Postprint: Physiological and Ecological Adaptation of Chromolaena odorata to Tropical Coral Islands

Authors: Liao Mengcheng, Liu Nan, Shuguang Jian

Date: 2021-04-13T00:00:00+00:00

Abstract

The environmental adaptability of invasive plants is fundamental to understanding their invasiveness. The Xisha Islands are tropical coral islands characterized by harsh environmental conditions such as high salinity, strong alkalinity, high temperature, intense light, and drought. In recent years, Chromolaena odorata has invaded some native plant communities in the Xisha Islands, potentially causing serious damage to the local fragile ecosystem. This study examined the leaf morphological and anatomical structures, physiological characteristics, and leaf nutrient element contents of C. odorata in forest gaps of native plant communities on the Xisha Islands and in suburban Wenchang City, aiming to investigate the adaptability of C. odorata to the special habitat of tropical coral islands. The results demonstrated that, compared with plants grown in Wenchang City, C. odorata on tropical coral islands exhibited thicker leaves, lower stomatal density, lower chlorophyll a and malondialdehyde contents, and higher superoxide dismutase and catalase activities, which facilitate adaptation to intense light and seasonal drought conditions on tropical coral islands and confer greater potential invasiveness. Therefore, strengthening monitoring and control of C. odorata is essential for the conservation and restoration of vegetation on tropical coral islands.

Full Text

Preamble

Ecophysiological Adaptability of Chromolaena odorata to Tropical Coral Islands

LIAO Mengcheng[1,2], LIU Nan[1], JIAN Shuguang[1*]
[1]CAS Engineering Laboratory for Vegetation Ecosystem Restoration on Islands

and Coastal Zones, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China
[2]University of Chinese Academy of Sciences, Beijing 100049, China

Abstract

Understanding the environmental adaptability of invasive plants is fundamental to assessing their invasiveness. The Xisha Islands represent tropical coral islands characterized by harsh environmental conditions including high salinity, strong alkalinity, high temperature, intense light, and drought. In recent years, Chromolaena odorata has invaded native plant communities on the Xisha Islands, potentially causing severe damage to these fragile ecosystems. This study investigated leaf morphological and anatomical structures, physiological characteristics, and leaf nutrient contents of C. odorata growing in forest gaps on tropical coral islands and in suburban Wenchang City, aiming to explore its adaptability to the unique habitats of tropical coral islands. The results showed that compared with plants from Wenchang, C. odorata from tropical coral islands exhibited thicker leaves, lower stomatal density, lower chlorophyll a and malondialdehyde contents, and higher superoxide dismutase and catalase activities. These traits facilitate its adaptation to strong light and seasonal drought conditions on tropical coral islands and contribute to its substantial invasive potential. Therefore, enhanced monitoring and control of C. odorata are essential during vegetation protection and restoration efforts on tropical coral islands.

Keywords: Chromolaena odorata; ecophysiological adaptability; invasiveness; tropical coral islands

Introduction

Chromolaena odorata, a perennial herb or subshrub belonging to the Asteraceae family, is native to Central America and has become a globally invasive weed. First discovered in China in 1934, it has since spread to Yunnan, Sichuan, Guangxi, Hainan, Guangdong, and other regions. This species produces numerous seeds that disperse easily, germinate quickly, and grow rapidly with strong sprouting ability, often forming monodominant communities in invaded areas. Such invasions severely suppress native plants and crops, reduce biodiversity, and impair ecosystem health and service functions. Previous domestic research on C. odorata has focused on allelopathy, ecophysiological adaptation, competitive effects, and risk assessment. However, studies on its ecophysiological adaptability to the special habitat of tropical coral islands remain unreported.

Tropical coral islands present extremely harsh environmental conditions, including high salinity, strong alkalinity, high temperature, intense light, and seasonal drought. Only a few well-adapted species such as Ceodes grandis, Guettarda speciosa, Cordia subcordata, Terminalia catappa, Scaevola sericea, Messerschmidia argentea, Ipomoea pescaprae, Canavalia maritima, and Thuarea involuta can successfully colonize these islands. Recent surveys have documented C.

odorata invading forest gaps in native plant communities, forming monodominant stands in some areas and threatening the ecological security of tropical coral islands.

Phenotypic plasticity and physiological adaptability are crucial determinants of plant invasiveness. As the primary organ for respiration and photosynthesis, leaves exhibit strong environmental adaptability, making leaf traits reliable indicators of plant responses to different habitats. This study compared leaf morphological and anatomical structures, physiological characteristics, nutrient contents, and rhizosphere soil physicochemical properties of C. odorata from Wenchang City and tropical coral islands. The objective was to investigate its adaptability to the unique environment of tropical coral islands and assess its invasiveness in island forest communities, providing a scientific basis for effective control strategies and protection of native vegetation.

