Postprint: Ecobiological Characteristics of Tournefortia argentea in the Xisha Islands

Authors: Cai Hongyue, Liu Nan, Wen Meihong, Ren Hai, Jian Shuguang

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Abstract

Tournefortia argentea is an evergreen small tree or shrub belonging to the genus Tournefortia in the family Boraginaceae, commonly found as a pioneer plant in tropical coastal and island environments of the Eastern Hemisphere, with important ecological, ornamental, and edible values. To understand the ecological adaptation mechanisms of T. argentea to tropical coral island environments and to provide fundamental data for its conservation, development, and utilization, this study analyzed naturally growing T. argentea on Dong Island of the Xisha Islands, examining its morphological and anatomical structures, physiological characteristics, leaf nutrient elements, and physicochemical properties of rhizosphere soil. The results demonstrate that T. argentea exhibits low stomatal density on leaf surfaces, small specific leaf area, well-developed spongy tissue, and high branch cavity ratio, indicating favorable water storage and drought resistance capacity. Its leaf surfaces are covered with dense white sericeous hairs that can reflect intense light and reduce water loss, facilitating adaptation to high-light and arid environments. The high proline content in leaves can effectively resist osmotic stress and provide a favorable living environment for cells. The soil where T. argentea grows is strongly alkaline with low nutrient and water content; however, its leaf nutrient element content remains normal, indicating high nutrient utilization efficiency and good adaptation to poor soil environments. T. argentea has low xylem density and fragile, easily broken branches, which can prevent being uprooted by strong typhoons, while the water-rich branches facilitate typhoon resistance and rapid canopy recovery. Therefore, T. argentea can well adapt to arid, high-light, and poor coastal sandy environments, showing promising application prospects for windbreak, sand fixation, and vegetation restoration on tropical coral islands (reefs) or coastal areas.

Full Text

Preamble

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Title: Ecological and Biological Characteristics of *Tournefortia argentea* in the Xisha Islands
Authors: CAI Hongyue[1],[2], LIU Nan[1], WEN Meihong[1],[2], REN Hai[1], JIAN Shuguang[1]*
[1]Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China
[2]University of Chinese Academy of Sciences, Beijing 100049, China

Abstract

Tournefortia argentea is an evergreen small tree or shrub belonging to the family Boraginaceae and genus *Tournefortia.* It is a common pioneer plant in tropical coastal and island habitats of the Eastern Hemisphere, possessing significant ecological, ornamental, and edible value. To understand its ecological adaptation mechanisms to tropical coral island environments and to provide foundational data for its conservation and utilization, this study investigated naturally growing *T. argentea* on Dongdao Island in the Xisha Islands, analyzing its morphological and anatomical structures, physiological characteristics, leaf nutrient elements, and rhizosphere soil physicochemical properties. The results demonstrate that *T. argentea* exhibits low stomatal density on leaf surfaces, small specific leaf area, well-developed spongy tissue, and high branch cavity ratios, indicating strong water storage and drought resistance capabilities. Its leaves are covered with dense white sericeous hairs that reflect intense light and reduce water loss, facilitating adaptation to high-light and arid conditions. The high proline content in leaves enables effective resistance to osmotic stress, providing a favorable intracellular environment. The soil supporting *T. argentea* is strongly alkaline with low nutrient and moisture content; however, normal leaf nutrient concentrations indicate high nutrient utilization efficiency and strong adaptation to impoverished soils. Low wood density makes branches fragile and prone to breakage, preventing uprooting by strong typhoons, while water-rich branches facilitate typhoon resistance and rapid canopy recovery. Consequently, *T. argentea* demonstrates robust adaptation to drought, intense light, and nutrient-poor coastal sandy environments, showing excellent potential for windbreak, sand fixation, and vegetation restoration in tropical coral islands (reefs) or coastal areas.

