DIFFERENTIAL LEAF PHYSIOLOGICAL AND ECOLOGICAL RESPONSES OF THE PIONEER SPECIES *RUELLIA SIMPLEX* AND *MIMOSA DIPLOTRICHA* ON TROPICAL CORAL ISLANDS

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Abstract. Tropical coral islands are of strategic importance, yet their ecological restoration is constrained by drought and nutrient-poor soils under high temperature and strong winds. To identify suitable pioneer species for vegetation recovery, we compared the physiological and ecological responses of *Ruellia simplex* and *Mimosa diplotricha* across three habitats: coastal sand in Shanwei (SW), soil-amended coral sand on Sansha Island (SS1), and native coral sand on Sansha Island (SS2). We measured leaf water content, soluble protein, antioxidant traits (SOD, GSH, MDA), nutrient stoichiometry (C, N, P and their ratios), metal elements (K, Ca), and photosynthetic pigments, and further integrated these traits through Mantel correlation analysis. Our results show that: (1) *R. simplex* maintained osmotic adjustment and redox balance through elevated Ca and K uptake and strong GSH accumulation, conferring high drought resilience; (2) *M. diplotricha* alleviated oxidative damage under moderate stress by enhancing SOD activity and soluble protein, but suffered sharp declines in pigments and antioxidant enzymes under extreme nutrient deficiency, indicating high environmental sensitivity; (3) Mantel analysis revealed that functional traits of *R. simplex* were relatively independent and coordinated by Ca as a central regulator, representing a "conservative" strategy, whereas traits of *M. diplotricha* were tightly coupled, reflecting an "investment-oriented" strategy. Taken together, *R. simplex* can provide stable long-term cover, while *M. diplotricha* may facilitate nutrient accumulation and community succession in improved habitats. Their complementary roles reduce vertical and horizontal energy exchange at the surface, limit water loss, and ultimately promote ecosystem recovery. This study provides a theoretical basis for differential species selection and management in tropical coral island restoration.

Keywords: *ecological restoration, landscape species, plant adaptability, plant introduction, tropical coral island*

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Introduction

Tropical coral islands are unique ecosystems that provides vital resources for fisheries, tourism, and national defense. Protecting these islands and ensuring their sustainable use is therefore of great importance. Their soils are typically composed of coarse, unconsolidated coral sands with low nutrient content and poor water-holding capacity (Wu et al., 2024; Sheng et al., 2025). Under global climate change, tropical cyclones have intensified, and these island ecosystems are frequently exposed to heat and strong winds. Rainwater remains only briefly in the exposed coral sands, aggravating freshwater shortages. Such conditions hinder vegetation development and impose long-term heat and drought stress on native plant communities, leading to ecosystem degradation (Cai et al., 2020; Macinnis-Ng et al., 2021; Zhou et al., 2023; Zhou et al., 2025). These challenges not only disrupt the ecological balance of tropical coral islands but also threaten the stability of their freshwater lenses, undermining sustainable development and utility (White et al., 2010; Wu et al., 2022). Establishing vegetation cover can effectively reduce soil moisture loss caused by wind and direct solar radiation, thereby improving soil conditions (Gray et al., 2024). Therefore, to establish vegetation diversity and improve habitat conditions on coral islands, it is necessary to introduce drought- and nutrient-tolerant pioneer species. Herbaceous plants, in particular, can rapidly colonize harsh environments, form extensive ground cover, and reduce soil water evaporation, thereby improving overall habitat quality (Park et al., 2024; Poorter et al., 2024). Thus, examining the physiological and ecological functional traits of introduced herbaceous plants is essential for identifying suitable species to restore tropical coral islands and promote their sustainable development.

When introduced into a new environment, plants adjust their functional traits to develop adaptive strategies that counteract unfavorable conditions (Ahrens et al., 2020; Wang et al., 2022). For example, under long-term heat and drought stress on tropical coral islands, sensitive vegetation may regulate stomatal conductance and leaf water content (LWC) to maintain normal cellular metabolism (Seleiman et al., 2021; Yan et al., 2023). The allocation of carbon (C), nitrogen (N), and phosphorus (P) in leaves also changes to support defense mechanisms against stress, while adjustments in potassium, calcium, and soluble protein levels contribute to osmotic regulation, reducing cell water potential and minimizing water loss to mitigate drought effects (Huang et al., 2025; Lei et al., 2025b). Responses of the photosynthetic pigment system further reflect survival–defense trade-offs, as plants downregulate photosynthesis to alleviate photodamage and allocate energy to stress resistance (Loggini et al., 1999). Concentrations of malondialdehyde (MDA), superoxide dismutase (SOD), and glutathione (GSH) in leaves may also shift markedly under drought stress to counteract oxidative damage (Zhu et al., 2020). Measuring these traits allows us to evaluate how species adjust water balance, nutrients, osmotic control, photosynthesis and antioxidant capacity to persist in extreme island environments (Wang et al., 2022; Liu et al., 2023).

Beyond their aesthetic contributions, the introduction of non-native landscape species presents unique ecological questions (Sheng et al., 2024; Ma et al., 2025; Meng et al., 2025). Their physiological responses and functional roles might differ significantly from native flora, making a dedicated investigation into their adaptability not merely an addition to existing knowledge, but a novel and necessary step for holistic restoration planning (Sheng et al., 2024; Ma et al., 2025; Meng et al., 2025). Landscape plants typically possess high ornamental value, with prominent flower colors, leaf

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colors, and floral scents. *Ruellia simplex* is a perennial ornamental herb with strong stress tolerance, capable of withstanding heat and drought, and grows well even in coastal sandy habitats such as Shanwei and Zhanjiang of tropical and subtropical city (Sheng et al., 2024; Meng et al., 2025; Sheng et al., 2025). It is also widely used for landscaping in tropical and subtropical regions, showing strong potential as a pioneer species (Cai et al., 2020). *Mimosa diplotricha*, in contrast, is a fast-growing perennial herb or shrubby plant with excellent nitrogen-fixing ability. Owing to its vigorous growth and regeneration capacity, it is commonly used as green manure and for soil improvement and erosion control. Both species have already been introduced to some tropical coral islands, but their growth status and physiological-ecological adaptability remain insufficiently assessed.

