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RESEARCH ARTICLE

Adaptive morpho-anatomical characteristics of the critically endangered plant *Myricaria laxiflora* in the Yangtze River Basin, China

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Abstract

Myricaria laxiflora, a National Class II critically endangered plant once declared extinct in the wild, is the only species in the genus *Myricaria* that occurs outside plateau regions and remains evergreen during winter. It serves not only as an ideal species for riparian zone restoration and soil conservation but also as a key model for studying genetic variation and ecological adaptation in plants. This species survives under alternating flood and drought conditions, exhibiting specialized anatomical traits in its roots, stems, and leaves. Using freezing microtome techniques, we investigated the anatomical adaptations of its roots, stems, leaves, and seeds to alternating flood and drought environments. The results showed that the roots develop a thickened periderm and large-diameter vessels, significantly enhancing water transport and stress resistance. The stems contain densely arranged phloem and xylem fibers, which enhance both mechanical strength and nutrient conduction efficiency. The leaves exhibit typical xeromorphic characteristics, including bifacial palisade tissues, a thick cuticle, and sunken stomata, which enable adaptation to intense light and drought stress. The seeds are small and lightweight, possessing hydrophobic lipid coatings and awn structures that facilitate efficient wind-and water-mediated dispersal. These integrated anatomical adaptations collectively enable *M. laxiflora* to thrive in the extreme riparian environments of the Yangtze River Basin, providing crucial theoretical foundations for its conservation and ecological restoration.

Keywords: Protected endangered plants, Adaptive anatomy, Aquatic plants, *Myricaria laxiflora*

Introduction

Myricaria laxiflora is an endemic, rare, and critically endangered species in the three gorges region. The construction of the three gorges hydropower station has led to severe habitat fragmentation in the hydro-fluctuation zone, resulting in drastically reduced populations. In 2006, it was assessed as Endangered (EN) on the IUCN Red List, reconfirmed as EN in the China.

Biodiversity Red List (2013), and later included as a National Grade II Protected Plant in the 2021 List of China's National Key Protected Wild Plants. This species endures complete submergence for five to six months each year while withstanding drought during dry seasons (Chen and Xie 2008). Such alternating flood and drought tolerance enables adaptation to extreme riparian environments-a rare trait among woody plants. As a characteristic species of the Three Gorges Reservoir hydro-fluctuation zone, it serves as an ideal model for studying ecological and evolutionary adaptations under specialized environmental conditions (Guan, et al. 2020, Doležal, et al. 2021).

The Himalayan region represents the center of origin and distribution for the genus *Myricaria*. *M. laxiflora* is the only species occurring outside plateau regions and the sole evergreen member of the genus during winter. It plays an important role in riverbank stabilization and soil conservation and is also used medicinally to treat burns. As the only low-altitude *Myricaria* species beyond plateau regions, understanding its characteristics is critically important for taxonomic and phylogenetic research within the genus and the Tamaricaceae family, as well as for investigating floristic features across seasonally flooded zones from high-altitude to subtropical regions in China (Liu, et al. 2006).

The unique morphological traits of *M. laxiflora* result from the interplay between genetic evolution and environmental adaptation. Studying these traits helps elucidate fundamental biological characteristics, reveals adaptive mechanisms, and guides conservation strategies (Li, et al. 2021). Its flood and drought tolerance qualifies it as a native species for ecological restoration in the Yangtze River hydro-fluctuation zones, where it forms green, wave-breaking, sand-fixing barriers (Chen, et al. 2019). As the only evergreen species in Myricaria, it represents an ideal candidate for landscape restoration and soil-water conservation in fluctuating zones and serves as a key model organism for research on plant genetics, ecological adaptation, and evolutionary biology.

To elucidate how *M. laxiflora* adapts to amphibious extremes-given that current research mainly focuses on biogeographic distribution, habitat features, associated species, ecological adaptability, and ex situ conservation, while morpho-anatomical research remains limited-this study conducts detailed anatomical analyses of vegetative organs using freezing microtome (cryo-sectioning) techniques (Hua, et al. 2012, Li et al. 2024). Through microscopic examination of roots, stems, and leaves, we assess structural parameters such as root diameter, vessel diameter, stem diameter, xylem and phloem thickness, leaf thickness, stomatal size, and palisade-spongy tissue organization. This approach aims to explore the relationship between anatomical traits and ecological adaptation to flooding disturbances, uncover drought-resistance mechanisms following water recession, and ultimately provide scientific insights into adaptive strategies and biodiversity conservation for amphibious endangered plants in the Yangtze River hydro-fluctuation zone.

