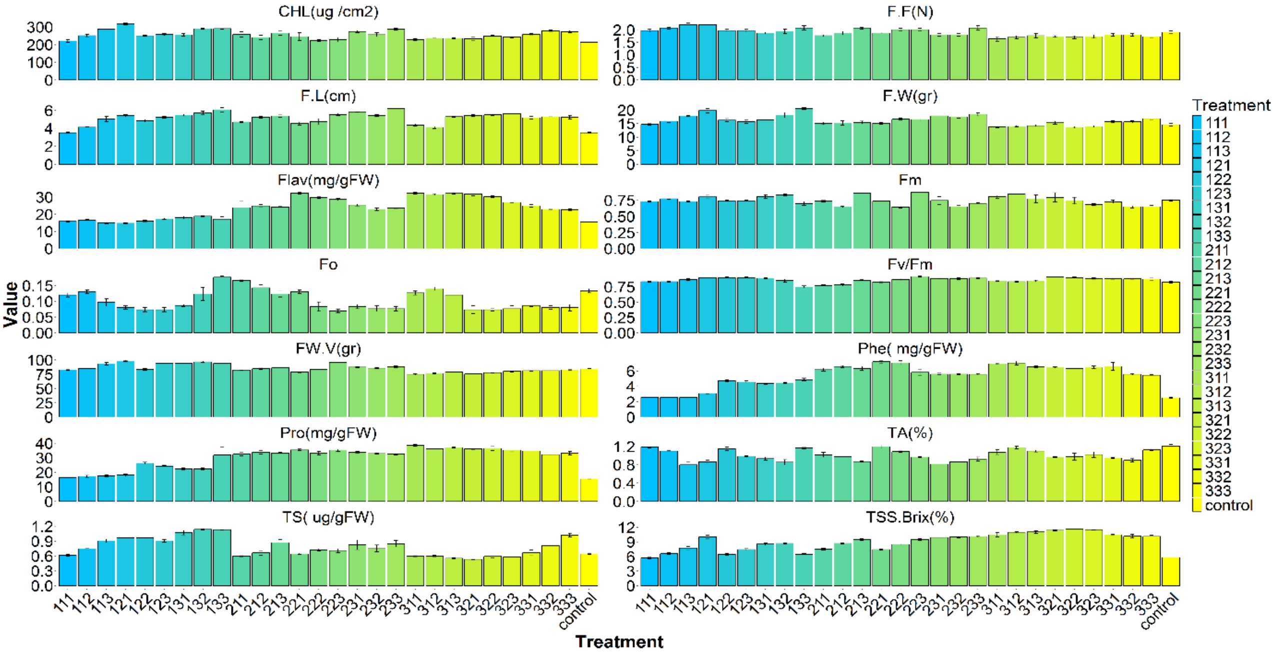


Fig. 1 Bar Plot of morphological, physiological, and biochemical traits of *Physalis* under combined treatments of drought stress, zinc, and Boron. Treatment codes are three-digit combinations in which the first digit represents drought level, the second represents Boron level, and the third represents zinc level. The control treatment is indicated as "control".

PCA Biplot

A principal component analysis (PCA) biplot (Fig. 3) was constructed to examine the two-dimensional distribution of the 27 samples based on physiological and biochemical traits. PC1 and PC2 accounted for 39.9% and 25.6% of the total variance, respectively, explaining a cumulative 65.5% of the overall variability. The samples were classified into nine distinct clusters. Cluster 1 (122, 123, 131) was associated with moderate fruit firmness and photosystem II efficiency (Fv/Fm). Cluster 2 (211, 212, 221, 222) showed moderate associations with titratable acidity (TA) and minimum fluorescence (Fo), indicating intermediate responses in fruit quality and stress-related parameters. Cluster 3 exhibited weak correlations with the measured traits, suggesting a limited treatment effect. Cluster 4 (111, 112, control) was generally characterized by lower fruit quality and biochemical performance. In contrast, Cluster 5 (121, 113, 132) showed higher fruit weight (FW), fruit volume (FWV), and total sugars (TS), demonstrating the positive influence of combined B and Zn treatments on growth and carbohydrate accumulation. Clusters 6 and 7 showed moderate associations with TA, Fo, and Fm, suggesting differential physiological responses under stress. Cluster 9 (321, 322, 323, 331) was characterized by the highest fruit firmness, along with elevated proline (Pro), total phenolic content (TPC), and total flavonoid content (TFC), indicating improved fruit quality under optimal treatment conditions (Fig. 3).

