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Physiological Response and Comprehensive Resistance Evaluation of East African Endemic *Aeollanthus repens* under Water and Heat Stress

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Abstract: *Aeollanthus repens*, native to East Africa, thrives in seasonally dry tropical biomes and boasts qualities ideal for both ornamental and ground cover purposes. However, despite its potential, its current resistance levels remain uncertain. Assessing its adaptability could offer valuable insights for its wider adoption and utilization. In this study, researchers employed 3-month-old cuttings of *A. repens*, subjecting them to six distinct environments by manipulating the temperature (25/20 °C and 35/30 °C) and soil moisture levels (100%, 20%, and 40%). Their leaf physiological and photosynthetic indices were assessed at intervals of 5, 10, and 15 days following exposure to stress. The findings unveiled that exposure to prolonged moisture, elevated temperatures, or a combination of both led to an increase in osmoregulatory substances in the leaves. This increase was accompanied by heightened enzyme activity and an increased intercellular carbon dioxide concentration, followed by a subsequent decline. Additionally, chlorophyll content, net photosynthetic rate, stomatal conductance, and transpiration rate exhibited a decreasing trend over time. Through a comprehensive assessment of stress tolerance utilizing a composite affiliation function value index, the study concluded that *A. repens* exhibits optimal growth in a certain high-temperature environments and demonstrates substantial resistance to waterlogging, drought, and simultaneous high-temperature stress. However, the resilience of *A. repens* appears to diminish under the compounded stresses of high temperature and drought.

Keywords: *Aeollanthus repens*; high-temperature stress; water stress; physiological response; resilience

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1. Introduction

In recent years, driven by the ongoing urbanization process, there has been growing emphasis on ecological considerations. Cities have responded by establishing extensive green spaces, leading to a surge in greenery. Within this context, plants play a pivotal role in shaping these green spaces [1]. Ground cover plants, in particular, serve as crucial elements in the landscape. They act as connectors between trees and shrubs, bridging the gap to lawns. Moreover, they provide an alternative to traditional lawns in areas challenged by poor soil quality, dense shade, or exposed tree roots. However, with the rise in global temperatures, coupled with increased rainfall in some regions, there is a heightened risk of severe flooding. Paradoxically, alongside flooding, regions traditionally characterized by humid climates are experiencing more frequent periods of extreme drought, attributed to global warming. Consequently, abiotic stresses such as high temperatures and moisture imbalances have emerged as primary factors impeding the normal growth and development of landscape plants [2–4]. In response to these evolving environmental challenges, research into plant resistance to high temperatures, drought, and flooding has become not only crucial but also pressing.

Leaves serve as the primary organs for absorbing water and nutrients essential for photosynthesis, playing a critical role in plant growth and survival. When plants encounter adverse conditions, such as stress, their leaves undergo physiological and morphological adjustments to adapt to the unfavorable environment [5]. Among the various metabolic responses, photosynthesis stands out as a sensitive indicator of plant reactions to environmental stress. It is intricately linked to plant growth and development, with the leaves serving as the primary sites for this vital process. Under the duress of high temperatures, water scarcity, or a combination of both, the leaf stomata tend to close, resulting in reduced stomatal conductance, a reduced transpiration rate, and reduced carbon dioxide absorption. Consequently, this leads to a decline in the net photosynthetic rate [6–8]. Moreover, as stress levels escalate, the leaves accumulate reactive oxygen species (ROS), triggering the degradation of photosynthetic pigments and diminishing their total chlorophyll content [9,10]. To counteract the damaging effects of ROS and maintain their balance, plants enhance the activity of enzymes involved in both ROS production and removal, such as catalase (CAT) and peroxidase (POD). However, as stress intensifies, the activity of these oxidative enzymes tends to decline [11]. Malondialdehyde (MDA), a harmful byproduct generated by plants during stressful conditions, typically increases to varying degrees. Elevated MDA levels signify greater damage inflicted by environmental stress on plants [12,13]. It is worth noting that in natural settings, environmental stress rarely occurs in isolation. Instead, plants often face a combination of adverse factors. The research indicates that multifactorial stress poses a more severe threat to plants compared to individual stressors, underscoring the complexity of plant responses to adverse environmental conditions [14–16].

Aeollanthus repens, belonging to the Lamiaceae family, is a charming ornamental plant admired for its lush appearance. This perennial herb typically stands between 0.2 and 0.7 m tall, boasting well-established roots. Its stems, characterized by branching and a cylindrical shape, produce stolon-like structures. Its leaves, tender, green, and rosulate, are oblanceolate, measuring around 2 cm in length and 0.5 cm in width. Both its stems and leaves are adorned with a white tomentum, adding to its visual appeal. The plant's elongated inflorescences bear striking flowers, sporting a lip-shaped, dark-purple corolla that gradually transitions to a lovely lavender hue over time. *A. repens* can be propagated using various methods, including seeds, cuttings, or providing adequate nutrients. Native to regions stretching from South Sudan to Mozambique, *A. repens* thrives in seasonally dry tropical biomes. Renowned for its adaptability to diverse habitats, it excels as a ground cover plant, displaying vigorous growth, enhancing landscapes, and demonstrating resilience to semi-shaded conditions and drought. Its versatility positions it as a promising candidate for greening urban spaces. However, despite its remarkable adaptability, there remains a noticeable gap in the research in exploring *A. repens*' response to high temperatures and water stress. The lack of systematic studies assessing its resistance and adaptability hampers its broader adoption as a ground cover plant. To address this knowledge gap, a study compared and analyzed the effects of high temperatures, moisture levels, and their combined stresses on the growth status, as well as the physiological and biochemical characteristics, of *A. repens*. Utilizing 3-month-old cuttings, the study aimed to shed light on the plant's response to adverse conditions, paving the way for its more informed use in landscaping and green space management.

This study aims to delve into the tolerance and physiological responses of *A. repens* under various temperature and water stress conditions. By subjecting the plant to different stressors, we seek to uncover new insights into the physiological mechanisms employed by drought-tolerant plants like *A. repens*. Ultimately, our findings will not only enhance our understanding of these mechanisms but also offer practical recommendations for utilizing *A. repens* effectively in landscaping projects.