Keywords: *Tournefortia argentea*; ecological and biological characteristics; stress resistance; exploitation and utilization

Introduction

Tournefortia argentea (Boraginaceae: *Tournefortia*) is a small tree or shrub commonly found as a pioneer species in tropical islands and coastal zones of the Eastern Hemisphere. In China, it is distributed only in Hainan and Taiwan, primarily in the Xisha and Nansha Islands. The plant reaches 1–5 m in height with robust branchlets densely covered in rusty or white pubescence [Figure 1: see original paper]B. Its succulent leaves are oblanceolate or obovate, with both surfaces bearing silky yellowish-white hairs [Figure 1: see original paper]B. The falcate cymes are terminal, arranged in corymbose patterns, with white tubular corollas 2.5–3 mm long [Figure 1: see original paper]C. The drupes are nearly spherical, approximately 5 mm in diameter, glabrous [Figure 1: see original paper]D, and enclosed by a waterproof shell adapted for seawater dispersal. The flowering and fruiting period occurs from April to June. Leaves cluster at branch apices in a rosette formation, and the silvery-white fine hairs create an aesthetically pleasing shimmering effect in sunlight [Figure 1: see original paper]A.

The leaves serve as both food and spice, tasting similar to celery, and constitute important pig fodder. The wood is used for house construction and small fishing boats, while branchlets serve as firewood. In Fiji, root extracts treat rheumatism, and leaf decoctions are used in steam baths for postpartum weakness. In Nauru, macerated meristematic tissues from stems and roots treat childhood rashes, diarrhea, and poisoning from spoiled fish. *T. argentea* tolerates intense light, strong winds, and salt spray well, requiring minimal management after establishment and exhibiting few pest or disease problems. It is widely distributed across Xisha Islands, dominating as the only shrub species on Dongdao Island' s southeastern coastal areas and on Shidao Island where vegetation is poorly developed. Eight species of macrofungi grow on its decayed or dead wood, underscoring its significant ecological functions and application value.

Current research on *T. argentea* has focused on morphology, community structure, phytochemical analysis, diseases, and mycorrhizal associations, yet studies on its ecological and biological characteristics in native Xisha Islands habitats remain unreported. Global climate change and intensifying human activities have significantly impacted the Xisha Islands' ecological environment, causing increasingly fragmented and patchy habitats for *T. argentea* and rising mortality rates, necessitating urgent conservation efforts. This study examined wild *T. argentea* on Dongdao Island, investigating morphological and anatomical structures, physiological traits, leaf nutrient elements, and rhizosphere soil physicochemical properties to provide foundational data for understanding its ecological adaptation mechanisms to coral island environments and to support conservation and utilization strategies.

1.1 Study Area Description

The Xisha Islands are a group of tropical coral islands in the northern South China Sea, comprising the Xuande Islands in the northeast and the Yongle Islands in the southwest, located at approximately 111°11 -112°54 E, 15°46 -17°08 N. Dongdao Island, oriented northwest-southeast with an elongated elliptical shape, is the second-largest island in the archipelago, covering 1.55 km^2 with elevations of 3-6 m. The island experiences a tropical maritime monsoon climate with mean annual temperatures of 26-27 °C. Annual precipitation averages 1500 mm but shows uneven seasonal distribution, with a distinct wet season (June-November, accounting for 87% of annual rainfall) and dry season (December-May, only 13% of annual rainfall). Strong winds and intense evaporation characterize the region, with annual evaporation approaching 2400 mm—nearly double the annual precipitation—and February-March evaporation exceeding rainfall by tenfold. Under such conditions of low rainfall, high evaporation, and poor water retention in sandy soils, normal plant growth requires strong adaptation to seasonal drought.

Dongdao Island supports rich, dense natural vegetation with 76 wild plant species. Known as possessing the last remaining primary forest in Xisha, its peripheral sand ridges host shrubs and small trees including *Scaevola sericea*, *T. argentea*, *Guettarda speciosa*, and *Morinda citrifolia*, while the central flat basin contains extensive *Pisonia grandis* forest covering approximately half the island area.

1.2 Methods

In July 2016, six healthy wild *T. argentea* individuals were selected on Dongdao Island. Rhizosphere soil and mature leaves and branches from the upper shoots were collected, placed in sealed bags with moist filter paper, and stored at 4 °C.

1.2.1 Morphological and Anatomical Characteristics

Specific leaf area (SLA) was measured using a LI-3000 leaf area meter, followed by oven-drying at 65 °C to constant weight for dry weight (DW) determination. SLA was calculated as LA/DW. Leaf dry matter content (LDMC) was calculated as leaf dry weight/fresh weight.