1.1 Study Sites and Sample Collection

The tropical coral island study site was located on Yongxing Island (112°20 E, 16°49 N) in the Xisha Islands, the largest island in the archipelago. The island has a tropical oceanic monsoon climate with a mean annual temperature of approximately 25.56°C and annual precipitation of about 1,400 mm. Rainfall is concentrated between June and November, accounting for approximately 86% of the annual total, resulting in severe seasonal drought during the dry season. The soil substrate consists of alluvial coral sand and phosphatic limestone soil with poor water retention and strong alkalinity. Chromolaena odorata grew vigorously in forest gaps within native plant communities, forming monodominant stands.

The Wenchang City study site was located in the suburban area (110°45 E, 19°31 N) with a mean annual temperature of approximately 24°C and a tropical oceanic monsoon climate. Annual precipitation averages about 1,800 mm, unevenly distributed with 80% concentrated between May and October. The soil type is coastal deposit sandy loam. Vigorous C. odorata populations were found in wastelands and along roadsides.

1.2 Experimental Materials

Sampling was conducted in early December 2019 during the dry season when plants were in a vigorous vegetative growth stage at both locations. On December 3, 2019, five forest gaps invaded by C. odorata were randomly selected on Yongxing Island, with sampling points spaced more than 20 m apart. At each point, one healthy plant was selected, and 8–10 mature leaves from the upper canopy were collected, sealed in plastic bags, and temporarily stored in a shipboard refrigerator. Rhizosphere soil samples (0–10 cm depth) were also collected beneath each plant and mixed into one composite sample from five different positions. The following day, leaf and soil samples were collected from the Wenchang suburban site using identical methods. All samples were transported to the laboratory for analysis of leaf morphological and anatomical structures, physiological characteristics, nutrient contents, and soil physicochemical properties.

1.3 Measurement Methods

1.3.1 Morphological and Anatomical Characteristics **Individual leaf area:** Leaf area (LA) was measured using a LI-3000 leaf area meter, and leaf number (N) was recorded to calculate individual leaf area (LA/N).

Leaf dry matter content: Fresh weight (FW) of leaves was measured using an electronic balance. Leaves were then oven-dried at 65°C to constant weight to obtain dry weight (DW), and leaf dry matter content (LDMC) was calculated as DW/FW.

Stomatal observation: Following the nail polish impression method of Fu et al. (2009), a layer of clear nail polish was applied to the lower leaf surface. After drying, the epidermis was peeled off with tweezers to prepare temporary sections. Under an XTS20 stereomicroscope, 10–15 random fields of view per leaf were examined. Stomatal number was recorded using a platelet grid counting method to calculate stomatal density, and stomatal length was measured.

Leaf cross-section observation: Following the method of Chang et al. (2012), sections were prepared and examined under an XTS20 stereomicroscope to measure and record leaf thickness and the thickness of upper epidermis, palisade tissue, spongy tissue, and lower epidermis.

1.3.2 Physiological Characteristics Chlorophyll content was determined following Li et al. (2000) and calculated using Arnon's (1949) formulas for chlorophyll a and b. Abscisic acid (ABA) content was measured by high-performance liquid chromatography (Wang et al., 2018). Total phenolics (Tp) content was determined using the Folin-Ciocalteu colorimetric method (Li, 2013). Malondialdehyde (MDA) content was measured by the thiobarbituric acid method (Sun et al., 2006). Antioxidant enzyme activities were determined as follows: catalase (CAT) by ultraviolet absorption (Aebi, 1984), peroxidase (POD) by the guaiacol method (Li et al., 2000), and superoxide dismutase (SOD) by the nitroblue tetrazolium (NBT) method (Li et al., 2000).

1.3.3 Leaf Nutrient and Soil Physicochemical Analyses Total nitrogen content in leaves was determined by the Kjeldahl method. Total phosphorus content was measured by the molybdenum-antimony colorimetric method. Total organic carbon (TOC) was determined by the potassium dichromate-sulfuric acid oxidation method (Dong, 1996). Soil physicochemical properties were analyzed following *Soil Physical and Chemical Analysis & Description of Soil Profiles* (Liu, 1996).

1.4 Data Analysis

Differences in leaf traits of C. odorata between habitats were analyzed using t-tests in Origin 2020b software.

Results

2.1 Morphological and Anatomical Characteristics

The leaf morphological and anatomical characteristics of C. odorata from both sites are presented in Table 1 . Plants from tropical coral islands showed significantly greater palisade tissue thickness and leaf thickness compared with those from Wenchang suburb. Conversely, Wenchang plants exhibited significantly greater stomatal guard cell length and stomatal density. No significant differences were observed in leaf dry matter content, individual leaf area, upper epidermis thickness, spongy tissue thickness, or lower epidermis thickness between the two habitats.

Table 1 Leaf morphological and anatomical characteristics of Chromolaena odorata growing in tropical coral island and Wenchang suburb

<table>
<tr><th>Index</th><th>Wenchang suburb</th><th>Tropical coral island</th></tr>
<tr><td>Leaf dry matter content (LDMC, %)</td><td colspan="2">0.245$±0.012a|0.242±0.013a||Leafareaperplant(cm^{2})|39.28±2.58a|36.93±1.71a||Thicknessofupperepide 2})|230.91±3.16a|212.30±$4.12b</td></tr>
</table>

Note: Different letters indicate significant differences (P<0.05), n=5. The same below.