To assess their potential for habitat improvement, we sampled leaves of *R. simplex* and *M. diplotricha* from three habitats: coastal sand in Shanwei city, soil-amended coral sand in Sansha city, and native coral sand in Sansha city. We measured key adaptive traits and compared their responses under habitats with different levels of drought stress. These results inform strategies for vegetation establishment, community succession, and the sustainable use of tropical coral islands.

Materials and methods

Study area

The study was conducted on the Sansha Islands, Hainan Province, China (111°11′–112°54′E, 15°46′–17°08′N), which lie in a tropical monsoon climate zone with a mean annual temperature of approximately 32.3℃ and an average annual precipitation of about 1500~2800 mm (Cai et al., 2020). The investigated island (112°44'E, 16°40'N), which have a total land area of approximately 1.6 km², are small and low-lying coral formations, with soils naturally rich in calcium and phosphorus but extremely poor in organic matter. Two herbaceous species, *R. simplex* and *M. diplotricha*, were selected from coastal sandy habitats in Shanwei city (115°54′E, 22°47′N), Guangdong (SW) and introduced to two experimental sites on Sansha city: a coral sand habitat amended with exogenous soil (SS1) and a native coral sand habitat without amendment (SS2). All three habitats fall within the tropical monsoon climate region, characterized by hot, rainy summers (June-August) and pronounced drought stress during the dry season. The geographical location and the main environmental characteristics of each site are presented in *Table 1*, respectively.

Table 1. *Description of sample plots*

Site	SW	SS1	SS2
Soil type	Marine sand	Coral sand with garden soil	Coral sand
Mean annual temperature (℃)	23.2℃	32.3℃	32.3℃
Mean annual precipitation (mm)	2200 mm	2800 mm	2800 mm
Soil organic carbon (g kg^{-1})	5.31	2.94	0.36
Soil water content (%)	10.10	5.02	3.24

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Sample collection

Sampling was carried out in mid-August 2023. At each site, we selected *R. simplex* and *M. diplotricha* individuals of similar size and condition. Mature, healthy leaves (3 treatments × 2 plants × 3 repeats) were taken from apical branches, sealed in plastic bags, stored at -4℃, and quickly returned to the lab for analysis (Lei et al., 2025a). For each species, three individual plants were sampled per site as biological replicates. In parallel, leaves from healthy and vigorous plants of the same batch were collected from their native habitat in Shanwei city, Guangdong, China, and used as controls.

Laboratory analysis

Leaf carbon (C) and nitrogen (N) contents were determined using an elemental analyzer (Total Organic Carbon Analyzer, TOC-VCSH, Shimadzu Hong Kong Limited, Japan). P content were measured using an Inductively Coupled Plasma Emission Spectrometer (ICP-OES, Avio 500, PE company, Japan) after the samples were digested with sulfuric acid-hydrogen peroxide (H_2SO_4-H_2O_2) (Chen et al., 2024; Li et al., 2024, 2025). Then, use an ICP-OES to analyze the leaf Ca and potassium (K) contents with perchloric acid and nitric acid. Leaf water content (LWC) was determined by the oven-drying (Electric hot air drying oven, DHG-9245A, Shanghai Yiheng Scientific Instrument Co., Ltd., China) and weighing (d = 0.01 mg Balance, NewClassic MF, MS105/A, Mettler-Toledo GmbH lm Langacher 448606 Greifensee, Switzerland) method (Ågren et al., 2012; Eslamiparvar et al., 2025).

The malondialdehyde (MDA) content in leaves was determined using the thiobarbituric acid method (Wang et al., 2008). Superoxide dismutase (SOD) activity was measured using the xanthine oxidase method (Wang et al., 2008; Sheng et al., 2025). Soluble protein content was determined by the Coomassie brilliant blue staining method (Li et al., 2024). Reduced glutathione (GSH) content was measured according to the method described by Nishimoto et al. (2017). The chlorophyll (a, b, and total) and carotenoid content in leaves was measured according to the method described by Macar et al. (2008), Hatier et al. (2013) and Hu et al. (2013) method.

Data analysis

Data were tested for normality (Shapiro-Wilk) and homogeneity of variance (Levene's), with transformations applied when needed. Differences between habitats and species were assessed by two-way ANOVA with Tukey's HSD ($p < 0.05$). Mantel tests were used to examine correlations among leaf traits, pigments, and nutrients. Data analyses and visualizations were conducted with *vegan*, *ggcor*, *ggplot2* and *corrplot* packages in R (v4.2.0), with *numpy* and *matplotlib* in Python (v 3.12), and Origin 2024.

Results

Leaf water content

Compared with the Shanwei coastal sand habitat (SW), leaf water content of *R. simplex* showed no significant changes in the soil-amended coral sand (SS1) or the native coral sand habitat (SS2) on Sansha Island. In contrast, *M. diplotricha* exhibited significantly higher leaf water content in both SS1 and SS2 ($p < 0.05$). Significant differences between the two species were also observed in SW and SS2 ($p < 0.05$).