Leaf structure was examined using conventional hand-sectioning techniques. Under optical microscopy, leaf thickness, spongy and palisade tissue thickness, upper epidermal thickness, stomatal guard cell size, and stomatal density were measured. Stomatal pore area index (SPI) was calculated as stomatal density $\times$ stomatal length^2.

Branch anatomy was analyzed using a Leica RM2235 microtome to obtain 20 m cross-sections. Images of vessel diameters were captured with a Leica DM4000B microscope and analyzed using ImageJ software to determine vessel diameter and density. Wood density was calculated as dry mass/fresh volume, with the mean of five branches representing average wood density. **Potential maximum hydraulic conductivity** was measured using the flushing method: 20 cm branches were placed in water-filled beakers, covered with black plastic bags until fully saturated, then flushed from a 50 cm water head to determine maximum conductivity, which reflects potential xylem hydraulic capacity. Maximum conductivity formula: Kmax = W/AΔt, where Kmax is maximum conductivity after repeated flushing ($g \cdot cm^{-2} \cdot s^{-1} \cdot MPa^{-1}$), W is water mass conducted (g), t is duration (s), and A is cross-sectional area (cm^2). Five replicates were measured for Alum/Axle (%) = (vessel area × vessel number)/branch cross-sectional area, and vulnerability index (VI) = vessel diameter/vessel density.

1.2.2 Physiological Characteristics

Chlorophyll content was extracted in 80% acetone and measured spectrophotometrically (UV-3802, Unico) at 663 nm and 645 nm to calculate chlorophyll a, chlorophyll b, total chlorophyll, and chlorophyll a/b ratio, with three replicates.

Soluble protein and abscisic acid (ABA) were measured with three replicates each. Soluble protein used the Coomassie brilliant blue method: 0.1 mL leaf extract mixed with 2.5 mL reagent, absorbance read at 595 nm. ABA was determined by high-performance liquid chromatography.

Proline and malondialdehyde (MDA) were measured with three replicates each. Proline used sulfosalicylic acid extraction and ninhydrin staining, absorbance read at 520 nm. MDA used the thiobarbituric acid method, reading absorbance at 532 nm and 600 nm.

Antioxidant enzyme activity and total phenolics were measured with three replicates each. Total antioxidant capacity (T-AOC) used the ferric reducing antioxidant power (FRAP) assay: under acidic conditions, Fe^{3+}-TPTZ reduces to Fe^{2+}-TPTZ, showing blue color with maximum absorption at 593 nm. Superoxide dismutase (SOD) activity used the nitroblue tetrazolium method, with one unit defined as 50% inhibition rate. Catalase (CAT) activity used UV absorption, with one unit defined as 1 nmol H_2O_2 degraded per gram fresh weight per minute. Total phenolics used the Folin-Ciocalteu method: under alkaline conditions, phenols reduce phosphotungstic-phosphomolybdic acid to blue compounds with peak absorption at 760 nm.

1.2.3 Leaf Element and Isotope Analysis

Fresh leaves were collected in the field and oven-dried at 60 °C. Total nitrogen (TN) was measured by the Kjeldahl method; total phosphorus (TP) by molybdenum-antimony colorimetry; total organic carbon (TOC) by potassium dichromate-sulfuric acid oxidation. $\delta^{13}C$ was determined using an isotope ratio mass spectrometer (IsoPrime100, IsoPrime, Manchester, UK), expressed in per mil (‰) using the international standard formula: $\delta(‰) = [(Rsam/Rstd) - 1] \times 1000$, where Rsam is sample relative abundance and Rstd is standard relative abundance. The carbon isotope standard is Pee Dee Belemnite (PDB) with RPDB = 0.0112372 and δ^{13}CPDB = 0‰.

1.2.4 Soil Physicochemical Properties

Surface litter was cleared from rhizospheres, and six 0–20 cm soil samples were collected, sealed, and stored at low temperature. After air-drying and sieving (2 mm), soil physicochemical properties were analyzed following standard methods.

1.3 Data Analysis

Data analysis and graphing used Microsoft Office Excel 2010 and Adobe Photoshop CC 2015.