The stomata (a) and cross section (b) of Chromolaena odorata growing in tropical coral island; The stomata (c) and cross section (d) of C. odorata growing in Wenchang suburb.

Figure 1 [Figure 1: see original paper] Leaf anatomical structure of Chromolaena odorata growing in tropical coral island and Wenchang suburb

2.2 Physiological Characteristics

The physiological characteristics of C. odorata are shown in Table 2 . Wenchang plants exhibited significantly greater chlorophyll a content and chlorophyll a/b ratio than tropical island plants, though both values were below the theoretical ratio of 3:1. Among the antioxidant enzymes (SOD, POD, CAT), SOD activity was significantly higher in tropical island plants, with no significant differences in POD or CAT activities. Additionally, MDA content was significantly higher in

Wenchang plants, while ABA and total phenolics contents showed no significant differences between habitats.

Table 2 Physiological characteristics of Chromolaena odorata growing in the tropical coral island and Wenchang suburb

Index	Wenchang suburb	Tropical coral island
Chlorophyll a content ($mg \cdot g^{-1}$)	1.274±0.066a	1.081±0.035b
Chlorophyll b content ($mg \cdot g^{-1}$)	0.529±0.033a	0.529±0.011a
Chlorophyll a/b	2.241±0.030a	2.110±0.020b
Abscisic acid (ABA) content ($\mu g \cdot g^{-1}$)	0.846±0.142a	0.984±0.061a
Malondialdehyde (MDA) content ($nmol \cdot g^{-1}$)	64.62±5.41a	45.56±5.39b
Total phenolics (Tp) ($mg \cdot g^{-1}$)	31.32±1.44a	29.77±0.16a
Superoxide dismutase (SOD) activity ($U \cdot g^{-1}$)	661.99±132.76b	1270.05±102.00a
Catalase (CAT) activity ($U \cdot g^{-1}$)	170.57±39.61a	231.48±48.78a
Peroxidase (POD) activity ($U \cdot g^{-1}$)	176.49±20.07a	114.20±19.14a

2.3 Leaf Nutrient Contents

The leaf nutrient contents of C. odorata are presented in Table 3 . Total organic carbon content was significantly higher in Wenchang plants compared with tropical island plants, while nitrogen and phosphorus contents showed no significant differences between habitats.

Table 3 Nutrient contents in leaves of Chromolaena odorata growing in the tropical coral island and Wenchang suburb

Index	Wenchang suburb	Tropical coral island
Total organic carbon content (TOC) ($g \cdot kg^{-1}$)	418.43±19.70a	370.37±3.76b
Total nitrogen content (TN) ($g \cdot kg^{-1}$)	32.93±2.27a	34.02±2.62a
Total phosphorus content (TP) ($g \cdot kg^{-1}$)	2.785±0.269a	3.616±0.406a
C/N ratio	13.446±1.005a	11.464±0.918a
C/P ratio	164.40±21.5	[illegible]

2.4 Rhizosphere Soil Physicochemical Properties

The rhizosphere soil physicochemical properties are shown in Table 4 . Tropical coral island soils were alkaline, with higher total organic carbon, total nitrogen, and total phosphorus contents than Wenchang soils, with total nitrogen and total phosphorus reaching significant levels.

Table 4 Physical and chemical properties of rhizosphere soil of Chromolaena odorata growing in the tropical coral island and Wenchang suburb

<table>
<tr><th>Index</th><th>Wenchang suburb</th><th>Tropical coral island</th></tr>
<tr><td>Total organic carbon content (%)</td><td colspan="2">1.86$±0.135a|3.80±0.816a||Totalnitrogencontent(TN)(g· kg{-1})|2.16±0.136b|5.17±1.07a||Totalphosphoruscontent(TP)(g · kg{-1})|0.228±0.033b|18.72±3.56a||pHvalue|6.468±0.281b|7.726±$0.119a</td></tr>
</table>

Discussion

3.1 Leaf Morphological and Anatomical Characteristics

Leaves exhibit substantial phenotypic plasticity during plant growth, enabling plants to adapt to different environmental conditions through modifications in leaf traits. Consequently, leaf characteristics serve as reliable indicators of plant adaptability to various habitats. Leaf dry matter content reflects a plant' s capacity for nutrient utilization and conservation, with higher values indicating stronger adaptability to harsh environments. Reducing individual leaf area (the ratio of total leaf area to leaf number) to decrease transpiration area represents an important adjustment mechanism for drought adaptation. In this study, no significant differences in leaf dry matter content or individual leaf area were observed between C. odorata from the two habitats.

Leaf thickness is an important indicator of drought resistance, as thicker leaves can retain more water. Leaves with thicker palisade tissue not only provide greater structural support but also more effectively reduce water loss under drought conditions. Tropical island C. odorata exhibited significantly greater leaf thickness and palisade tissue thickness than Wenchang plants, demonstrating adaptation to the pronounced seasonal drought on tropical coral islands.