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Analysis of variance indicated that habitat (Fs = 57.56, $p < 0.001$), species ($p < 0.01$), and their interaction ($p < 0.01$) all had significant effects on leaf water content (*Fig. 1*).

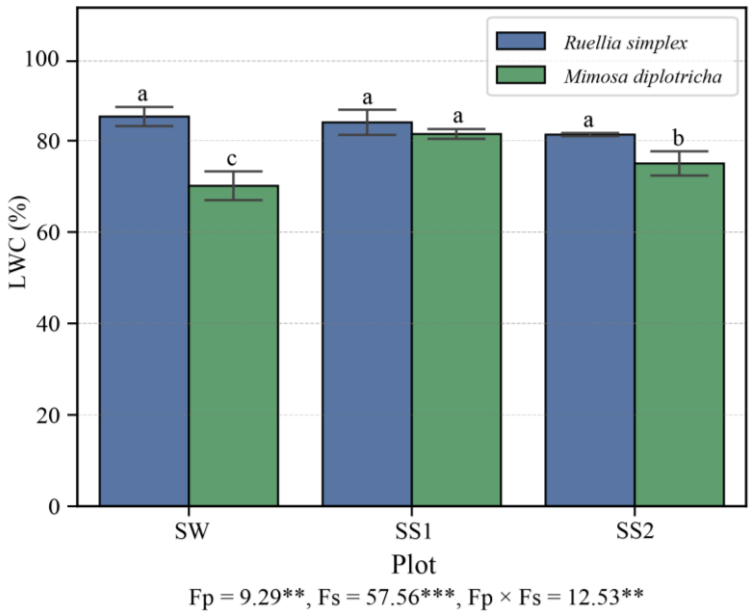

Figure 1. *Leaf water content of Ruellia simplex and Mimosa diplotricha in three habitats: coastal sand in Shanwei (SW), soil-amended coral sand in Sansha (SS1), and native coral sand in Sansha (SS2). Note: Habitat (Fs), species (Fp), and their interaction (Fp × Fs) represent the main and interactive effects from two-way ANOVA. SW, SS1, and SS2 denote the same habitats throughout all figures, and Fp, Fs, and Fp × Fs indicate the same statistical factors in subsequent figures*

Leaf antioxidant content

As shown in *Fig. 2*, leaf antioxidant traits were significantly affected by habitat, species, and their interaction, with marked differences observed both within species across habitats and between species within the same habitat ($p < 0.05$). Compared with SW, leaf GSH concentrations of *R. simplex* and *M. diplotricha* were significantly higher in both SS1 and SS2 ($p < 0.05$). Specifically, GSH in *R. simplex* increased by 61.38% and 102.76% in SS1 and SS2, respectively, while *M. diplotricha* increased by 42.31% and 23.06% (*Fig. 2a*). Leaf MDA in *R. simplex* increased by 21.55% in SS1 and 46.19% in SS2 ($p < 0.05$). By contrast, MDA in *M. diplotricha* decreased by 29.17% in SS1 but increased by 35.68% in SS2 ($p < 0.05$) (*Fig. 2b*). For SOD activity, only *M. diplotricha* in SS1 showed a significant increase (74.83%), whereas *M. diplotricha* in SS2 and *R. simplex* in both habitats exhibited significant decreases of 17.24%, 73.31%, and 43.22%, respectively (*Fig. 2c*). In *R. simplex*, soluble protein decreased by 11.73% in SS1 and increased slightly by 2.04% in SS2, both significantly different from SW ($p < 0.05$). In *M. diplotricha*, soluble protein concentrations were significantly higher in both SS1 and SS2 than in SW, with increases of 8.38% and 18.99%, respectively ($p < 0.05$) (*Fig. 2d*). Overall, *R. simplex* showed higher GSH and SOD but lower MDA and soluble protein than *M. diplotricha*, except under SS1 where MDA was higher and SOD lower in *R. simplex* than in *M. diplotricha*.

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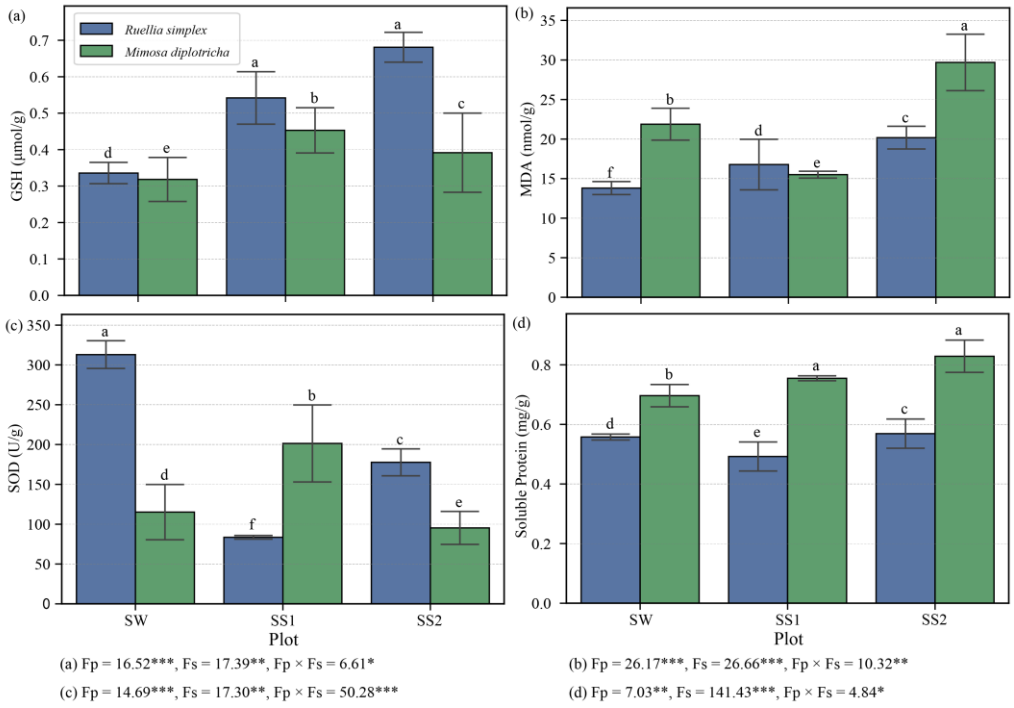