Overall, drought stress negatively affected fruit length, weight, and firmness. Foliar application of Boron (200 ml/L) and Zinc (2 g/L) under moderate drought stress (50% field capacity) produced the most favorable results by enhancing fruit growth, total soluble solids (TSS), chlorophyll content, and photosystem II efficiency. Moreover, the combined treatment increased Pro, TPC, and TFC levels, suggesting activation of antioxidant defense and osmoprotective pathways. The strong positive correlations observed between Pro–TPC (r = 0.90) and TPC–TFC (r = 0.86) indicate coordinated stress-response mechanisms. Zinc application contributed to chloroplast stabilization and maintenance of photosynthetic pigments, whereas Boron improved cell wall integrity and facilitated carbohydrate translocation, collectively mitigating drought-induced stress effects. In conclusion, PCA and correlation analyses demonstrate that foliar application of Boron and Zinc synergistically enhances drought tolerance, improves photosynthetic efficiency, and promotes fruit quality in *Physalis* species. The combined treatment under 50% field capacity represents the most effective experimental condition.

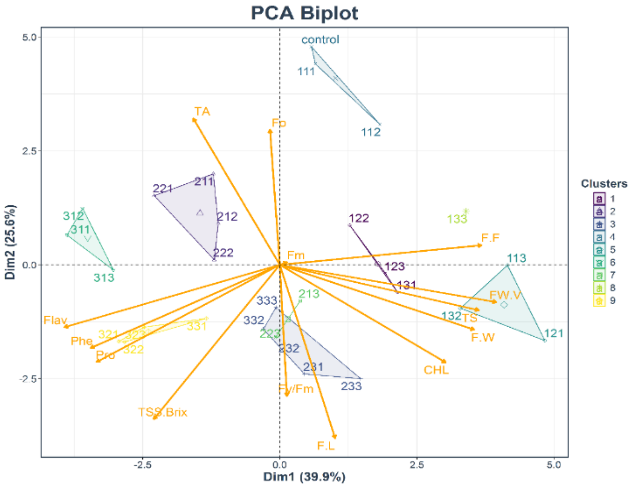


Fig. 3 Principal Component Analysis (PCA) Biplot of *Physalis* Treatments Grouped by Cluster Analysis Based on Morphological, Physiological, and Biochemical Traits

This study demonstrated that combined B + Zn mitigated the negative effects of water limitation, enhancing fruit quality, photosynthetic efficiency, and secondary metabolite accumulation. Drought stress markedly reduced fruit length and weight, consistent with previous reports on impaired cell expansion and fruit development [19, 20]. The combination of moderate B (200 ml/L) and Zn (2 g/L) alleviated these reductions, likely by stabilizing cell walls and membranes. Zn plays a key role in enzyme activation and auxin metabolism [21, 26], while B supports cell wall construction and sugar translocation [22], collectively improving nutrient uptake and osmotic balance. Under drought, total soluble solids (TSS) and titratable acidity (TA) increased, as previously observed in water-limited conditions [11]. Moderate drought (50–75% field capacity) combined with B + Zn further enhanced TSS and total sugars, indicating stimulated carbohydrate metabolism and osmoprotectant synthesis, which can improve fruit sweetness and flavor. Total chlorophyll content also increased under specific B + Zn treatments, reflecting improved stability of photosynthetic pigments. Zn maintains chloroplast structure and supports chlorophyll biosynthesis [9, 23], while B contributes to membrane function, together improving light capture in PSII. The strong negative correlation between Fo and Fv/Fm (r = -0.94) confirmed drought-induced PSII damage, which was minimized by the combined B + Zn application.

Additionally, proline, total phenolics (TPC), and flavonoids (TFC) increased under drought, especially with low Zn and moderate B, indicating activation of antioxidant defenses. Proline, as an osmolyte, stabilizes cellular structures and reduces ROS effects [4, 20]. Strong correlations between Pro–TPC (r = 0.90) and TPC–TFC (r = 0.86) suggest coordinated regulation of osmolytes and phenolic compounds, as observed in physalis and tomato [10]. In summary, foliar B and Zn synergistically enhanced drought tolerance in P. alkekengi by stabilizing photosynthesis, improving osmotic and antioxidant responses, and maintaining fruit quality.

CONCLUSION

Foliar application of boron (B) and zinc (Zn) improved drought tolerance in *P. alkekengi* by enhancing fruit growth, quality, photosynthetic efficiency, and antioxidant accumulation. Among all treatments, 200 ml/L B + 2 g/L Zn under moderate drought (50% field capacity) produced the best results, with increased fruit weight, total soluble solids, chlorophyll content, and elevated proline, phenolics, and flavonoids. These effects highlight the synergistic role of B and Zn in maintaining cellular stability and metabolic balance under water stress. In summary, combined foliar B and Zn application provides an effective strategy to mitigate drought stress and improve fruit quality in *P. alkekengi*, offering practical guidance for sustainable cultivation under limited water conditions.

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Data Availability

All data are included in the manuscript

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No specific financial credit was used in this experiment.

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