2.1 Morphological and Anatomical Characteristics

Field observations revealed succulent leaves covered with dense white sericeous hairs on both surfaces, preventing water loss. Microscopic examination showed isobilateral leaves with single-layered, tightly arranged epidermal cells lacking conspicuous cuticles. Both upper and lower epidermis contained long columnar palisade tissue cells, with multilayered, loosely arranged spongy tissue in the middle. Semi-transparent sericeous hairs occurred on both surfaces, denser on the upper epidermis [Figure 2: see original paper]A. Morphological characteristics (Table 1) showed specific leaf area of 84.88 $\mathrm{cm^2 \cdot g^{-1}}$, leaf thickness of 534.47 m, upper epidermal stomatal density of 86.67 $\mathrm{n \cdot mm^{-2}}$, and lower epidermal stomatal density of 120 $\mathrm{n \cdot mm^{-2}}$. The palisade/spongy tissue ratio was 0.16, indicating far more developed spongy tissue. Stem xylem contained abundant water-storage parenchyma cells and vessels [Figure 2: see original paper]B.

2.2 Physiological Characteristics

Chlorophyll a and b contents were 0.21 $\mathrm{mg \cdot g^{-1}}$ and 0.14 $\mathrm{mg \cdot g^{-1}}$ respectively, with a chlorophyll a/b ratio of 1.55 (Table 2). Soluble protein content was high at 43.64 $\mathrm{mg \cdot g^{-1}}$, while abscisic acid levels were low at 2.80 $\mathrm{g \cdot g^{-1}}$. Antioxidant enzyme activities were substantial: CAT activity was 21.05 $\mathrm{U \cdot g^{-1}}$ and SOD activity was 133.78 $\mathrm{U \cdot g^{-1}}$. MDA and total phenolics were low at 12.27 $\mathrm{nmol \cdot g^{-1}}$ and 8.76 $\mathrm{mg \cdot g^{-1}}$ respectively, while proline content was remarkably high at 1167.09 $\mathrm{g \cdot g^{-1}}$.

2.3 Leaf Nutrients and Soil Physicochemical Properties

Leaf nutrient concentrations (Table 3) showed highest total organic carbon (400.73 $\mathrm{g \cdot kg^{-1}}$) and lowest total phosphorus (2.99 $\mathrm{g \cdot kg^{-1}}$), with an N/P ratio of 5.89 and stable carbon isotope ratio of -25.70‰. Rhizosphere soil analysis (Table 4) revealed only 3.4% water content, pH 8.26 (alkaline), high calcium (74.28 $\mathrm{g \cdot kg^{-1}}$), magnesium (5.60 $\mathrm{g \cdot kg^{-1}}$), potassium (275.05 $\mathrm{mg \cdot kg^{-1}}$), and iron (753.55 $\mathrm{mg \cdot kg^{-1}}$), but extremely low total phosphorus (2.35 $\mathrm{mg \cdot kg^{-1}}$).

3.1 Adaptation to Arid Environments

Through long-term self-regulation and evolution, plants develop specific morphological structures to adapt to environmental changes. Stomata are the primary channels for gas exchange and water transpiration, controlling photosynthetic and transpiration capacity. Interspecific stomatal density ranges from 5-1000 $\text{n} \cdot \text{mm}^{-2}$, with extreme drought reducing density. *T. argentea* showed upper epidermal stomatal density of 86.67 $\text{n} \cdot \text{mm}^{-2}$ and lower epidermal density of 120 $\text{n} \cdot \text{mm}^{-2}$—relatively low levels—indicating adaptation to Xisha Islands' water-deficient habitats through reduced stomatal density and diminished transpiration. The dense white sericeous hairs covering both leaf surfaces effectively reflect intense light while reducing air movement across the leaf surface, preventing water loss and decreasing transpiration.

Specific leaf area (SLA), the ratio of leaf area to dry weight, represents a functional trait reflecting plant-environment interactions. SLA is typically larger in resource-rich environments and smaller in barren or harsh conditions. Dominant Xisha Islands species such as *Pisonia grandis* (166.84 $\text{cm}^2 \cdot \text{g}^{-1}$) and *Cordia subcordata* (205.06 $\text{cm}^2 \cdot \text{g}^{-1}$) show substantially higher SLA than *T. argentea* (84.88 $\text{cm}^2 \cdot \text{g}^{-1}$). This low SLA indicates relatively thick leaves capable of storing more water, adapting to water scarcity during dry seasons.