2. Results

2.1. *Effects of High Temperature, Moisture, and Combined Stress on the Photosynthesis and Morphology of A. repens*

Throughout the experiment, both the control group and the high-temperature stress group displayed robust health, showing no signs of surface damage. However, in the high-temperature and waterlogging group, as well as the waterlogging-only group, the plants exhibited blackened, rotting leaves at their bases, accompanied by the emergence of aerial roots. Interestingly, the high-temperature waterlogging group exhibited a greater proliferation of aerial roots compared to the ambient temperature waterlogging group. Drought stress initially did not manifest any noticeable changes in the plants, but by the fifth day, slight yellowing of the basal leaves began to appear. By the 10th day, this yellowing intensified, and by the 15th day, the plants exhibited overall softening and collapse. High-temperature stress combined with drought stress showed no significant impact on the plants until the fifth day, after which they began to exhibit signs of softening and wilting. (Figure 1).

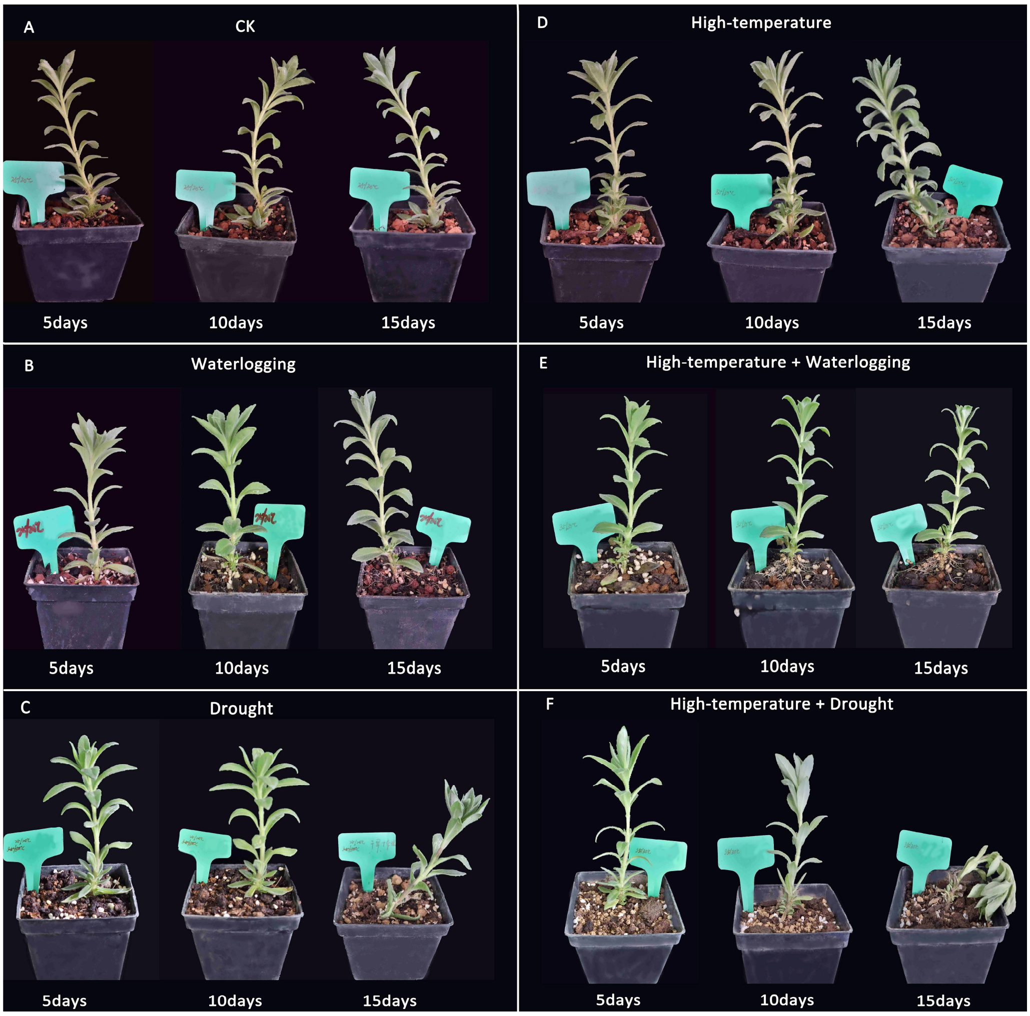

Figure 1. Illustrates the diverse morphological characteristics exhibited by *A. repens* across different temperature and humidity conditions at three specific time intervals. (**A**) The growth status of the plants in the control group; (**B**) the growth status of the plants in the waterlogging stress group; (**C**) the growth status of the plants in the drought stress group; (**D**) the growth status of the plants in the high-temperature stress group; (**E**) the growth status of the plants in the high-temperature and waterlogging stress group; (**F**) the growth status of the plants in the high-temperature drought stress group.

A. repens displayed a consistent decrease in its chlorophyll content, net photosynthetic rate (Pn), transpiration rate (Tr), and stomatal conductance (Gs) over the course of the experiment under various environmental stresses. Interestingly, the intercellular carbon dioxide concentration (Ci) showed a fluctuating pattern, initially decreasing and then increasing(Table 1). When exposed solely to high-temperature stress, Tr, Ci, and Gs did not exhibit significant changes compared to the control group. However, in the presence of waterlogging, drought, or a combination of high-temperature and waterlogging stresses, both Tr and Gs showed notable reductions compared to the control group. Specifically, Tr and Gs reached their lowest values after 15 days of exposure to high-temperature drought stress. In the waterlogging group, Ci showed a decline followed by an increase, with the lowest value recorded on the 10th day, significantly lower than the control group. Conversely, in response to high-temperature drought stress, the Ci values generally increased over time, reaching their peak after 15 days, significantly higher than the control group. Overall, these findings indicate that *A. repens* experienced the most significant damage when subjected to combined compound stresses, while single high-temperature stress had the least impact.

Table 1. Effect of high-temperature and water stress on photosynthetic parameters *A. repens*. Note: CK: "control group", W: "waterlogging stress group", D: "drought stress group", H: "high-temperature stress group", HW: "high-temperature and waterlogging stress group", HD: "high-temperature and drought stress group". Statistical significance was determined using one-way ANOVA, followed by Duncan's multiple range test. Different lowercase letters indicate significant differences among different treatment according to DMRT ($p < 0.05$).