Stomata, as channels controlling water and gas exchange, are highly sensitive to environmental changes. Stomatal density across different plant species ranges from 5 to 1,000 $n \cdot mm^{-2}$. Under severe drought conditions, plants typically exhibit lower stomatal density. Research on six drought-resistant shrubs in northwestern arid and semi-arid regions revealed stomatal densities ranging from 39.5 to 227.5 $n \cdot mm^{-2}$, all relatively low levels, suggesting that reduced stomatal density enhances drought resistance. Compared with Wenchang plants, tropical island C. odorata had lower stomatal density, which helps reduce water loss through transpiration and adapt to seasonal drought. Changes in stomatal length also represent an important adaptation to drought. Studies on two Agropyron cristatum varieties with different drought resistance levels found that more drought-resistant varieties had shorter stomata. In this study, tropical island C. odorata had shorter stomata, indicating stronger drought resistance. These findings are consistent with research on Solidago canadensis growing in different habitats. Overall, C. odorata demonstrates considerable plasticity in leaf morphological and anatomical structures, reflecting strong adaptability to the harsh environment of tropical coral islands.

3.2 Physiological Characteristics

Chlorophyll is essential for light energy absorption in plants, with chlorophyll a primarily absorbing long-wavelength red light and chlorophyll b absorbing short-wavelength blue-violet light. The chlorophyll a/b ratio indicates plant growth status and photosynthetic potential. Both populations showed chlorophyll a/b ratios below the theoretical value of 3:1, which facilitates light energy absorption and photosynthesis. The chlorophyll a/b ratio typically correlates negatively with drought resistance. The significantly lower chlorophyll a/b ratio in tropical island C. odorata indicates greater drought tolerance. Additionally, excessive light intensity can cause photoinhibition in plants. Reducing chlorophyll content is an important strategy to avoid capturing excess energy that leads to photoinhibition. Chlorophyll a serves as the primary photosynthetic pigment in light reaction centers, and its reduction helps decrease the transfer of excess light energy to photosystem reaction centers, thereby reducing damage from intense light. Compared with Wenchang plants, tropical island C. odorata had lower chlorophyll a content, demonstrating adaptation to the high light stress on tropical coral islands.

During normal plant growth, reactive oxygen species such as hydrogen peroxide are continuously produced and scavenged in a balanced state. However, environmental stresses (drought, salinity, high light) can disrupt this balance, causing free radical accumulation and cellular damage. SOD, POD, and CAT are common antioxidant enzymes that protect plants from excessive reactive oxygen species. SOD catalyzes the conversion of superoxide radicals (O_2^-) to H_2O_2 and O_2, while POD and CAT catalyze H_2O_2 decomposition. Together, these enzymes reduce damage from superoxide anion and hydroxyl radicals. Compared with the antioxidant enzyme activities of Canavalia maritima (SOD: 395.23 $U \cdot g^{-1}$, POD: 105.39 $U \cdot g^{-1}$, CAT: 143.27 $U \cdot g^{-1}$) and the selected suitable species Catharanthus roseus (SOD: 867.78 $U \cdot g^{-1}$, POD: 92.35 $U \cdot g^{-1}$, CAT: 199.94 $U \cdot g^{-1}$) on tropical coral islands, C. odorata in this study exhibited higher activities of all three antioxidant enzymes. Elevated antioxidant enzyme activity enhances plant adaptability under stress conditions.

When plants experience severe stress, reactive oxygen species production can exceed scavenging capacity, leading to membrane peroxidation. MDA, as the final product of membrane lipid peroxidation, effectively reflects the degree of cell membrane damage. In this study, tropical island C. odorata showed significantly lower MDA content but higher SOD and CAT activities than Wenchang plants, suggesting that high antioxidant enzyme activity in tropical island plants substantially reduced stress-induced membrane damage. This finding aligns with research on hybrid rice showing a negative correlation between MDA content and SOD and CAT activities.

3.3 Nutrient Utilization Efficiency of C. odorata

Carbon forms the backbone of biological macromolecules, and leaf carbon content represents leaf construction cost. Correlations among traits in the leaf economics spectrum reflect the trade-off between investment in leaf construction and photosynthetic capacity. Leaves following a "rapid return" strategy typically exhibit high photosynthetic capacity and low leaf carbon content. Compared with Wenchang plants, tropical island C. odorata had lower leaf carbon content, consistent with findings for Scaevola sericea, Arachis hypogaea, and Cocos nucifera transplanted to tropical coral islands. This suggests that C. odorata invests more energy in enhancing photosynthetic capacity rather than leaf construction costs to adapt to the high-light environment of tropical coral islands.

Nitrogen and phosphorus are essential nutrients that constitute proteins and nucleic acids and are required in large quantities during growth. Their contents and ratios significantly affect photosynthesis, respiration, and other vital activities, reflecting plant nutrient requirements and growth status. Both total nitrogen and phosphorus contents in tropical island C. odorata exceeded global averages for terrestrial plants (20.1 and 1.99 $g \cdot kg^{-1}$, respectively), indicating good growth conditions. Research suggests that N/P ratios below 14 indicate nitrogen limitation, while ratios above 16 indicate phosphorus limitation. The N/P ratio of 9.58 for tropical island C. odorata is similar to that of native tropical coral island plants, indicating nitrogen-limited growth. Previous studies have shown that C. odorata prefers habitats with high nitrogen and phosphorus availability. The relatively high nitrogen and phosphorus contents in tropical coral island habitats may therefore facilitate the growth, reproduction, and further spread of C. odorata.