Materials and Methods

Study area

During the dry season, around October each year, water levels decline in the Yangtze River, exposing cobble beaches on which the submerged, dormant branches of *M. laxiflora* initiate vegetative growth, transitioning to reproductive growth by November to December. Plant materials and seeds were collected from natural populations in Tongzi Town, Jiang'an County, Yibin City, Sichuan Province (105°02'05.65"E, 28°46'35.26"N; elevation 247 m) on 4 January 2024 (Fig. 1). The site experiences a mean annual temperature of approximately 18°C, annual precipitation of 1,050-1,618 mm, and an average sunshine duration of 1,199 hours, with plants growing on cobble-rich beaches. In March 2024, roots, stems, and leaves were sampled from five mature, uniformly growing plants. From 25 individuals (2-5 years old), 25 lateral root samples and 50 stem samples with leaves were collected. Lateral roots and leaves were preserved in FAA fixative (50% ethanol: Formaldehyde: Acetic acid=18:1:1 v/v), vacuum-sealed, and transported for subsequent analysis.

Morphological characterization

Plant height was measured before leaf and flower collection from 25 individuals. Samples were transported to the Taxonomy Laboratory, Department of Biology, Yibin University, for analysis. Transverse leaf sections were examined under an OLYMPUS CX41 light microscope, and micrographs were captured. Comprehensive morphological descriptions of the plant and its organs (roots, stems, leaves, flowers, inflorescences, fruits, and seeds) were documented based on standard taxonomic references. Quantitative measurements of each organ were recorded and analyzed descriptively.

Anatomical description

Section preparation: Samples were cleaned, and central tissue portions were sectioned into approximately 1 cm × 1 cm pieces. These were immediately fixed in FAA (70% ethanol: Formalin: Acetic acid=90:5:5 v/v) for >24 h. For cryo-sectioning, fixed tissues were rinsed with distilled water, trimmed, and immersed in a 1:1 mixture of Sakura OCT embedding compound and water for 1-2 h. Tissues were embedded in OCT compound, frozen at -20°C for 10 minutes in a Leica CM1950 cryostat, and sectioned at 10-15 μm thickness once the embedding medium turned opaque. Sections were mounted on slides using 20% glycerol as a mounting medium for temporary preparations.

Figure 1. Location of the study area in the upper Yangtze River Basin, China. Distribution of remnant *Myricaria laxiflora* populations on Chengjiang Island, Yibin City, red stars indicate the four populations sampled for anatomical materials and habit of *M. laxiflora* plants inhabiting cobble beaches within the hydro-fluctuation zone.

Results

Morphological description and morphometrics

Plant habit: *Myricaria laxiflora* is an erect shrub with a woody perennial base, evergreen and reaching heights of 1.5-2 m. The sampled population in this study averaged 1.5 m in height, exclusively inhabiting exposed gravel banks along the upper Yangtze River with sparse vegetation. It predominantly coexists with another endangered species, *Plantago fengdouensis*, in extreme riparian zones subjected to alternating flood-drought conditions.

Root: The plant has a well-developed taproot system penetrating deeply into the soil, typically distributed within 2-3 m under normal conditions. The periderm of roots, rhizomes, or stolons exhibits fissures, with 2-7 adventitious buds clustered at nodes.

Stem: Adventitious fibrous roots emerge from the base of rhizomes or erect stems. Branches on perennial upright stems often shed, leaving triangular white to grayish-white scars. Older branches are smooth with shallow longitudinal grooves after dry seasons, colored vermilion, reddish-brown, purplish-brown, or violet-black. Current-year shoots are emerald-green, dark green, purplish-red, or reddish-brown. Leaves densely spiral on young shoots, sessile, papery, predominantly lanceolate or oblong, 2-4 mm long × 0.8-1.2 mm wide, apex obtuse or acute, base slightly expanded and concave with narrow membranous margins.

Leaves: Leaves densely cover current-year green shoots, papery, sessile, lanceolate or oblong, 2-4 mm × 0.8-1.2 mm, apex obtuse or acute, base slightly expanded with narrow membranous margins, often curved inward forming semi-amplexicaul leaves. Foliage is predominantly light green, while young leaves on new shoots may appear magenta or purplish-red.