Index		Chlorophyll Content/[SPAD]	Net Photosynthetic Rate /[μmol·(m^2·s)$^{-1}$]	Stomatal Conductance /[mol·(m^2·s)$^{-1}$]	Carbon Dioxide Concentration /[μmol·mol^{-1}]	Stomatal Conductance /[mmol·(m^2·s)$^{-1}$]
CK	5 d	38.1 ± 0.5 b	8.68 ± 0.56 a	0.132 ± 0.011 a	1240 ± 17 b	2500 ± 27 a
	10 d	38.3 ± 0.6 b	10.21 ± 0.48 a	0.168 ± 0.009 a	1241 ± 29 b	3100 ± 31 a
	15 d	38.3 ± 0.3 b	10.34 ± 0.32 a	0.143 ± 0.007 a	1240 ± 57 b	2300 ± 25 a
W	5 d	37.0 ± 1.7 b	6.75 ± 0.12 ab	0.081 ± 0.001 b	1194 ± 89 c	1600 ± 47 b
	10 d	33.1 ± 2.4 c	5.25 ± 0.31 c	0.070 ± 0.004 b	1034 ± 46 d	900 ± 36 b
	15 d	26.2 ± 0.4 d	2.90 ± 0.19 d	0.036 ± 0.002 bc	1235 ± 35 c	800 ± 23 b
D	5 d	30.4 ± 0.9 d	6.11 ± 0.48 bc	0.100 ± 0.010 ab	1213 ± 48 b	1500 ± 19 b
	10 d	28.2 ± 1.5 d	4.18 ± 0.21 c	0.053 ± 0.002 bc	1097 ± 57 cd	1200 ± 13 b
	15 d	17.5 ± 1.7 e	1.58 ± 0.03 d	0.033 ± 0.002 bc	1254 ± 46 b	700 ± 27 b
H	5 d	38.9 ± 0.2 b	8.82 ± 0.04 a	0.143 ± 0.003 a	1258 ± 49.4 b	3000 ± 109 a
	10 d	42.4 ± 1.1 a	9.99 ± 0.32 a	0.145 ± 0.009 a	1248 ± 86 b	2600 ± 69 a
	15 d	36.5 ± 3.0 b	6.42 ± 0.26 b	0.109 ± 0.006 ab	1234 ± 54 b	2300 ± 181 a
HW	5 d	33.8 ± 1.3 c	5.53 ± 0.11 bc	0.080 ± 0.003 b	1043 ± 68 cd	1400 ± 79 b
	10 d	25.6 ± 0.5 d	2.93 ± 0.03 cd	0.032 ± 0.001 bc	1294 ± 88 b	1200 ± 67 b
	15 d	14.3 ± 1.3 f	1.64 ± 0.07 d	0.027 ± 0.001 c	1270 ± 99 b	800 ± 70 b
HD	5 d	28.8 ± 2.0 d	4.18 ± 0.19 c	0.078 ± 0.005 b	1027 ± 37 d	1100 ± 78 b
	10 d	12.3 ± 0.1 f	1.44 ± 0.07 d	0.027 ± 0.001 c	1238 ± 49 b	1500 ± 46 b
	15 d	7.6 ± 0.1 g	−2.13 ± 0.08 e	0.021 ± 0.001 c	1591 ± 65 a	300 ± 13 c

2.2. *Effects of High-Temperature and Water Stress on A. repens' Cell Membranes*

Malondialdehyde serves as a key marker of lipid peroxidation within cell membranes and carries a certain degree of toxicity. As the content of malondialdehyde increases, so does the potential harm to plants. Throughout the duration of sustained moisture, high-temperature stress, and both single and combined stress environments, the MDA content exhibited significant variation, generally displaying an upward trajectory with prolonged stress exposure (Figure 2B). Notably, in environments characterized by combined stressors, the MDA content was markedly higher compared to those subjected to single stressors by the 15th day (Figure 2C). Furthermore, the MDA content observed under the drought stress treatment surpassed that of the waterlogging stress treatment. Conversely, the trend in the MDA content in response to high-temperature stress was less pronounced and did not significantly differ from that of the control group (Figure 2A). These observations suggest that *A. repens* experienced greater damage under combined stress conditions than under single stress, with drought stress inflicting more harm compared to waterlogging stress, while high-temperature stress exhibited the least discernible impact on the MDA content.

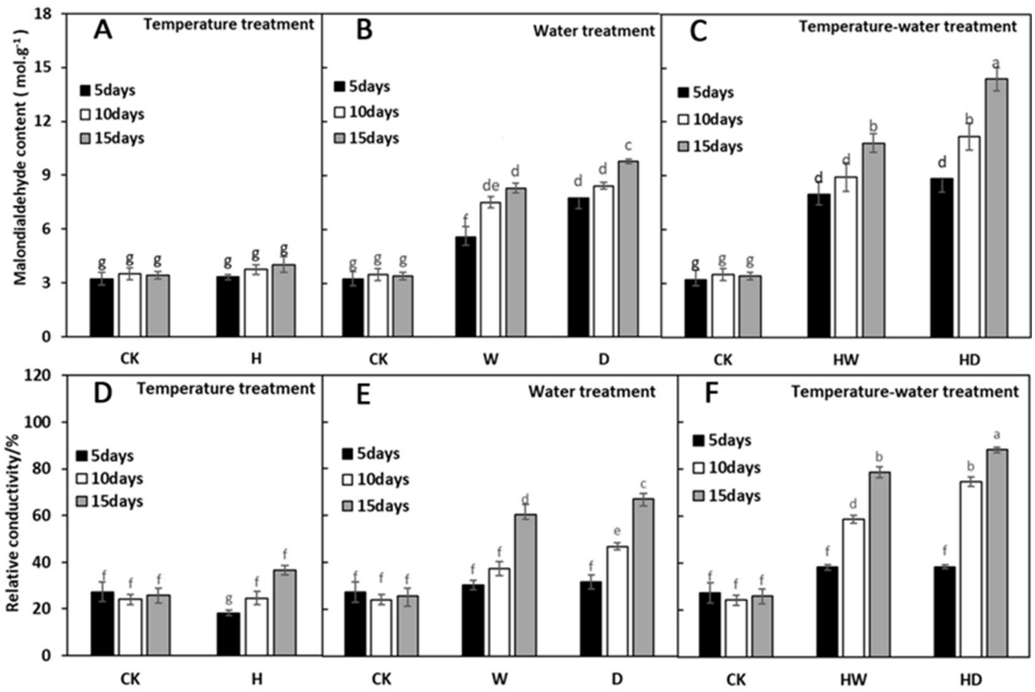

Figure 2. A. *Aeollanthus repens* degree of plant tissue stress injury under different treatment conditions. MDA content (**A**–**C**), relative conductivity (**D**–**F**). CK: "control group", W: "waterlogging stress group", D: "drought stress group", H: "high-temperature stress group", HW: "high-temperature and waterlogging stress group", HD: "high-temperature and drought stress group". Statistical significance was determined using one-way ANOVA, followed by Duncan's multiple range test. Different lowercase letters indicate significant differences among different treatments according to DMRT ($p < 0.05$). Error bars represent the standard error of the mean.