Conclusion

Compared with Wenchang plants, C. odorata from tropical coral islands exhibited adaptive morphological and anatomical characteristics (thicker leaves, lower stomatal density) and physiological traits (lower chlorophyll a content, higher SOD and CAT activities, lower MDA content) that enable it to cope with the harsh environmental conditions of drought and intense light on tropical coral islands. The fertile soils in forest gaps of native tropical coral island communities further facilitate C. odorata growth. Consequently, C. odorata poses a significant risk of large-scale invasion into native plant communities on tropical coral islands, necessitating strengthened monitoring and control measures.

References

AEBI H, 1984. Methods in enzymology: oxygen radicals in biological systems[M]. American: Academic Press:121-126.

ARNON DI, 1949. Copper enzymes in isolated chloroplasts-polyphenoloxidase in beta-vulgaris[J]. Plant Physiol, 24(1): 1-15.

CAO F, 2008. Morphology and anatomy of invasive biological characteristics and sexual reproduction control of an invasive plant, Solidago canadensis[D]. Nanjing: Nanjing Agricultural University:22-23. [Cao Fei, 2008. Study on the morphological and anatomical characteristics of invasive biology and control of sexual reproduction of Solidago canadensis[D]. Nanjing: Nanjing Agricultural University: 22-23.]

CHANG YQ, XU WY, MU LQ, et al., 2012. Effects of drought stress on anatomical structure of leaves of three species of shrubs and their drought resistances[J]. J Ne For Univ, 40(3): 36-40. [Chang Yingqiao, Xu Wenyuan, Mu Liqang, et al., 2012. Effects of drought stress on leaf anatomical structure of three ornamental shrubs and their drought resistance analysis[J]. Journal of Northeast Forestry University, 40(3): 36-40.]

DONG M, 1996. Survey, observation and analysis of terrestrial biocommunities[M]. Beijing: Standards Press of China:152-155. [Dong Ming, 1996. Survey, observation and analysis of terrestrial biocommunities[M]. Beijing: Standards Press of China: 152-155.]

FU QS, LI HL, CUI J, et al., 2009. Effects of water stress on photosynthesis and associated physiological characters of Capsicum annuum L.[J]. Sci Agric Sin, 42(5): 1859-1866. [Fu Qiushi, Li Hongling, Cui Jian, et al., 2009. Effects of water stress on photosynthesis and related physiological characteristics of pepper[J]. Scientia Agricultura Sinica, 42(5): 1859-1866.]

GENG YP, ZHANG WJ, LI B, et al., 2004. Phenotypic plasticity and invasiveness of alien plants[J]. Biodivers Sci, 12(4): 447-455. [Geng Yupeng, Zhang Wenju, Li Bo, et al., 2004. Phenotypic plasticity and invasiveness of alien plants[J]. Biodiversity Science, 12(4): 447-455.]

HAN G, LI SX, XU P, et al., 2006. Analyisis of drought resistance on anatomical structure of leave of six species of shrubs[J]. J NW For Univ, 21(4): 43-46. [Han Gang, Li Shaoxiong, Xu Peng, et al., 2006. Analysis of drought resistance of leaf anatomical structure of six shrub species[J]. Journal of Northwest Forestry University, 21(4): 43-46.]

HAN TT, LIU N, SONG GM, et al., 2018. Eco-physiological characteristics of Morinda citrifolia[J]. J Trop Subtrop Bot, 26(1): 33-39. [Han Taotao, Liu Nan, Song Guangman, et al., 2018. Study on eco-physiological characteristics of Morinda citrifolia[J]. Journal of Tropical and Subtropical Botany, 26(1): 33-39.]

HETHERINGTON AM, WOODWARD FI, 2003. The role of stomata in sensing and driving environmental change[J]. Nature, 424(6951): 901-908.

HUANG J, LIU N, REN H, et al., 2019. Physiology and biochemical characteristics of Canavalia maritime under stress[J]. J Trop Subtrop Bot, 27(2): 157-163. [Huang Jing, Liu Nan, Ren Hai, et al., 2019. Analysis of physiological and biochemical characteristics of stress resistance in Canavalia maritime[J]. Journal of Tropical and Subtropical Botany, 27(2): 157-163.]

HUA C, WANG RL, 2003. Changes of sod and cat activities and mda content during senescence of hybrid rice and three lines leaves[J]. Acta Bot Boreal-Occident Sin, 23(3): 406-409. [Hua Chun, Wang Renlei, 2003. Changes of SOD and CAT activities and MDA content during senescence of hybrid rice and three lines leaves[J]. Acta Botanica Boreali-Occidentalia Sinica, 23(3): 406-409.]