Flowers: Racemose, indeterminate inflorescences terminate the shoots and measure 5-25 cm in length, sparsely arranged along the stem. Bracts lanceolate or ovate-lanceolate, 5-8 mm × 1.5-2 mm, acuminate with narrow membranous margins. Pedicels 2-5 mm long. Sepals lanceolate or oblong, 2-4 mm × 1-1.5 mm, apex rounded or acute, persistent with membranous edges. Petals obovate, alternating with sepals, 5-8 mm × 2-3 mm, pink, pale purple, or magenta, concave with prominent longitudinal veins, persistent. Filaments basally extended, 1/2-1/3 fused; anthers basifixed, dehiscing longitudinally; pollen spherical. Ovary conical, 4-6 mm long; stigma capitate; 3 carpels synorganized into a single locule.

Fruit and seeds: Capsules narrowly conical, 6-8 mm long; 27-61 capsules per inflorescence, each containing 150-190 seeds. Seeds 1-1.5 mm long: basal 1/3 flattened-fusiform, orange-yellow; apical 2/3 an awn column (>50% densely covered by silvery-white pubescence), glossy. Capsules mature in a basipetal sequence and dehisce longitudinally into three valves; infructescences form elongated seed columns that are primarily dispersed by wind.

Anatomical characterization of *Myricaria laxiflora*

The root: The perennial lateral roots of *M. laxiflora* exhibit nearly circular cross-sections with secondary structures comprising periderm, secondary phloem, and secondary xylem (Fig. 2-A, Tab. 1). The periderm consists of orderly arranged rectangular cells, with partially sloughed outer layers forming residual structures (Fig. 2-B). Three distinct layers are observable: Phellem (cork), phellogen (cork cambium), and phelloderm, featuring suberized, tightly packed cell walls that stain dark yellowish-brown (Fig. 2-E). Replacing the primary cortex and epidermis, the periderm functions as a secondary protective barrier. Well-developed secondary vascular tissues include secondary xylem (occupying ~1/3 of the cross-section), vascular cambium, and secondary phloem. The xylem contains vessels (large vessels ≈ 3 × diameter of small ones), xylem rays, parenchyma, and abundant fibers with thickened walls clustered around vessels (Fig. 2-C). Secondary phloem comprises sieve elements, companion cells, sclereids, phloem fibers (polygonal with conspicuously thickened walls), and parenchyma (Fig. 2-F). The annular vascular cambium consists of 3-5 layers of compact rectangular cells; those adjacent to phloem differentiate into phloem cells after producing 2-7 layers (Fig. 2-D).

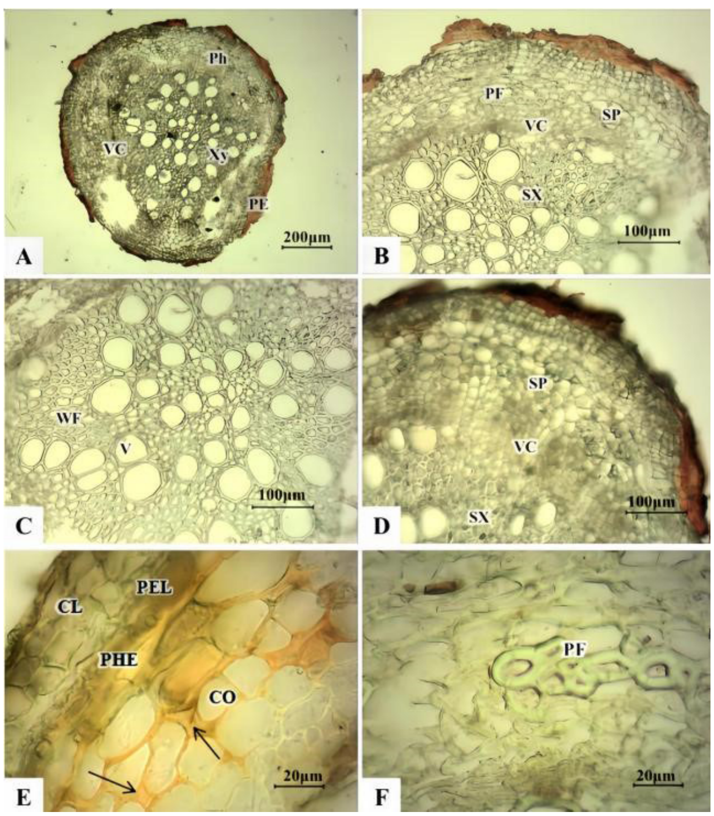

Figure 2. Anatomical structure of the root of *Myricaria laxiflora* under microscope. (A) Transverse section of root; (B) Partial cross section of roots; (C) Xylem conduit; (D) Vascular cambium; (E) Peridermis; (F) Phloem; Note: VC: Vascular cambia; Ph: Phloem; Xy: Xylem; PE: Perithelium; PF: Phloem fibers; SP: Secondary phloem; SX: Secondary xylem; WF: Wood fiber; V: Vascular; CL: Cork layer; PEL: Phellogen; PHE: Phelloderm; CO: Cortex.