The leaf conductivity of *A. repens* exhibited notable differences compared to the control group across various environmental conditions. After 5 days of the experiment, in the high-temperature environment, the leaf conductivity was significantly lower than that of the control group (Figure 2D). By the 10th day of the experiment, no significant changes were observed in the high-temperature/normal water and normal temperature/waterlogged environments when compared to the control group (Figure 2E). However, significant changes were noted in the normal temperature/drought and high-temperature/water stress environments, with the conductivity changes ranking as high-temperature, drought > high-temperature, waterlogged > normal temperature, drought. Moving to the 15th day of the experiment, there was still no significant change in the high-temperature/normal water environment compared to the control group. However, in the compound stress environments, significant changes were observed compared to single stress conditions, with drought stress exhibiting significant changes compared to waterlogging stress. The combined stress of high temperature and drought had the most significant effect on membrane lipid peroxidation in *A. repens* (Figure 2F). The leaf conductivity and leaf malondialdehyde content showed that single high-temperature stress did not significantly worsen the membrane lipid peroxidation. However, other stress environments did increase the membrane lipid peroxidation in the plants to varying degrees.

2.3. Effect of High-Temperature and Water Stress on Antioxidant Enzyme Activities of A. repens

There were notable variations in the trend in peroxidase (POD) activity observed in *A. repens* across different treatments. Specifically, under high-temperature and drought stress treatment, the POD activity initially experienced an increase, followed by a rapid decline as the stress duration progressed. The peak activity was recorded at 10 days, reaching a maximum value 11.8 times higher than that of the control group (Figure 3C). In contrast, under other stress treatments, including high-temperature/moisture combined stress, the POD activity demonstrated a consistent increasing trend with prolongation of the stress time. Moreover, the POD activity was significantly higher under high-temperature/moisture combined stress compared to single stress conditions (Figure 3B). Furthermore, it was observed that POD activity changed more rapidly under high-temperature environments compared to ambient temperature conditions (Figure 3A).

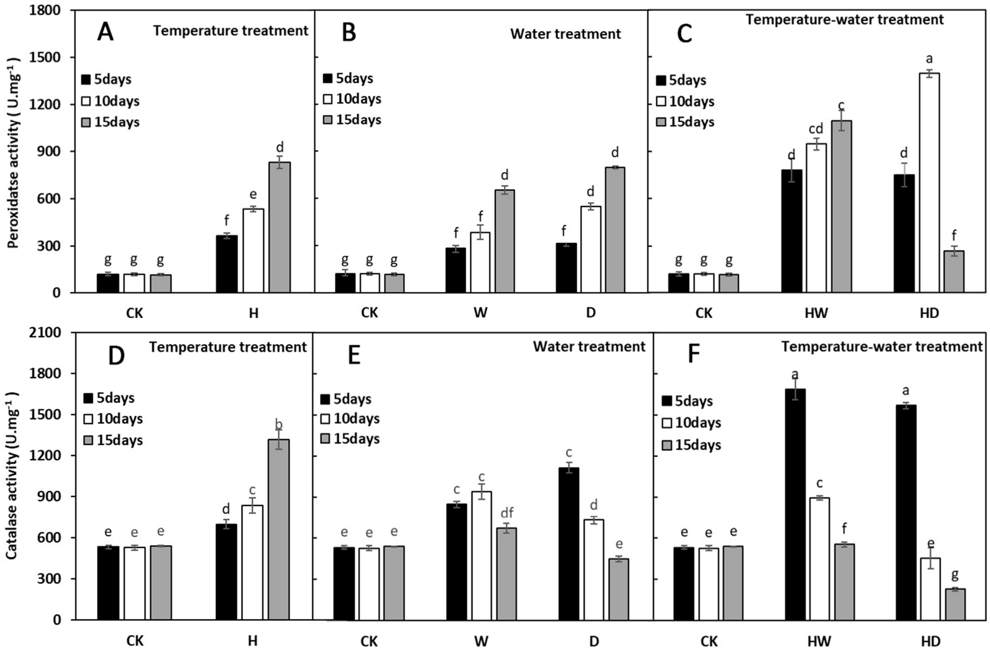

Figure 3. Alterations in enzyme activities in *A. repens* under various treatment conditions. (**A**–**C**) peroxidase activity, (**D**–**F**) catalase activity. CK: "control group", W: "waterlogging stress group", D: "drought stress group", H: "high-temperature stress group", HW: "high-temperature and waterlogging stress group", HD: "high-temperature and drought stress group". Statistical significance was determined using one-way ANOVA, followed by Duncan's multiple range test. Different lowercase letters indicate significant differences among different treatment according to DMRT ($p < 0.05$). Error bars represent the standard error of the mean.

The changes in the catalase (CAT) activity in *A. repens* varied across different environmental treatments. Specifically, under high-temperature stress treatment, the CAT activity exhibited a continuous increase with a prolonged stress duration (Figure 3D). Conversely, under the waterlogging stress treatment, the CAT activity initially increased and then decreased over time (Figure 3E). In environments characterized by ambient temperature/drought, a high temperature and waterlogging, as well as a high temperature and drought, the CAT activity peaked on the fifth day of stress exposure (Figure 3F), During this period, the CAT activity was notably elevated, with its levels 1.3, 3.2, and 2.9 times higher than that of the control group environment, respectively. The high-temperature environment led to an overall increase in the enzyme activity, whereas the combined stress conditions exhibited more pronounced changes in the oxidase activity under high-temperature stress conditions.