The palisade/spongy tissue ratio of 0.16 reduces light absorption and prevents damage from excess light energy. Well-developed spongy tissue combined with low stomatal density maintains high internal gas exchange efficiency under minimal transpiration, conferring drought resistance. Compared with general drought-tolerant trees, *T. argentea* shows lower wood density (0.57 $\text{g} \cdot \text{cm}^{-3}$), larger vessel diameter (60.49 m), and potential hydraulic conductivity of 16.86 $\text{kg} \cdot \text{m}^{-1} \cdot \text{MPa}^{-1} \cdot \text{s}^{-1}$, indicating strong water transport capacity adapted to high evaporation rates. Compared with *C. subcordata*, *T. argentea* exhibits lower wood density, higher branch cavity ratio (13.96%), and highly developed water-storage parenchyma with prominent pith, enabling rapid water absorption and storage during limited dry-season rainfall.

Stable carbon isotope ratio (δ^{13}C) reflects plant photosynthetic and transpiration processes, estimating water use efficiency (WUE). δ^{13}C values positively correlate with WUE—higher values indicate greater efficiency. *T. argentea* showed δ^{13}C of -25.70‰, higher than the average -27.01‰ reported for desert shrubs, confirming high WUE and drought resistance.

3.2 Adaptation to Adversity and Oxidative Stress

Tropical coral island (reef) environments are harsh, characterized by drought, high temperature, intense light, high salinity, strong alkalinity, and lack of true soil, limiting colonizing species. Adversity induces metabolic changes that serve as important stress-resistance indicators. Proline acts as an osmoticum in osmoregulation; under water deficit, massive proline synthesis increases tolerance and protects cellular structure. *T. argentea* leaf proline content (1167.09 $\text{g} \cdot \text{g}^{-1}$)

far exceeds that of *C. subcordata* (200.78 $\text{g} \cdot \text{g}^{-1}$) and *P. grandis* (158.61 $\text{g} \cdot \text{g}^{-1}$), demonstrating substantial proline synthesis under drought, intense light, wind-induced heat, and seasonal salt-spray osmotic stress.

Plants possess antioxidant systems to scavenge reactive oxygen species. Antioxidants inhibit lipid peroxidation initiation, converting peroxides to harmless substances. *T. argentea* showed total antioxidant capacity (T-AOC) of 60.75 $\text{U} \cdot \text{g}^{-1}$, comparable to high levels in colored potatoes. Chlorophyll a (0.21 $\text{mg} \cdot \text{g}^{-1}$) and b (0.14 $\text{mg} \cdot \text{g}^{-1}$) contents were lower than in *P. grandis* and *C. subcordata*, reducing light energy absorption and controlling reactive oxygen generation from excess photosynthetic energy, thereby minimizing oxidative damage to cellular substructures and demonstrating strong adaptation to high-light stress.

Malondialdehyde (MDA), a primary lipid peroxidation product, reflects membrane damage levels. Under drought, reactive oxygen accumulation beyond scavenging capacity exacerbates lipid peroxidation, typically elevating MDA. However, *T. argentea* maintained low MDA levels, likely due to developed water-storage structures and high proline content enhancing stress resistance and protecting membrane lipids from oxidative damage.

3.3 Adaptation to Poor Soil and Sea Winds

Coastal sandy beaches experience strong winds, intense direct and reflected sunlight, and salt spray. Soil analysis (Table 4) revealed nitrogen deficiency (0.13%) and extremely low phosphorus (2.35 $\text{mg} \cdot \text{kg}^{-1}$). High free calcium carbonate in coral sand reduces phosphorus availability, intensifying soil infertility, while low water content (3.4%) and high pH (8.26) alter nutrient supply and bioavailability. Under such conditions, leaf carbon content reflects both carbon assimilation capacity and adaptation to harsh environments. *T. argentea* leaf total organic carbon (400.73 $\text{g} \cdot \text{kg}^{-1}$), total nitrogen (17.603 $\text{g} \cdot \text{kg}^{-1}$), and total phosphorus (2.99 $\text{g} \cdot \text{kg}^{-1}$) all fall within normal plant nutrient ranges, indicating good growth status and strong nutrient absorption/utilization capacity adapted to impoverished coastal habitats.