JIN YM, LI LX, 2012. Comparative study on relationship between leaf anatomical structure and drought resistance of Fontanesia fortunei carr., Forsythia suspense vahl., and Syringa microphylla diels[J]. J NE Agric Univ, 43(1): 116-121. [Jin Yanming, Li Liangxi, 2012. Comparative study on relationship between leaf anatomical structure and drought resistance of Fontanesia fortunei carr., Forsythia suspense vahl., and Syringa microphylla diels[J]. Journal of Northeast Agricultural University, 43(1): 116-121.]

KOERSELMAN W, MEULEMAN AFM, 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation[J]. J Appl Ecol, 33(6): 1441-1450.

LI B, CHEN XM, LI TY, et al., 2015. Comparison of the anatomical structures of the leaves of two different drought-resistant Agropyron cristatum[J]. Jiangsu J Agric Sci, 43(9): 247-249. [Li Bo, Chen Xuemei, Li Tieyuan, et al., 2015. Comparison of the anatomical structures of the leaves of two different drought-resistant Agropyron cristatum[J]. Jiangsu Journal of Agricultural Sciences, 43(9): 247-249.]

LI HS, 2000. Principles and techniques of plant physiological biochemical experiment[M]. Beijing: Higher Education Press: 134–168. [Li Hesheng, 2000. Principles and techniques of plant physiological biochemical experiment[M]. Beijing: Higher Education Press: 134-168.]

LI M, WANG GX, 2002. Effect of drought stress on activities of cell defense enzymes and lipid peroxidation in Glycyrrhiza uralensis seedings[J]. Acta Ecol Sin, 22(4): 503-507. [Li Ming, Wang Genxuan, 2002. Effect of drought stress on activities of cell defense enzymes and lipid peroxidation in Glycyrrhiza uralensis seedings[J]. Acta Ecologica Sinica, 22(4): 503-507.]

LI YL, CUI JY, SU YZ, 2005. Specific leaf area and leaf dry matter content of some plants in different dune habitats[J]. Acta Ecol Sin, 23(2): 304-311. [Li Yulin, Cui Jianyuan, Su Yongzhong, 2005. Specific leaf area and leaf dry matter content of some plants in different dune habitats[J]. Acta Ecologica Sinica, 23(2): 304-311.]

LIU GS, 1996. Soil physical and chemical analysis & description of soil profiles[M]. Beijing: Standards Press of China:31-38. [Liu Guangsong, 1996. Soil physical and chemical analysis & description of soil profiles[M]. Beijing: Standards Press of China: 31-38.]

LI J, MA XX, LI SX, et al., 2013. Determination of total phenols in Dendrobii officinalis Caulis[J]. Chin J Exp Tradit Med Formul, 19(24): 60-62. [Li Juan, Ma Xiaoxue, Li Shunxiang, et al., 2013. Determination of total phenols in Dendrobii officinalis Caulis[J]. Chinese Journal of Experimental Traditional Medical Formulae, 19(24): 60-62.]

LI J, LIU N, REN H, et al., 2016. Ecological adaptability of 7 plants to tropical coral island environment[J]. Ecol Environ Sci, 25(5): 790-794. [Li Jie, Liu Nan, Ren Hai, et al., 2016. Ecological adaptability of 7 plants to tropical coral island environment[J]. Ecology and Environmental Sciences, 25(5): 790-794.]

LI XQ, WEI CQ, WANG YB, et al., 2017. Risk assessment of the invasive plant Chromolaena odorata [J]. For Sci, 42(5): 59-62. [Li Xiangqin, Wei Chunqiang, Wang Yunbo, et al., 2017. Risk assessment of the invasive plant Chromolaena odorata[J]. Forestry Science & Technology, 42(5): 59-62.]

LI XF, WANG J, ZHU CH, et al., 2017. Effects of mixed sowing proportion on the competitive ability between Stylosanthes guianensis cv. Reyan No. 2 and Chromolaena odorata during early growth [J]. Chin J Trop Crop, 38(8): 1411-1417. [Li Xuefeng, Wang Jian, Zhu Chaohua, et al., 2017. Effects of mixed sowing proportion on the competitive ability between Stylosanthes guianensis cv. Reyan No. 2 and Chromolaena odorata during early growth[J]. Chinese Journal of Tropical Crops, 38(8): 1411-1417.]

LI ZZ, LIU DH, ZHAO SW, et al., 2014. Mechanisms of photoinhibition induced by high light in Hosta grown outdoors[J]. Chin J Plant Ecol, 38(7): 720-728. [Li Zhizhen, Liu Donghuan, Zhao Shiwei, et al., 2014. Mechanisms of photoinhibition induced by high light in Hosta grown outdoors[J]. Chinese Journal of Plant Ecology, 38(7): 720-728.]

LUO Q, LIU H, WU GL, et al., 2018. Using functional traits to evaluate the adaptability of five plant species on tropical coral islands[J]. Acta Ecol Sin, 38(4): 1256-1263. [Luo Qi, Liu Hui, Wu Guilin, et al., 2018. Using functional traits to evaluate the adaptability of five plant species on tropical coral islands[J]. Acta Ecologica Sinica, 38(4): 1256-1263.]