2.4. Effects of High-Temperature, Water, and Combined Stress on the Osmotic Regulation of *A. repens*

Soluble sugars, soluble proteins, and proline play crucial roles in helping plants regulate their osmotic pressure, particularly in response to environmental stressors. These substances increase to mitigate the effects of unfavorable conditions, aiding plants in adapting to challenging environments. Changes in SS, SP, and Por content are often observed in response to moisture, a high temperature, and their combined stresses.

During the experimental period, the soluble sugar content of *A. repens* showed a general increase with the duration of stress exposure. Notably, its concentration under combined stress had a greater impact compared to that under single stressors, with water stress resulting in significantly higher levels than high-temperature stress. While the difference between high-temperature stress and the control was not statistically significant (Figure 4A), the interaction effect for stress and time in the other environments was highly significant. The soluble sugar content peaked on the 15th day of exposure to a high temperature and drought, reaching three times the content of the control (Figure 4C). Additionally, there was a slight increase in the soluble sugar content under drought stress compared to waterlogging stress, although none of the changes reached the significance observed in the combined stress environments (Figure 4B). Similarly, the soluble protein content of *A. repens* displayed varying degrees of increase under the water and high-temperature stress treatments within the 15-day timeframe. The rate of increase under combined stress was significantly higher than that under single stress conditions. The highest soluble protein content was observed for the high-temperature/drought treatment on the 10th day for single stress and on the 15th day for combined stress (Figure 4F). The soluble protein content remained unchanged under the high-temperature stress conditions until the 15th day (Figure 4D). However, the protein content significantly increased in both the flooding and drought environments, with no significant difference observed between the two (Figure 4E).

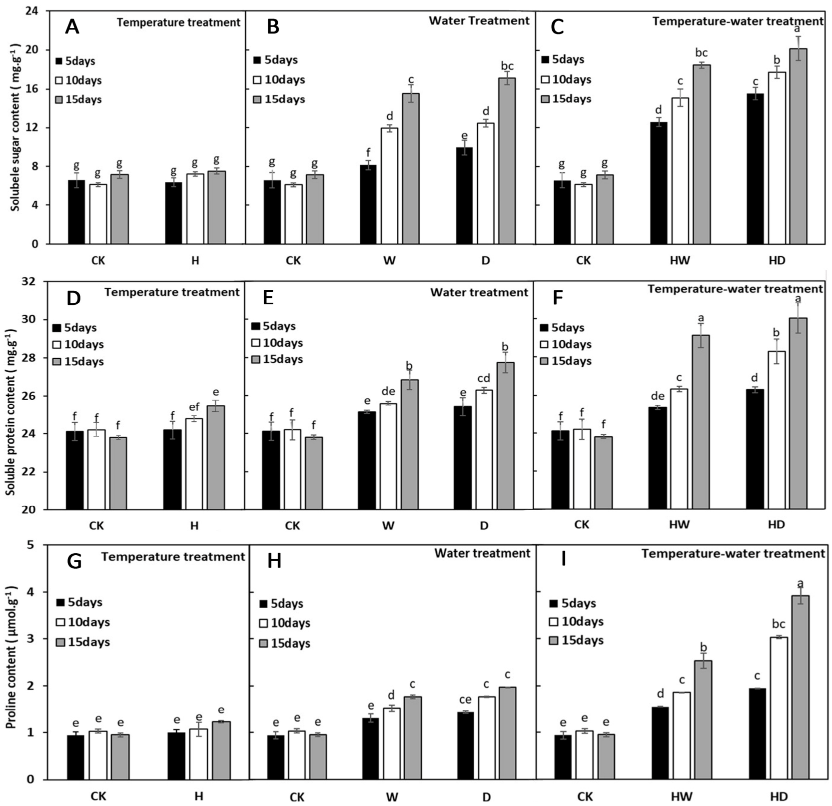

Figure 4. Changes in the content of osmolytes in *A. repens* under various treatments. (**A**–**C**) Soluble sugar content, (**D**–**F**) soluble protein content, (**G**–**I**) proline content. CK: "control group", W: "waterlogging

stress group", D: "drought stress group", H: "high-temperature stress group", HW: "high-temperature and waterlogging stress group", HD: "high-temperature and drought stress group". Statistical significance was determined using one-way ANOVA, followed by Duncan's multiple range test. Different lowercase letters indicate significant differences among different treatment according to DMRT ($p < 0.05$). Error bars represent the standard error of the mean.

At the 10th day mark, the proline content in *A. repens* subjected to drought stress was notably higher than that in the plants under waterlogging stress(Figure 4H). By the 15th day, under the high-temperature/drought stress treatment, the proline content reached its peak, registering 3.9 times higher than that of the control group (Figure 4I). Conversely, there were no significant changes observed in the proline content under high-temperature stress conditions until the 15th day (Figure 4G).

The study revealed that as the stress intensity increased, *A. repens* responded by regulating itself and augmenting its content of osmoregulatory substances to alleviate the effects of high-temperature and water stress. Under combined high-temperature and water stress, the levels of SS, SP, and Por were higher compared to those under single stress conditions. Moreover, single high-temperature stress had a lesser impact on the levels of SS and Por. By the 15th day of stress exposure, the osmoregulatory substance content was 1.26 times higher that of the control group. In treatments involving high-temperature and water stress, the proline content of *Aeollanthus repens* increased with the duration of stress, showing a significant rise. Notably, the rise in proline content was more pronounced under combined stress conditions compared to single stress.

2.5. Comprehensive Evaluation of the Tolerance of A. repens to Different Growing Environments

Based on the D-values calculated using the membership function, the resistance of *A. repens* under six environmental conditions was comprehensively evaluated and integrated (Table 2). The D-values for *A. repens* in the control group and under the high-temperature stress, waterlogging stress, drought stress, high-temperature and waterlogging stress, and high-temperature and drought stress treatments were 0.70, 0.68, 0.48, 0.45, 0.44, and 0.34, respectively. These values indicate that the control group and high-temperature stress environments were more conducive to the growth of *A. repens*. However, when compared to the other six groups, the growth of *A. repens* was somewhat inhibited under the conditions of waterlogging stress, drought stress, high-temperature and drought stress, and high-temperature and waterlogging stress.