The Xisha Islands experience frequent typhoons during July-September, with massive waves capable of moving sand ridges and inundating supratidal vegetation. *T. argentea* exhibits open canopies with sparse branches, low wood density, underdeveloped mechanical tissues, yet highly developed water-storage parenchyma and large pith cavities. Fragile, easily broken branches prevent whole-plant uprooting during typhoons, while water-rich branches enable rapid post-typhoon canopy recovery, representing a clear survival strategy for coastal environments.

The combination of water-storage capacity in branches and leaves, dense white sericeous hairs reflecting light and reducing water loss, high proline content for osmotic stress tolerance, fragile branches preventing typhoon uprooting, and high nutrient utilization efficiency enables *T. argentea* to thrive in drought, alkalinity, and intense light conditions characteristic of tropical coral islands (reefs). Additionally, its unique and aesthetically pleasing foliage and growth form offer broad application prospects for vegetation restoration and landscaping in tropical coral islands or coastal regions.

References

CAI QS, 2013. Plant physiology test [M]. Beijing: China Agriculture Press. [Cai Qingsheng, 2013. Plant Physiology Experiment [M]. Beijing: China Agricultural University Press.]

CHEN CY, FU CH, HSIAO WW, et al, 2007. First Report of Southern Blight of Silvery Messerschmidia Seedlings in Taiwan [J]. Plant Dis, 91(9): 1198-1198.

CHEN T, FENG HY, XU SJ, et al, 2002. Stable carbon isotope composition of desert plant leaves and water-use efficiency [J]. Journal of Desert Research, 22(3):288-291. [Chen Tuo, Feng Huyuan, Xu Shijian, et al., 2002. Carbon isotope composition of desert plant leaves and water use efficiency [J]. Journal of Desert Research, 22(3):288-291.]

Flora of China Editorial Committee CAS, 1989. Flora of China [M]. Beijing: Science Press, 64(2):33-34. [Editorial Committee of Flora of China, Chinese Academy of Sciences, 1989. Flora of China Volume 64, Part 2 [M]. Beijing: Science Press, 64(2):33-34.]

GUAN LL, LIU N, WEI Q, et al, 2008. Comparison of leaf construction costs between three invasive species and three native species in South China [J]. J Trop Subtrop Bot, 16(2):95-103. [Guan Lanlan, Liu Nan, Wei Qiang, et al., 2008. Response of chlorophyll fluorescence characteristics of three vine species to simulated sulfur dioxide pollution in South China [J]. Journal of Tropical and Subtropical Botany, 16(2):95-103.]

KNIGHT JD, LIVINGSTON NJ, KESSEL CV, 1994. Carbon isotope discrimination and water-use efficiency of six crops grown under wet and dryland conditions [J]. Plant Cell Environ, 17(2):173-179.

LAMUELA-RAVENTÓS RM, SINGLETON VL, ORTHOFER R, 1999. Analysis of Total Phenols and Other Oxidation Substrates and Antioxidants by Means of Folin-Ciocalteu Reagent [M]// Exercises in general chemistry and qualitative analyses /. J. Wiley & sons, 152-178.

LAN XY, 2011. Effects of arbuscular mycorrhiza inoculation on the physiology of *Scaevola sericea* and *Messerschmidia argentea* under salt stress [D]. Taichung City: National Chung Hsing University. [Lan Xingyu, 2011. Physiological effects of arbuscular mycorrhizal inoculation on *Scaevola sericea* and *Messerschmidia argentea* under salt stress [D]. Taichung City: National Chung Hsing University.]

LI LJ, LI TH, BI ZS, 1988. Description of Paracel Islands macro fungi [J]. Edible Fungi of China, 1(1): 019. [Li Lijia, Li Taihui, Bi Zhishu, 1988. Description of macrofungi from the Xisha Islands [J]. Edible Fungi of China, 1(1): 019.]

LI R, DANG W, CAI J, et al, 2016.Relationships between xylem structure and embolism vulnerability in six species of drought tolerance trees [J]. Chin J Plant Ecol, 40 (3): 255-263. [Li Rong, Dang Wei, Cai Jing, et al., 2016. Relationships between xylem structure and embolism vulnerability in six drought-tolerant tree species [J]. Chinese Journal of Plant Ecology, 40(3):255-263.]