Figure 2. *Leaf glutathione (GSH), malondialdehyde (MDA), superoxide dismutase (SOD), and soluble protein contents in Ruellia simplex and Mimosa diplotricha grown in coastal sandy soil of Shanwei (SW), coral sand amended with external soil in Sansha (SS1), and pristine coral sand in Sansha (SS2)*

Leaf carbon, nitrogen, and phosphorus ecological stoichiometry

Fig. 3a shows that *R. simplex* and *M. diplotricha* differed in their carbon allocation strategies, which were mainly affected by species and the species × habitat interaction ($p < 0.05$). Leaf C concentration in *R. simplex* increased significantly across SW, SS1, and SS2 ($p < 0.05$), whereas no significant differences were observed for *M. diplotricha*, despite a decreasing numerical trend. After introduction into SS2, the significant difference in leaf C between the two species observed in SW was no longer apparent (*Fig. 3a*). For nitrogen, both species showed consistent allocation patterns, primarily influenced by habitat ($p < 0.05$). Although leaf N content decreased numerically in both species, neither interspecific nor habitat-level differences reached statistical significance ($p > 0.05$) (*Fig. 3b*). Leaf P content was significantly influenced by habitat ($p < 0.05$). Both species showed significantly higher P in SS1 and SS2 compared with SW, except that *R. simplex* and *M. diplotricha* did not differ significantly in SS1. In contrast, leaf P content of *R. simplex* was significantly higher than that of *M. diplotricha* in both SW and SS2 ($p < 0.05$) (*Fig. 3c*). For C:N ratio, the two species differed significantly only in SW ($p < 0.05$), whereas no significant differences were detected in SS1 or SS2 (*Fig. 3d*). Habitat had a significant effect ($p < 0.05$), with both species showing higher C:N ratios in SS1 and SS2 compared with SW (*Fig. 3d*). Leaf C:P and N:P ratios of *R. simplex* were consistently lower than those of *M. diplotricha* across habitats. Under the significant effects of habitat and species ($p < 0.05$), both C:P and N:P ratios of the two species decreased significantly in SS1 and SS2 compared with SW (*Fig. 3e, f*).

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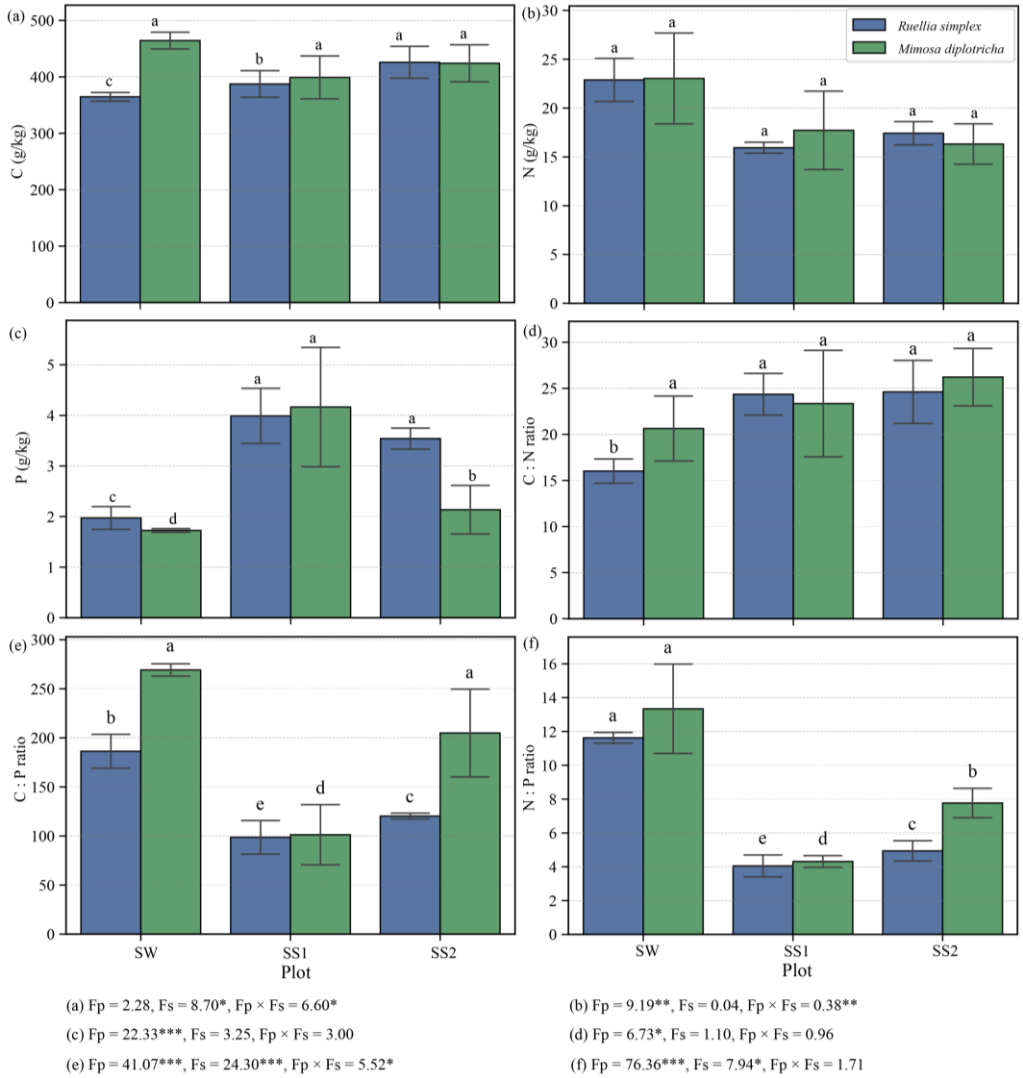