PAN X, QIU Q, LI JY, et al., 2015. Drought resistance evaluation based on leaf anatomical structures of 25 shrubs on the tibetan plateau[J]. J South Chin Agric Univ, 36(2): 61-68. [Pan Xin, Qiu Quan, Li Jiyue, et al., 2015. Drought resistance evaluation based on leaf anatomical structures of 25 shrubs on the tibetan plateau[J]. Journal of South China Agricultural University, 36(2): 61-68.]

PAN YM, TANG SQ, WEI CQ, et al., 2019. Tolerance of seed germination in two native species to the allelopathic effect of Chromolaena odorata and the competition between them[J]. Acta Ecol Sin, 39(19):7302-7310. [Pan Yumei, Tang Saichun, Wei Chunqiang, et al., 2019. Tolerance of seed germination in two native species to the allelopathic effect of Chromolaena odorata and the competition between them[J]. Acta Ecologica Sinica, 39(19): 7302-7310.]

POORTER L, BONGERS F, 2006. Leaf traits are good predictors of plant performance across 53 rain forest species[J]. Ecology, 87(7): 1733-1743.

QIU D, WU GL, LIU L, et al., 2019. Spatial-temporal variation of leaf dry matter content and specific leaf area of Cinnamomum camphora in urban area[J]. J Yunnan Univ Nat Sci Ed, 41(3):609-618. [Qiu Dong, Wu Ganlin, Liu Ling, et al., 2019. Spatial-temporal variation of leaf dry matter content and specific leaf area of Cinnamomum camphora in urban area[J]. Journal of Yunnan University (Natural Sciences Edition), 41(3): 609-618.]

QUAN GM, ZHANG JE, XU HQ, et al., 2009. Biological characteristics and control strategies of alien invasive plant Eupatorium odoratum[J]. Chin Agric Sci Bull, 25(9): 236-243. [Quan Guoming, Zhang Jiaen, Xu Huaqin, et al., 2009. Biological characteristics and control strategies of alien invasive plant Eupatorium odoratum[J]. Chinese Agricultural Science Bulletin, 25(9): 236-243.]

SMITH M, BARNEY JN, VARNON KM, et al., 2020. Climate drives differences in the germination niche of a globally distributed invasive grass[J]. J Plant Ecol, 13(2): 195-203.

SONG GM, LIU N, JIAN SG, et al., 2018. Physiological and biological characteristics of Terminalia catappa[J]. J Trop Subtrop Bot, 26(1): 40-46. [Song Guangman, Liu Nan, Jian Shuguang, et al., 2018. Physiological and biological characteristics of Terminalia catappa[J]. Journal of Tropical and Subtropical Botany, 26(1): 40-46.]

SUN Q, HU JJ, GONG YH, 2006. Plant physiology test technique[M]. Yangling: Northwest Agriculture & Forestry University Press:176-177. [Sun Qun, Hu Jingjiang, Gong Yuehua, 2006. Plant physiology research technology[M]. Yangling: Northwest Agriculture & Forestry University Press: 176-177.]

TONG SH, LIU N, WANG J, et al., 2020. Ecological and physiological adaptabilities of Catharanthus roseus to tropical coral island[J]. Guihaia, 40(3): 384-394. [Tong Shenghong, Liu Nan, Wang Jun, et al., 2020. Ecological and physiological adaptabilities of Catharanthus roseus to tropical coral island[J]. Guihaia, 40(3): 384-394.]

TONG Y, JIAN SG, CHEN Q, et al., 2013. Vascular plant diversity of the Paracel Islands, China[J]. Biodivers Sci, 21(3): 364-374. [Tong Yi, Jian Shuguang, Chen Quan, et al., 2013. Vascular plant diversity of the Paracel Islands, China[J]. Biodiversity Science, 21(3): 364-374.]

WANG ML, FENG YL, 2005. Effects of soil nitrogen levels on morphology, biomass allocation and photosynthesis in Ageratina adenophora and Chromoleana odorata[J]. J Plant Ecol, 29(5): 697-705. [Wang Manlian, Feng Yulong, 2005. Effects of soil nitrogen levels on morphology, biomass allocation and photosynthesis in Ageratina adenophora and Chromoleana odorata[J]. Chinese Journal of Plant Ecology, 29(5): 697-705.]

WANG ML, FENG YL, LI X, 2006. Effects of soil phosphorus level on morphological and photosynthetic characteristics of Ageratina adenophora and Chromolaena odorata[J]. Chin J Appl Ecol, 17(4): 4602-4606. [Wang Manlian, Feng

Yulong, Li Xin, 2006. Effects of soil phosphorus level on morphological and photosynthetic characteristics of Ageratina adenophora and Chromolaena odorata[J]. Chinese Journal of Applied Ecology, 17(4): 4602-4606.]