LIN ZF, LI SS, LIN GZ, 1984. Superoxide dismutase activity and lipid peroxidation in relation to senescence of rice leaves [J]. Acta Bot Sin,26(6): 605-615. [Lin Zhifang, Li Shuangshun, Lin Guizhu, et al., 1984. Relationship between superoxide dismutase activity, lipid peroxidation and senescence of rice leaves [J]. Acta Botanica Sinica, 26(6): 605-615.]

LIU GS, 1996. Soil physical and chemical analysis & description of soil profiles [M].Beijing: Standards Press of China. [Liu Guangsong, 1996. Soil Physical and Chemical Analysis & Description of Soil Profiles [M]. Beijing: Standards Press of China.]

LIU XT, GE CD, ZOU XQ, et al, 2017. Carbon, Nitrogen geochemical characteristics and their implications on environmental change in the lagoon sediments of the Dongdao Island of Xisha Islands in South China Sea [J]. Acta Oceanol Sin, 39(6):43-54. [Liu Xiaotong, Ge Chendong, Zou Xinqing, et al., 2017. Geochemical characteristics of carbon and nitrogen in lagoon sediments of Dongdao Island, Xisha Islands and their implications for environmental change [J]. Acta Oceanologica Sinica, 39(6):43-54.]

MANNER HI, ELEVITCH CR, 2006. *Tournefortia argentea* (tree heliotrope) [J]. Traditional Tree Initiative: Species Profiles for Pacific Island Agroforestry, 1-12.

OGIHARA K, MIYAGI Y, HIGA M, et al, 1997. Pyrrolizidine alkaloids from *Messerschmidia argentea*[J]. Phytochemistry, 44(3): 545-547.

OGIHARA K, NAKAZATO R, NISHI Y, et al, 2002. DPPH-radical scavenging constituents from the twigs of *Messerschmidia argentea* (III) [J]. Bull. Fac. Sci. Univ. Ryukyus, (74)73-80.

PEI B, ZHANG GC, ZHANG SY, et al, 2013.Effects of soil drought stress on photosynthetic characteristics and antioxidant enzyme activities in *Hippophae rhamnoides* Linn. seedings [J]. Acta Ecol Sin, 2013, 33(5): 1386-1396. [Pei Bin, Zhang Guangcan, Zhang Shuyong, et al., 2013. Effects of soil drought stress on photosynthetic characteristics and antioxidant enzyme activities in *Hippophae rhamnoides* Linn. seedlings [J]. Acta Ecologica Sinica, 33(5):1386-1396.]

Plant Survey Team of Xisha Islands, Guangdong Institute of Botany, 1977. The plants and vegetation of the Xisha Islands in China [M]. Beijing: Science Press. [Plant Survey Team of Xisha Islands, Guangdong Institute of Botany, 1977. Plants and Vegetation of the Xisha Islands of China [M]. Beijing: Science Press.]

REN H, PENG SL, SUN GC, et al, 1997. The ecological comparison of *Psychotria rubra* and *Rhodomyrtus tomentosa* in South China [J]. Chin J Plant Ecol, 21: 386-392

REN SJ, YU GR, JIANG CM, et al, 2012. Stoichiometric characteristics of leaf carbon, nitrogen, and phosphorus of 102 dominant species in forest ecosystems along the North-South Transect of East China [J]. Chin J Appl Ecol, 23(3):581-586. [Ren Shujie, Yu Guirui, Jiang Chunming, et al., 2012. Stoichiometric characteristics of leaf carbon, nitrogen, and phosphorus of 102 dominant species in forest ecosystems along the North-South Transect of East China [J]. Chinese Journal of Applied Ecology, 23(3):581-586.]

SHIPLEY B, VU TT, 2002. Dry matter content as a measure of dry matter concentration in plants and their parts [J]. New Phytol, 153(2):359-364.

SUN CZ, WANG C, CAI ZZ, et al, 2013. Determination of flavonoids, phenolic acids and abscisic acid in honeys of different floral origins by HPLC [J]. Food Sci, 34(10):281-285. [Sun Chongzhen, Wang Chao, Cai Zizhe, et al., 2013. Determination of abscisic acid, flavonoids and phenolic acids in honeys of different floral origins by HPLC [J]. Food Science, 34(10):281-285.]