Figure 3. *Leaf carbon (C), nitrogen (N), phosphorus (P) contents and their stoichiometric ratios (C:N, C:P, and N:P) in Ruellia simplex and Mimosa diplotricha grown in coastal sandy soil of Shanwei (SW), coral sand amended with external soil in Sansha (SS1), and pristine coral sand in Sansha (SS2)*

Potassium and calcium in leaves

Leaf K and Ca concentrations in *R. simplex* and *M. diplotricha* were significantly affected by habitat, species, and their interaction ($p < 0.05$), with the exception that K was only weakly influenced by habitat ($p > 0.05$) (*Fig. 4*). Overall, *R. simplex* exhibited significantly higher leaf K and Ca concentrations than *M. diplotricha.* In *R. simplex*, leaf K decreased significantly in both SS1 and SS2, whereas Ca increased significantly ($p < 0.05$) (*Fig. 4*). In contrast, *M. diplotricha* showed significant increases in both K and Ca in SS1 and SS2 ($p < 0.05$), although the magnitude of change was much smaller than in *R. simplex* (*Fig. 4*).

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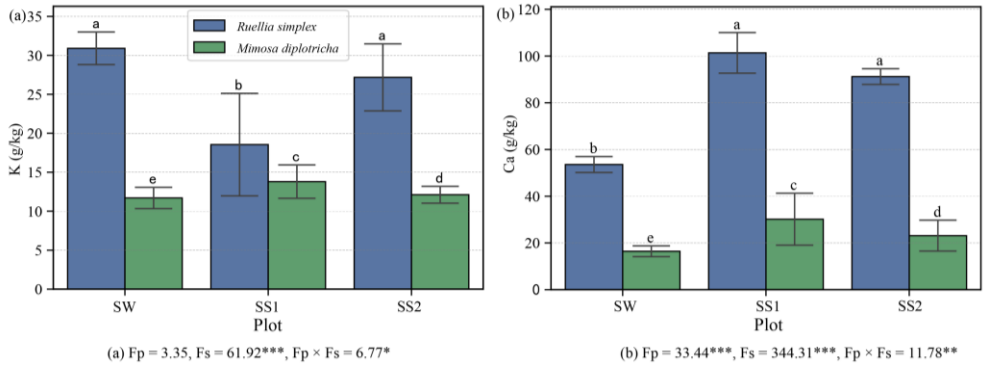

Figure 4. *Potassium (K) and calcium (Ca) contents in leaves of Ruellia simplex and Mimosa diplotricha grown in coastal sandy soil of Shanwei (SW), coral sand amended with external soil in Sansha (SS1), and pristine coral sand in Sansha (SS2)*

Ecological responses of photosynthetic pigments in leaves

Leaf chlorophyll a, chlorophyll b, total chlorophyll, and carotenoid concentrations in *R. simplex* and *M. diplotricha* were significantly affected by habitat, species, and their interaction ($p < 0.05$). In SW, all four pigments in *R. simplex* were significantly lower than those in *M. diplotricha* ($p < 0.05$). After introduction into SS1 and SS2, this pattern reversed, with *R. simplex* showing significantly higher pigment concentrations than *M. diplotricha* ($p < 0.05$). With increasing stress, pigment concentrations in both species declined significantly (*Fig. 5*). The magnitude of pigment loss was smaller in R. simplex than in *M. diplotricha* (*Fig. 5*).