Table 2. Comprehensive evaluation indicators of *A. repens* under high-temperature and water stress: (a) chlorophyll content, (b) soluble protein content, (c) soluble sugar content, (d) proline content, (e) peroxidase activity, (f) catalase activity, (g) malondialdehyde content, (h) net photosynthetic rate, (i) relative conductivity, (j) stomatal conductance, (k) intercellular carbon dioxide concentration, (l) transpiration rate, (m) D-value according to membership function. CK: "control group", W: "waterlogging stress group", D: "drought stress group", H: "high-temperature stress group", HW: "high-temperature and waterlogging stress group", HD: "high-temperature and drought stress group". The numbers 1, 2, and 3 correspond to days 5, 10, and 15, respectively.

Processing	a	b	c	d	e	f	g	h	i	j	k	l	m	Position
CK1	0.88	0.95	0.97	1.00	0.00	0.21	1.00	0.87	0.13	0.75	0.38	0.78	0.68	1
CK2	0.88	0.94	1.00	0.97	0.00	0.20	0.98	0.99	0.09	1.00	0.38	1.00		
CK3	0.88	1.00	0.93	0.99	0.00	0.21	0.98	1.00	0.11	0.83	0.38	0.72		
W1	0.85	0.79	0.86	0.88	0.11	0.42	0.79	0.71	0.17	0.41	0.30	0.45	0.48	3
W2	0.73	0.71	0.59	0.80	0.21	0.49	0.62	0.59	0.27	0.34	0.01	0.21		
W3	0.53	0.52	0.33	0.72	0.42	0.30	0.55	0.40	0.60	0.10	0.37	0.18		
D1	0.66	0.74	0.73	0.83	0.16	0.61	0.59	0.66	0.20	0.54	0.33	0.43	0.44	4
D2	0.59	0.60	0.55	0.72	0.34	0.34	0.53	0.51	0.41	0.22	0.12	0.31		
D3	0.28	0.37	0.22	0.66	0.53	0.15	0.41	0.30	0.70	0.08	0.40	0.14		

Table 2. *Cont.*

Processing	a	b	c	d	e	f	g	h	i	j	k	l	m	Position
H1	0.90	0.94	0.98	0.98	0.19	0.32	0.99	0.88	0.00	0.83	0.41	0.94	0.70	2
H2	1.00	0.84	0.92	0.96	0.33	0.42	0.95	0.97	0.10	0.84	0.39	0.81		
H3	0.83	0.73	0.90	0.90	0.60	0.75	0.93	0.69	0.26	0.60	0.37	0.71		
HW1	0.75	0.75	0.54	0.79	0.52	1.00	0.58	0.61	0.29	0.40	0.03	0.38	0.45	5
HW2	0.52	0.60	0.36	0.69	0.65	0.46	0.49	0.41	0.59	0.08	0.47	0.38		
HW3	0.19	0.15	0.12	0.47	0.77	0.22	0.32	0.30	0.87	0.04	0.43	0.17		
HD1	0.61	0.60	0.33	0.66	0.50	0.92	0.50	0.51	0.29	0.39	0.00	0.27	0.34	6
HD2	0.13	0.28	0.17	0.63	1.00	0.15	0.29	0.29	0.81	0.04	0.37	0.43		
HD3	0.00	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	1.00	0.00		

2.6. Correlation Analysis

The correlation analysis of various indicators of A. repens under water and high-temperature stresses provides valuable insights into the physiological changes occurring within the plant under six stress treatment environments (Table 3). Notably, moisture and high-temperature stress exerted a significant impact on A. repens, evidenced by the strong positive correlations between photosynthetic characterization indices such as Pn, Gs, Tr, and chlorophyll content. Moreover, in terms of the physiological indices, highly significant positive correlations were observed between soluble sugars, soluble proteins, proline, malondialdehyde, relative conductivity, and POD activity. Interestingly, D-values, serving as a comprehensive measure of resistance, exhibited significant correlations with all the indices except Ci.

Table 3. Correlation analysis of physiological indices in cultivars of *A. repens* exposed to high-temperature and water stress. (a) chlorophyll content, (b) soluble protein content, (c) soluble sugar content, (d) proline content, (e) peroxidase activity, (f) catalase activity, (g) malondialdehyde content, (h) relative conductivity, (i) net photosynthetic rate, (j) stomatal conductance, (k) intercellular carbon dioxide concentration, (l) transpiration rate, (m) D-value according to membership function. * $p < 0.05$, ** $p < 0.01$.

	a	b	c	d	e	f	g	h	i	j	k	l	m
a	1.00												
b	−0.96 **	1.00											
c	−0.94 **	0.94 **	1.00										
d	−0.90 **	0.93 **	0.88 **	1.00									
e	−0.93 **	0.91 **	0.95 **	0.78 **	1.00								
f	−0.92 **	0.89 **	0.90 **	0.71 **	0.96 **	1.00							
g	−0.94 **	0.94 **	0.96 **	0.92 **	0.92 **	0.86 **	1.00						
h	−0.97 **	0.97 **	0.94 **	0.88 **	0.93 **	0.91 **	0.91 **	1.00					
i	0.94 **	−0.95 **	−0.96 **	−0.91 **	−0.92 **	−0.87 **	−0.96 **	−0.94 **	1.00				
j	0.87 **	−0.88 **	−0.93 **	−0.78 **	−0.93 **	−0.88 **	−0.91 **	−0.90 **	0.95 **	1.000			
k	−0.45 *	0.44 *	0.24	0.53 *	0.21	0.19	0.29	0.47 *	−0.33	−0.17	1.00		
l	0.76 **	−0.80 **	−0.88 **	−0.79 **	−0.78 **	−0.73 **	−0.88 **	−0.77 **	0.88 **	0.91 **	−0.05	1.00	
m	0.93 **	−0.93 **	−0.95 **	−0.92 **	−0.88 **	−0.85 **	−0.97 **	−0.92 **	0.96 **	0.92 **	−0.31	0.92 **	1.000

3. Discussion

Plants undergo numerous factors influencing their growth and development, among which temperature and moisture stand out as pivotal environmental elements [17]. Chlorophyll, crucial for absorbing light energy during photosynthesis and converting it into chemical energy, directly impacts the efficiency of leaf photosynthesis [18–20]. Parameters such as Pn, Tr, Ci, and Gs serve as vital indicators of leaf photosynthesis efficiency [21]. In response to high-temperature and water stress, plants initially exhibit stomatal limitation as an early stress response. However, as the stress severity escalates, their non-stomatal limitations gradually become more prominent, contributing significantly to a decline in the leaf net photosynthetic rate [22].