SUN Q, HU JJ, 2006. Plant physiology test technique [M]. Yangling: N Agr For Univ Press. [Sun Qun, Hu Jingjiang, Gong Yuehua, 2006. Plant Physiology Research Techniques [M]. Yangling: Northwest A&F University Press.]

TANG ZC, 1984. Plant Physiol Commun, 1: 15-21. [Tang Zhangcheng, 1984. Accumulation of proline in plants under stress conditions and its possible significance [J]. Plant Physiology Communications, 1: 15-21.]

TONG Y, JIAN SG, CHEN Q, et al, 2003.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 Xisha Islands, China [J]. Biodiversity Science, 21(3): 364-374.]

VILE D, SHIPLEY B, GARNIER E, 2006. Ecosystem productivity can be predicted from potential relative growth rate and species abundance [J]. Ecol Lett, 9(9): 1061-1067.

WANG XH, LIU N, REN H, et al, 2017. The ecological and biological characteristics of *Pisonia grandis* [J]. Guihaia, 37(12):1489-1497. [Wang Xinhui, Liu Nan, Ren Hai, et al., 2017. Ecological and biological characteristics of *Pisonia grandis* [J]. Guihaia, 37(12):1489-1497.]

WANG Y, PAN ZC, LI XP, et al, 2017. Differences in anthocyanin content and total antioxidant capacity of potato tubers with different flesh colour [J]. Food Nutr China, 23(2):66-69. [Wang Ying, Pan Zhechao, Li Xianping, et al., 2017. Analysis of anthocyanin content and total antioxidant capacity in potatoes with different flesh colors [J]. Food and Nutrition in China, 23(2):66-69.]

WU SH, CHEN HW, JIAN SG, et al, 2017. The biological characteristics of *Cordia subcordata* on tropical coral island in China [J]. Ecol Sci, 36(6):57-63. [Wu Shuhua, Chen Haowen, Jian Shuguang, et al., 2017. Biological characteristics of *Cordia subcordata* on tropical coral islands in China [J]. Ecological Science, 36(6):57-63.]

XIONG X, ZHANG HL, WU JP, et al, 2016. ^{13}C and ^{15}N isotopic signatures of plant soil continuum along a successional gradient in Dinghushan Biosphere Reserve [J]. Chin J Plant Ecol, 40(6): 533-542. [Xiong Xin, Zhang Huiling, Wu Jianping, et al., 2016. Carbon and nitrogen isotopic characteristics of plant-soil continuum along a forest successional sequence in Dinghushan [J]. Chinese Journal of Plant Ecology, 40(6):533-542.]

YIN YQ, HU JB, DENG MJ, 2007. Latest development of antioxidant system and responses to stress in plant leaves [J]. Chin Agric Bull, 23(1):105-110. [Yin Yongqiang, Hu Jianbin, Deng Mingjun, 2007. Research progress on antioxidant system in plant leaves and its response to stress [J]. Chinese Agricultural Science Bulletin, 23(1):105-110.]

ZHANG CN, ZHAO XP, LIANG F, et al, 2014. Variations of vessel characteristics of branches in *Quercus mongolica* canopy [J]. Sci Silva Sin, 50(10):152-157. [Zhang Chaonan, Zhao Xiping, Liang Fang, et al., 2014. Variations in vessel characteristics of branches at different canopy positions in *Quercus mongolica* [J]. Scientia Silvae Sinicae, 50(10):152-157.]

ZHU SD, CHEN YJ, CAO KF, et al, 2015. Interspecific variation in branch and leaf traits among three *Syzygium* tree species from different successional tropical forests [J]. Funct Plant Biol, 42(4):423-432.

ZHU YH, 2016. Patterns of variations in leaf trait and responses to environmental changes in oriental oak (*Quercus variabilis*) across Eastern Asia [D]. Shanghai: Shanghai Jiao Tong University. [Zhu Yanhua, 2013. Patterns of variation in leaf traits and responses to environmental changes in oriental oak (*Quercus variabilis*) across East Asia [D]. Shanghai: Shanghai Jiao Tong University.]

ZOU Q, 2000. Guideline of experiments in plant physiology [M].Beijing: Chin Agr Press. [Zou Qi, 2000. Guidelines for Plant Physiology Experiments [M]. Beijing: China Agriculture Press: 56-59.]

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

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