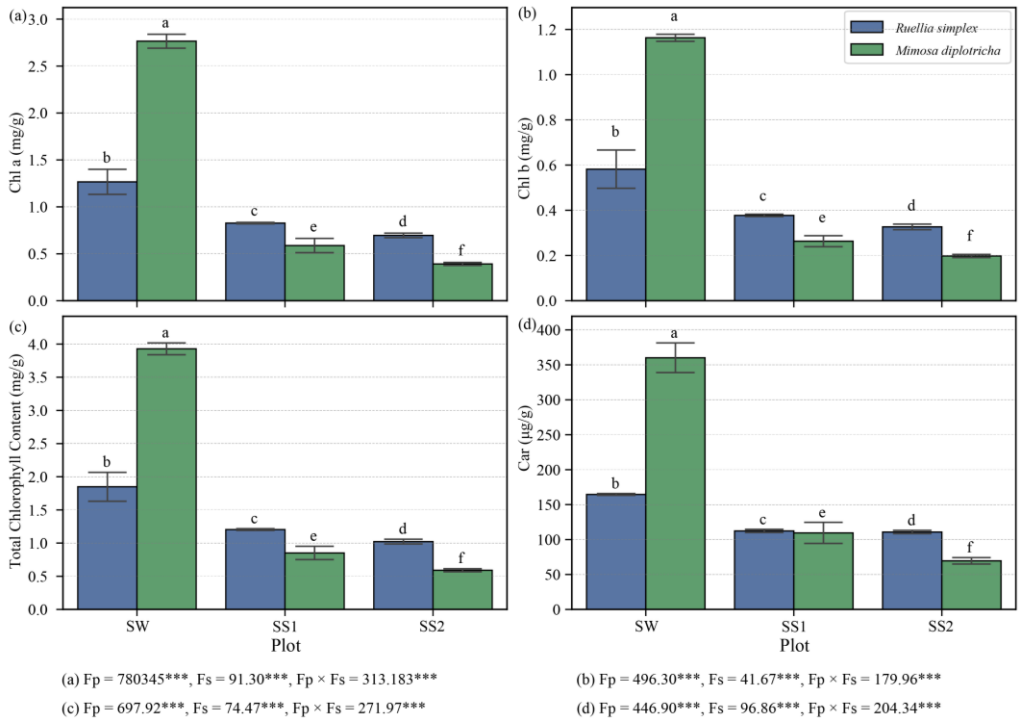

Figure 5. *Leaf pigment contents (Chl a, Chl b, total chlorophyll, and carotenoids) of Ruellia simplex and Mimosa diplotricha in coastal sandy soil of Shanwei (SW), coral sand amended with external soil in Sansha (SS1), and pristine coral sand in Sansha*

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Correlation between different physiological and ecological indicators of leaves

To further elucidate the coordinated regulation among leaf physiological and ecological traits, a Mantel test was conducted using four key stress-response indicators-LWC, soluble protein, and leaf K and Ca concentrations-to examine their overall associations with other functional traits. As shown in *Fig. 6a*, analysis of the full dataset revealed that under heat and water stress, variation in LWC was significantly correlated with carbon content and photosynthetic pigments ($p < 0.01$). Leaf Ca was significantly associated with P, GSH, and pigment concentrations ($p < 0.01$), while soluble protein and K were significantly correlated only with MDA and SOD, respectively ($p < 0.01$). When analyzed separately, *R. simplex* and *M. diplotricha* exhibited distinct ecological response strategies. In *M. diplotricha* (*Fig. 6c*), LWC, K, and Ca were all strongly influenced by P ($p < 0.05$); in addition, LWC was significantly associated with MDA and pigments, and soluble protein was also significantly correlated with MDA and pigments ($p < 0.05$). In contrast, R. simplex showed significant correlations among most traits, but LWC and soluble protein were not strongly affected by other physiological indicators (*Fig. 6b*). Only leaf Ca was consistently associated with multiple factors ($p < 0.01$), and K was correlated only with SOD ($p < 0.05$). These patterns highlight the strong adaptive capacity of R. simplex to withstand heat and drought stress.

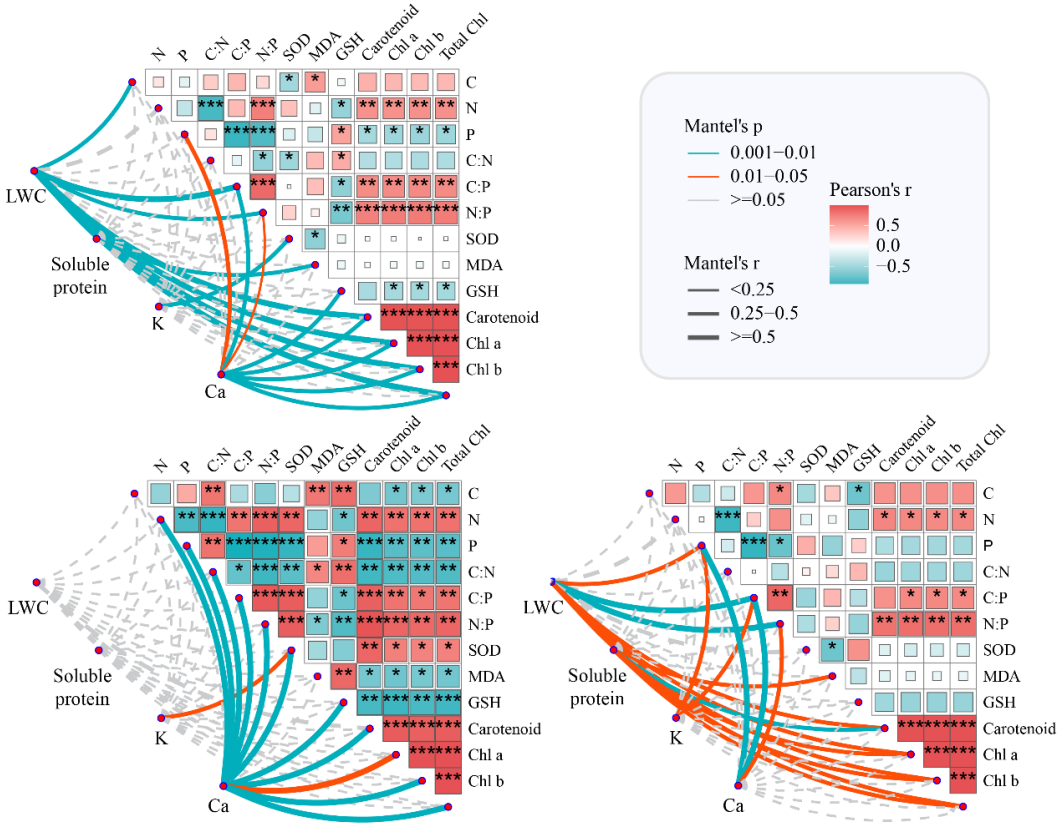

Figure 6. *Mantel analysis of physiological and ecological traits of Ruellia simplex and Mimosa diplotricha. Note: "*", "**", and "***" indicate $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively*

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Discussion

In water-limited environments, plants rely on osmotic adjustment to maintain cellular water balance and sustain normal metabolic processes under drought stress. Our results revealed clear differences between the two species in their drought-resistance strategies. For example, *M. diplotricha* showed a significant increase in leaf water content, suggesting that it may cope with drought stress by enhancing tissue hydration (*Fig. 7*). In contrast, *R. simplex* may depend on alternative mechanisms to withstand water deficit. In general, high leaf water content is considered an important indicator of drought resistance, reflecting a plant's water retention capacity and hydration status (Macar et al., 2008). However, maintaining high leaf water content often requires plants to regulate osmolyte concentrations, thereby lowering cellular water potential to promote water uptake and retention (Sehar et al., 2021).