WANG MY, 2016. Present status of surface water environment in Wenchang in Hainan Province and countermeasures[J]. J Anhui Agric Sci, 44(5): 279-281. [Wang Minying, 2016. Present status of surface water environment in Wenchang in Hainan Province and countermeasures[J]. Journal of Anhui Agricultural Sciences, 44(5): 279-281.]

WANG W, LE SF, HE TY, et al., 2018. Determination of abscisic acid in Medicago sativa cv. by high performance liquid chromatography[J]. Anal Instrum, 49(2): 53-57. [Wang Wei, Le Shengfeng, He Tianyu, et al., 2018. Determination of abscisic acid in Medicago sativa cv. by high performance liquid chromatography[J]. Analytical Instruments, 49(2): 53-57.]

WEI W, HOU YP, PENG SL, et al., 2017. Effects of light intensity on growth and biomass allocation of invasive plants Mikania micrantha and Chromolaena odorata [J]. Acta Ecol Sin, 37(18):6021-6028. [Wei Wei, Hou Yuping, Peng Shaolin, et al., 2017. Effects of light intensity on growth and biomass allocation of invasive plants Mikania micrantha and Chromolaena odorata[J]. Acta Ecologica Sinica, 37(18): 6021-6028.]

WRIGHT IJ, REICH PB, WESTOBY M, et al., 2004. The worldwide leaf economics spectrum[J]. Nature, 428(6985): 821-827.

WU BX, 1981. The primary studies on Eupatorium odoratum community in southern Yunnan[J]. J Chin West Nor Univ(Nat Sci Ed), 2(1): 40-64. [Wu Bangxing, 1981. The primary studies on Eupatorium odoratum community in southern Yunnan[J]. Journal of China West Normal University (Natural Sciences Edition), 2(1): 40-64.]

WU JR, ZHAO HB, PAN HJ, et al., 2007. Effects of soil water regimes on the growth of the exotic invasive plant: Chromolaena odorata[J]. Ecol Environ Sci, 16(3): 935-938. [Wu Jinrong, Zhao Houben, Pan Huanyu, et al., 2007. Effects of soil water regimes on the growth of the exotic invasive plant: Chromolaena odorata[J]. Ecology and Environmental Sciences, 16(3): 935-938.]

XIAO DM, WANG M, JI LZ, et al., 2004. Influence of water stress on growth and biomass allocation of dominant tree species in mixed forest of broad-leaved and Korean pine at Changbai Mountain[J]. Chin J Ecol, 23(5):93-97. [Xiao Dongmei, Wang Miao, Ji Lanzhu, et al., 2004. Influence of water stress on growth and biomass allocation of dominant tree species in mixed forest of broad-leaved and Korean pine at Changbai Mountain[J]. Chinese Journal of Ecology, 23(5): 93-97.]

XU DQ, ZHANG YZ, ZHANG RX, et al., 1992. Photoinhibition of photosynthesis in plants[J]. Plant Physiol Comm, 28(4): 237-243. [Xu Daquan, Zhang Yuzhong, Zhang Rongxian, et al., 1992. Photoinhibition of photosynthesis in plants[J]. Plant Physiology Communications, 28(4): 237-243.]

XU ZZ, ZHOU GS, 2008. Responses of leaf stomatal density to water status and its relationship with photosynthesis in a grass[J]. J Exp Bot, 59(12): 3317-3325.

YANG Y, LAI YC, LI N, et al., 2010. Ecological and biological characteristics of Clerodendrum splendens[J]. J Anhui Agric Sci, 38(19): 10040-10043. [Yang Yong, Lai Yongchao, Liu Nan, et al., 2010. Ecological and biological characteristics of Clerodendrum splendens[J]. Journal of Anhui Agricultural Sciences, 38(19): 10040-10043.]

ZHANG LL, SUN FF, WEN DZ, 2009. Effects of irradiance and soil moisture on antioxidants and lipid peroxidation products in Mikania micrantha and Chromolaena odoratum[J]. Chin J Plant Ecol, 33(5): 974-983. [Zhang Lingling, Sun Fangfang, Wen Dazhi, 2009. Effects of irradiance and soil moisture on antioxidants and lipid peroxidation products in Mikania micrantha and Chromolaena odoratum[J]. Chinese Journal of Plant Ecology, 33(5): 974-983.]

ZHANG MS, TAN F, 2001. Relationship between ratio of chlorophyll a and b under water stress and drought resistance of different sweet potato varieties[J]. Seed, 21(4): 23-25. [Zhang Mingsheng, Tan Feng, 2001. Relationship between ratio of chlorophyll a and b under water stress and drought resistance of different sweet potato varieties[J]. Seed, 21(4): 23-25.]

ZHOU XY, CAO FL, 2005. Effects of soil salt stress on the activity of protective enzymes and peroxidation in three warm-season turfgrasses[J]. For Res, 18(3): 336-341. [Zhou Xingyuan, Cao Fuliang, 2005. Effects of soil salt stress on the activity of protective enzymes and peroxidation in three warm-season turfgrasses[J]. Forest Research, 18(3): 336-341.]

Note: Figure translations are in progress. See original paper for figures.