To understand the photosynthetic behaviors of *A. repens* seedlings, we investigated their gas exchange under varying conditions, including water availability, temperature, and high-temperature/water composite stresses. Our study revealed significant reductions in the chlorophyll content and net photosynthesis rate of *A. repens* under drought, waterlogging, and high-temperature stress conditions. Additionally, its stomatal conductance and transpiration rate exhibited continuous decreases with an increasing stress duration under all the tested conditions(Figure 5). These findings suggest that *A. repens'* leaves regulate water metabolism by lowering their stomatal conductance to maintain normal physiological processes. The observed decrease in the intercellular CO_2 concentration under waterlogging and drought stress, followed by an increase under high-temperature and water stress, implies that *A. repens* leaves prioritize reducing their water loss by lowering their stomatal conductance, even at the expense of CO_2 uptake. This reduced CO_2 uptake hampers the timely replenishment of consumed CO_2, resulting in a decline in the net photosynthetic rate [22–24]. Furthermore, the intercellular CO_2 concentration gradually increased with the worsening of leaf damage during high-temperature and water combined stress, indicating that the plant leaves were mainly constrained by non-stomatal factors at this stage. A high temperature exacerbated the damage caused by water stress to *A. repens*, leading to a decrease in the CO_2 assimilation rate in the leaves, an increase in the intercellular CO_2 concentration, and a continuous decrease in the net photosynthetic rate [25]. Consequently, the plants' adaptability to the environment decreased. Interestingly, the chlorophyll content of the plants in the high-temperature stress group did not show a significant change, suggesting that a high-temperature environment is more suitable for *A. repens*. However, in the waterlogging group, the drought stress group, and the high-temperature and waterlogging group, the chlorophyll content and net photosynthesis rate initially remained high but declined significantly afterward. Nonetheless, throughout the stress process, the leaves remained in the state of an early stress response characterized by stomatal restriction, indicating strong resistance of the plant in such environments. In contrast, the plants under high-temperature and drought stress exhibited a sustained chlorophyll content and net photosynthetic rate until the fifth day of stress, followed by a decline. The leaf responses transitioned from stomatal limitation to a non-stomatal limitation state, resulting in leaf structure damage. Nonetheless, the plant displayed strong tolerance to high temperatures and high humidity, as well as water stress at a normal temperature. In conclusion, it is imperative to enhance water management during summer and avoid prolonged periods of drought or waterlogging in daily cultivation practices to prevent unnecessary harm to the plant.

MDA content and relative conductivity serve as crucial indicators of oxidative damage to cell membranes, reflecting the extent of harm inflicted upon a plant [26]. Our study observed a significant increase in the MDA content under both single water stress and high-temperature water composite stress conditions(Figure 5). Specifically, the MDA content was higher during drought stress compared to waterlogging stress, and combined stress led to a higher MDA content compared to single stress conditions. Notably, there was no significant change in the MDA content in the high-temperature stress group and control groups. These findings suggest that combined stresses result in more severe damage to *Aeollanthus repens* than single stresses, with drought stress inducing more damage than waterlogging stress. Furthermore, the equilibrium between the accumulation and removal of reactive oxygen species in the body of *A. repens* under high-temperature stress conditions indicates that the plant's oxidative stress response remains balanced. Moreover, the relative conductivity of the plant leaves exhibited a similar trend to the MDA content, highlighting the direct correlation between increased cell membrane permeability and membrane lipid peroxidation in *A. repens*. Consequently, the membrane damage incurred during plant stress significantly impacts plant photosynthesis.

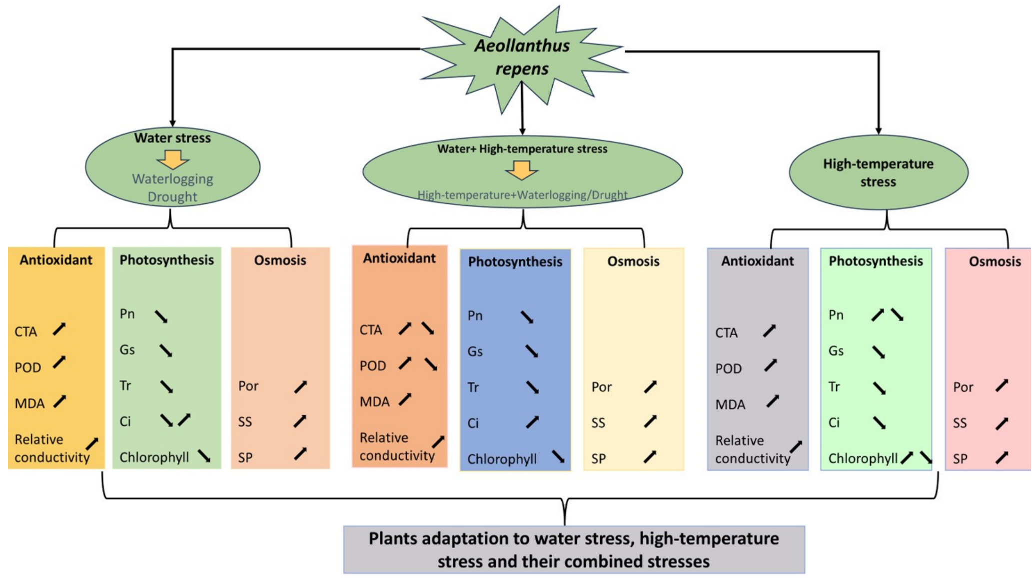

Figure 5. The possible adaptive mechanisms of *Aeollanthus repens* in a high-temperature and water stress environment.

In adverse environments, such as those characterized by increased levels of reactive oxygen species (ROS), plants respond by enhancing the production of protective enzymes like peroxidase (POD) and catalase (CAT) to mitigate the oxidative damage to their cell membranes [27,28]. In our study, the enzyme activity in the plants was found to increase under high-temperature conditions more than at ambient temperatures, suggesting that high temperatures enhance enzyme activities(Figure 5), consistent with previous research by Han et al. [29]. Under conditions of waterlogging, drought, and combined high-temperature and waterlogging stress, the CAT activity initially increases and then declines, while the POD activity continues to rise. This pattern indicates that plants maintain a dynamic balance between the production and scavenging of reactive oxygen species under these stress conditions, consistent with previous research by Mi et al. [14]. However, under combined high-temperature and drought stress, both the CAT and POD activities initially surge and then diminish. This trend suggests that with an increasing severity of stress, the overall antioxidant enzyme activity decreases, thereby disrupting the balance between reactive oxygen species production and scavenging in plants.