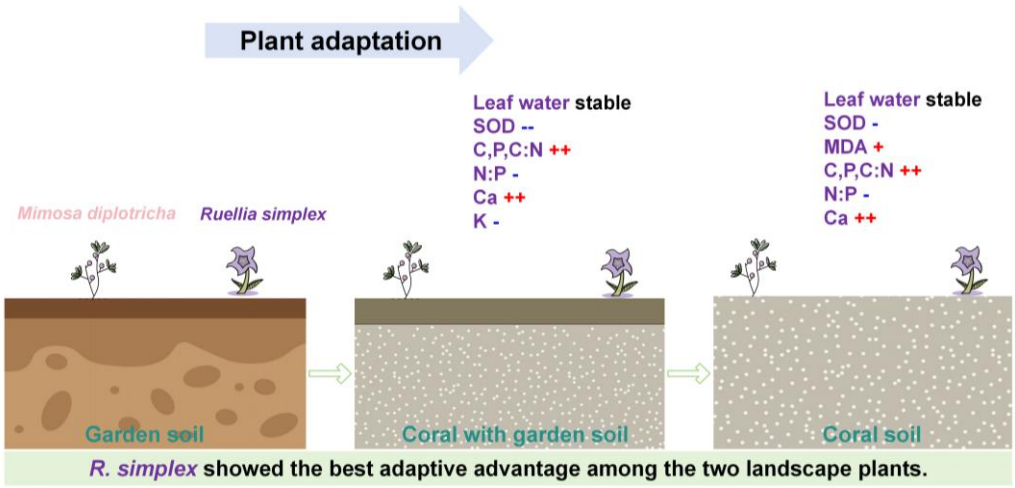

Figure 7. *Schematic diagram illustrating the changes in soil physicochemical properties and the corresponding physiological responses of Ruellia simplex and Mimosa diplotricha across the three treatments (SW, SS1, and SS2)*

K and Ca are two key inorganic osmolytes in plant cells. At the onset of water deficit, plants often accumulate K^+ to rapidly lower cellular water potential and maintain turgor pressure (Sardans et al., 2021). In this study, *M. diplotricha* exhibited higher K concentrations in drier habitats (SS1 and SS2), whereas *R. simplex* showed the opposite trend. This indicates that the two species adopt different osmotic adjustment strategies under the same stress conditions, consistent with their patterns of leaf water content. *M. diplotricha* maintained higher leaf hydration through K accumulation, while reduced K in *R. simplex* may facilitate stomatal closure, thereby minimizing transpirational water loss (Yang et al., 2021). Ca plays a broader role in stress signaling. Drought stress induces increases in cytosolic Ca^{2+}, triggering stomatal regulation, stress-responsive gene expression, and stabilization of cellular structures, which help mitigate drought damage (Sehar et al., 2021; Yang et al., 2021). After introduction into SS1 and SS2, Ca levels increased significantly in both species, with a greater increase in *R. simplex*. This suggests that *R. simplex* may rely more heavily on stress-induced responses such as stomatal closure and membrane stabilization. These findings align with previous reports that drought-tolerant species often maintain elevated tissue Ca

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levels together with organic osmolyte accumulation, thereby sustaining turgor, reducing oxidative damage, and enhancing drought resistance (Sehar et al., 2021; Huang et al., 2023).

In addition to inorganic osmolytes, organic osmolytes play indispensable roles in resisting drought stress. In this study, *M. diplotricha* showed significantly elevated soluble protein concentrations under both SS1 and SS2 drought conditions, whereas *R. simplex* exhibited a significant decline in SS1. This reflects differences in stress-response thresholds and adaptive pathways between the two species. In general, moderate drought stress induces the synthesis of protective proteins, leading to increased soluble protein concentrations that enhance enzymatic activity and stabilize cellular structures (Maleki et al., 2024). For instance, soluble protein concentrations in cotton leaves are higher under drought than under normal conditions, confirming that drought induces the accumulation of protective proteins (Li et al., 2010). However, when drought is either mild or severe, protein synthesis may decline or degradation may occur, resulting in reduced soluble protein concentrations and lower metabolic activity, thereby conserving energy (Mohammadkhani et al., 2008; Xiong et al., 2022). In this study, the decrease of soluble protein in *R. simplex* under mild stress in SS1 may be related to reduced protein synthesis, allowing more energy to be allocated to drought defense. Overall, *M. diplotricha* tends to maintain cell water potential and leaf hydration by increasing osmolytes such as K and soluble proteins, consistent with its significantly higher leaf water content under drought. By contrast, *R. simplex* relies more on stomatal regulation and Ca-mediated signaling to maintain tissue hydration, consistent with the relatively stable leaf water content observed across habitats. These strategies reflect different pathways of drought adaptation: the former actively stores water by raising intracellular osmotic pressure, while the latter passively conserves water by reducing water loss.