Table 1. Related data on the anatomical structure of *Myricaria laxiflora*.

Morphological trait	Root ($\bar{x} \pm S_{\bar{x}}$)	Stem ($\bar{x} \pm S_{\bar{x}}$)	Leave ($\bar{x} \pm S_{\bar{x}}$)
Diameter	1006.35 ± 32.69	865.83 ± 24.43	-
Thickness of cork layer	32.98 ± 5.46	-	-
Phloem thickness	91.9 ± 9.43	115 ± 12.4	-
Xylem radius	287.03 ± 11.38	169.73 ± 16.7	-
Large catheter diameter	56.16 ± 4.02	18.67 ± 1.3	-
Small catheter diameter	14.8 ± 2.1	7.67 ± 0.81	-
Stratum corneum thickness	-	4.67 ± 0.43	-
Epidermal thickness	-	14 ± 3.4	-
Cortical thick walled tissue thickness	-	60 ± 6.1	-
Blade thickness	-	-	325.36 ± 12.29
Upper epidermal keratin thickness	-	-	3 ± 0.31
Lower epidermal keratin thickness	-	-	3.26 ± 0.19
palisade tissue thickness	-	-	25.33 ± 3.14
Sponge tissue thickness	-	-	33.33 ± 3.69

The stem: Current-year stems display four regions: epidermis, cortex, vascular cylinder, and pith (Fig. 3-A, B). The epidermis contains a single layer of regularly arranged cells covered by a prominent cuticle (Tab. 1). The cortex comprises 7-10 cell layers: 4-6 outer layers of sclerenchyma (some containing red inclusions that impart stem coloration, Fig. 3-B) and 3-4 inner layers of chlorenchyma with large intercellular spaces (Fig. 3-C). During secondary growth initiation, cells interior to primary phloem resume division forming fascicular cambium, while medullary ray cells develop interfascicular cambium, jointly establishing a wavy cambial ring (Fig. 3-B) that later becomes continuous (Fig. 3-A). Collateral vascular bundles are densely arranged, with phloem consisting of 3-8 outer fiber layers and 4-7 inner parenchyma layers. Pith parenchyma contains sparse inclusions, surrounded by 2-3 layers of thickened cells forming a perimedullary zone (Fig. 3-F).