Proline, soluble sugars, and soluble proteins play pivotal roles as osmoregulatory substances and antioxidant defense mechanisms within plant cells. When plants are subjected to adverse conditions, these substances accumulate to a certain extent, facilitating the binding of more water molecules and increasing the content of bound water, thereby mitigating their detrimental effects [30–32]. In our study, the contents of proline, soluble sugars, and soluble proteins in *A. repens'* leaves significantly increased during single moisture stress and combined high-temperature/moisture stress conditions (Figure 5). However, they were not significantly affected by single high-temperature stress environments, consistent with previous research by Li et al and Ramachandra et al [33,34].

Plants' resistance to heat and water stress is determined by a multitude of factors, and relying on a single indicator may not accurately gauge their resilience. In our experiment, we selected 12 stress tolerance indicators to comprehensively evaluate the adaptability and stress tolerance of *A. repens* using fuzzy membership function analysis. The results revealed that the plants exhibited satisfactory growth in both ambient and high-temperature environments and displayed high resistance to waterlogging stress, combined high-temperature and waterlogging stress, and drought stress conditions. Overall, the plants demonstrated excellent adaptation to both prolonged high humidity and transient drought stress environments.

In summary, *A. repens* exhibited diverse trends across various indices under high-temperature and water stress environments, reflecting the multifaceted impacts of these conditions on the plant. Using principal component analysis and the membership function, we discerned that the plant thrived within both the high-temperature and control groups. Additionally, it displayed robust tolerance to waterlogging stress, drought stress, and a high temperature combined with waterlogging stress, with a notable degree of tolerance observed in the high-temperature/drought environment. These findings underscore the plant's strong adaptability to waterlogging environments and some resilience to drought conditions, thriving particularly well in high-temperature settings. *A. repens* demonstrates remarkable adaptability to climates characterized by high temperatures, high humidity, and occasional extreme droughts. During the growth phase of *A. repens*, it is advisable to maintain loose and permeable soil with adequate moisture levels. Furthermore, refined water management practices should be employed under high-temperature conditions to prevent prolonged waterlogging or drought stress. This information provides valuable insights for the successful cultivation of *A. repens*.

4. Materials and Methods

4.1. Experimental Materials

In this study, *A. repens* cuttings were used as the experimental materials. In mid-March 2023, 180 healthy growing branches of a uniform thickness and length were selected for the sterilized cuttings. The cuttings were transplanted into a plastic basin with a height of 10 cm and an inner diameter of about 10 cm. The substrate in the pots was peat soil, perlite, and vermiculite (2:1:1), and the soil ranged in pH from 6.5 to 7.5. Cuttings with a plant height of 15 $\pm$ 3 cm and a growth period of 3 months were chosen as our experimental material.

4.2. Experimental Treatments

A total of 180 cuttings were pretreated in an artificial climatic chamber for 7 days. The temperature was set to fluctuate between 25 °C during the day and 20 °C at night, with a photoperiod of 14 h of light and 10 h of darkness. Indoor humidity was maintained at 50%, and the light intensity was set at 10,000 lux. Following this adaptation period, *A. repens* was subjected to six different environmental treatments. These treatments included ambient temperatures of 25/20 °C with 40% soil moisture (control group), 100% soil moisture (waterlogging group), and 20% soil moisture (drought group), as well as ambient temperatures of 35/30 °C with 40% soil moisture (high-temperature group), 100% soil moisture (high-temperature and waterlogging group), and 20% soil moisture (high-temperature and drought group). The plant samples were selected 5, 10, and 15 days after the experiment, with the samples taken from the top to the bottom of the plant at the 5th to 8th functional leaf. Each treatment consisted of 30 plants per treatment with 10 replicates. Throughout the experiment, photographs were taken to document the changes in the plant morphology.

4.3. Measurement Indicators and Methods

4.3.1. Measurement of Indicators of the Photosynthetic Properties

Functional leaves located at nodes 4-6 from the top were carefully selected for analysis. Using a LI-6800 photosynthesizer (LI-COR, Inc., Lincoln, NE, USA), measurements of the net photosynthetic rate (Pn), stomatal conductance (Gs), transpiration rate (Tr), and intercellular carbon dioxide concentration (Ci) were conducted between 9:00 and 11:00 on a sunny day. Following determination of the photosynthetic parameters, the total chlorophyll content of the leaves was assessed using a handheld chlorophyll meter.

4.3.2. Measurement of the Physiological Indicators

Various biochemical markers were measured using Solarbio kits. These markers comprised soluble protein (SP), soluble sugar (SS), proline (Pro), MDA, POD, and CAT.

4.3.3. Comprehensive Evaluation of Resistance to High-Temperature Waterlogging Stress Conditions

The membership function fuzzy comprehensive evaluation method was used to evaluate the resistance of *Aeollanthus repens* under different environmental conditions. The formula for calculating the subordinate function values U(Xi) and the sum of the membership functions (D) is as follows [35]:

$$U(Xi) = \frac{Xi - Xmin}{Xmax - Xmin} \tag{1}$$

$$\mathrm{D} = \sum_{i=1}^{n} \mathrm{U(Xi)(i = 1, 2, , n)} \tag{2}$$

The membership functions for each principal component are determined using Equation (1), denoted as U(Xi), where Xi represents the value of the ith principal component for each species. This equation incorporates the ratio of an index with a minimum value of Xmin and a maximum value of Xmax. A higher value of D in the comprehensive evaluation indicates the greater resistance of *Aeollanthus repens* in that specific environment. Based on the D value, the plant's capacity to adapt to its environment is categorized into four grades: non-resistant, weakly resistant, moderately resistant, and highly resistant, corresponding to D values less than 0.2, between 0.2 and 0.4, between 0.4 and 0.6, and between 0.6 and 1, respectively.

4.4. Data Analysis

The data provided were organized and analyzed using both Excel 2010 and SPSS 20 software. One-way ANOVA was employed to compare the differences among various experimental groups. Additionally, principal component analysis and correlation analysis were conducted using SPSS 20 software. To streamline the analysis, the original indicators were transformed into new composite indicators.

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