Drought stress triggers excess ROS, driving lipid peroxidation and oxidative damage. Plants counter this with enzymatic defenses such as SOD and non-enzymatic antioxidants like GSH (Zhu et al., 2020). In this study, *M. diplotricha* showed significantly elevated SOD activity and reduced MDA concentrations in the soil-amended SS1 habitat, indicating that enhanced enzymatic activity efficiently scavenged ROS and alleviated lipid peroxidation. This is consistent with the established mechanism whereby increased MDA under stress is typically accompanied by enhanced antioxidant enzyme activity, with SOD dismutating superoxide radicals (Khaleghi et al., 2019; Meng et al., 2025). However, under more severe drought (SS2), SOD activity in *M. diplotricha* declined slightly relative to the control, likely due to enzyme inactivation or inhibited synthesis, leading to MDA accumulation (Duan et al., 2023). In contrast, SOD activity in *R. simplex* declined continuously under stress (73% in SS1 and 43% in SS2), suggesting that energy reallocation may reduce investment in enzymatic defenses, weakening ROS scavenging and resulting in greater MDA accumulation (Liu et al., 2023). Meanwhile, GSH functioned as a direct free radical scavenger in both species. GSH concentrations increased significantly in both species under drought, with particularly large increases in *R. simplex*, suggesting a greater reliance on non-enzymatic antioxidant pathways, consistent with previous findings (Nishimoto et al., 2017; Meng et al., 2025).

On the photosynthetic side, Chl a, Chl b and total chlorophyll declined in both species in SS1 and SS2. This reflects reduced photosynthesis but also a likely adaptive downregulation of light harvesting to prevent excess ROS (Loggini et al., 1999).

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Carotenoids accumulated, consistent with their role in energy dissipation and singlet oxygen quenching via the xanthophyll cycle. Overall, the two species showed distinct but also overlapping responses in antioxidant and photoprotection strategies.

Drought alters not only water and light use but also nutrient elemental stoichiometry (Wang et al., 2022). Carbon allocation reflects trade-offs between growth and defense, and in this study the two species adopted contrasting strategies. Under stress, *R. simplex* significantly increased leaf carbon concentration, while *M. diplotricha* showed the opposite trend. This pattern supports the idea that *R. simplex* may reduce metabolic activity while increasing osmolytes and non-structural carbohydrates to stabilize cellular structures, whereas *M. diplotricha* may allocate more energy to carbon-based defense. The increase in leaf C:N ratio under stress in both species further supports this interpretation. Following introduction to the coral islands, leaf nitrogen decreased significantly while phosphorus increased, which may reflect both stress-induced responses and differences in soil nutrient availability. This is consistent with previous findings that coral island soils are richer in phosphorus (Li et al., 2025). The associated declines in C:P and N:P may support ATP/NADPH efficiency and photosystem repair, but also indicate a shift from N limitation in sandy habitats to P limitation on coral sands (Zhang et al., 2018; Wang et al., 2023). As a legume, *M. diplotricha* offsets N limitation via fixation, aiding its establishment. Thus, *M. diplotricha* fits a "high-investment, high-defense" strategy, maintaining metabolism and repair, while R. simplex follows a "low-investment, conservative" path, reducing costs and stabilizing structures. This stoichiometric divergence complements their water, antioxidant, and photosynthetic strategies, forming a coherent adaptive system.

The overall Mantel analysis indicated that plants adapt to drought stress through multiple pathways of water regulation and osmotic adjustment. These include increasing LWC to sustain photosynthesis and antioxidant systems, and elevating Ca concentrations to activate stress-responsive mechanisms and maintain growth. However, species differed in their adaptive strategies. *R. simplex* tended to rely on Ca-mediated responses, emphasizing reduced metabolism and structural stabilization of cells and tissues as a means of stress adaptation. In contrast, *M. diplotricha* adopted a more integrated strategy. Alongside increased Ca for structural stability, it invested additional energy to substantially elevate LWC and soluble protein concentrations, thereby sustaining metabolic activity under stress. From the perspective of physiological adaptation, both species can tolerate the hot and drought-prone conditions of tropical coral islands. In terms of ecological application, *R. simplex* shows strong resistance and can provide long-term cover on bare coral sands, reducing evaporation and improving the microenvironment. *M. diplotricha*, being fast-growing and capable of N fixation, can enhance soil fertility in improved habitats. Together, the two species represent a complementary "stabilization + improvement" strategy for vegetation restoration on tropical coral islands.

Conclusion

This study systematically investigated the physiological and ecological responses of *R. simplex* and *M. diplotricha* in three contrasting habitats: coastal sandy soils in Shanwei (SW), coral sands amended with external soil in Sansha (SS1), and pristine coral sands in Sansha (SS2). Our results revealed that *M. diplotricha* copes with drought stress by markedly increasing leaf water content, accumulating potassium ions and

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soluble proteins, and activating antioxidant enzymes, reflecting a "high-investment, high-defense" strategy. Owing to its rapid growth and nitrogen-fixing capacity, this species can effectively improve soil fertility. In contrast, *R. simplex* maintained relatively stable leaf water content by reducing potassium, increasing calcium, elevating reduced glutathione, and downregulating photosynthetic pigments to stabilize cellular structures. This "low-investment, conservative" strategy confers strong stress tolerance and enables persistent coverage of bare substrates, thereby reducing water loss and improving microhabitat conditions. When combined, the two species can enhance surface vegetation cover, minimize energy exchange across vertical and horizontal interfaces, and jointly achieve a "stabilization + improvement" restoration outcome: stabilizing substrates while enhancing soil quality and promoting vegetation establishment. Future work should focus on designing habitat- and stage-specific species assemblages and monitoring the long-term succession of other stress-tolerant species, in order to establish a robust framework for vegetation restoration and sustainable management on tropical coral islands.

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