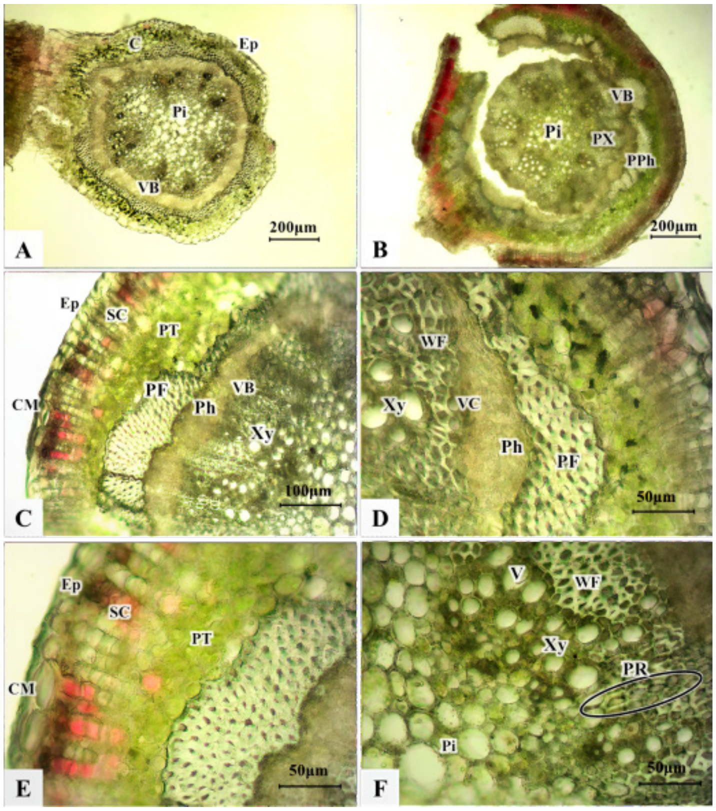

Figure 3. Anatomical structure of a stem of *Myricaria laxiflora* under microscope. (A,B) Transverse section of stem; (C) Partial cross section of stem; (D) vascular bundle; (F) pith and xylem; Note: EP: epidermis cell; C: Cortex; Pi: pith; VB: Vascular bundle; PX: Secondary xylem; PPh: Secondary phloem; CM: Corneum; SC: Sclerenchyma cell; PF: Phloem fibers; PH: Phloem; Xy: Xylem; WF: Wood fobre; VC: Vascular cambia; V: Vascular; PR: Pith ray.

The leaf: Leaf cross-sections are lunate with three domains: Epidermis, mesophyll, and veins (Tab. 1). The isolateral structure features 1-2 layered palisade tissues (total 25.33 μm thick) on both surfaces, with tightly packed marginal cells and loosely arranged central cells (Fig. 4-B). Spongy tissue is reduced, comprising irregular cells with large air spaces. Midribs contain collateral bundles organized adaxially to abaxially as: epidermis (subrectangular cells in pentagonal arrays with rounded anticlinal walls and localized thickenings), 2-3 parenchyma layers, xylem, phloem, 3-4 parenchyma layers, and epidermis. Amphistomatic leaves (with more stomata on stem-clasping surfaces) bear multicellular radiocytic stomata (with ≥ 5 radiating subsidiary cells and a diameter of approximately 50 μm) containing sunken guard cells and substomatal chambers (Fig. 4A).

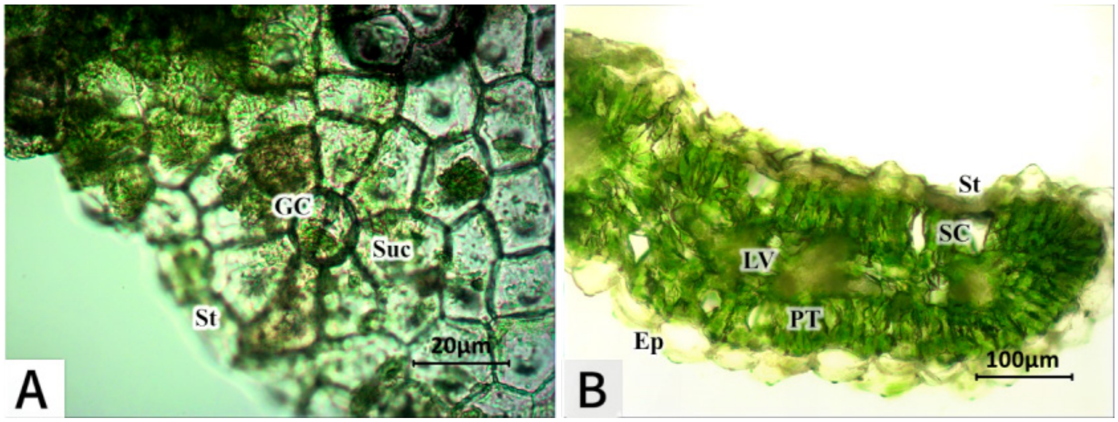

Figure 4. Anatomical structure of the leaves of *Myricaria laxiflora* under microscope. (A) Stomatal apparatus; (B) Transverse section of leaf; Note: ST: Stomatal apparatus; GC: Guard cell; Suc: Subsidiary cells; LV: Leaf vein; SC: Subatomatal chamber; PT: Palisade tissue; EP: Perithelim cell.

The seed: Fruits are narrowly triangular capsules containing 20-100 almond-shaped seeds. Fresh seeds are light tan, turning dark brown after one year with roughened surfaces (Fig. 6-E). Embryos are linear with erect cotyledons occupying >50% volume. Internal cells exhibit longitudinal alignment: large/loose centrally and small/dense peripherally. The radicle zone contains transversely palisade-like cells overlain by dense cytoplasmic meristematic cells connecting to regularly arranged hypocotyls (Fig. 5-A). A lacuna formed by degraded parenchyma exists between this zone and the micropyle (Fig. 5-B). Cotyledons show prominent vascular systems (Fig. 5-C). The seed coat detaches easily, bearing hydrophobic lipids; pappus-tipped seeds have spirally based unicellular trichomes (Fig. 6-D).

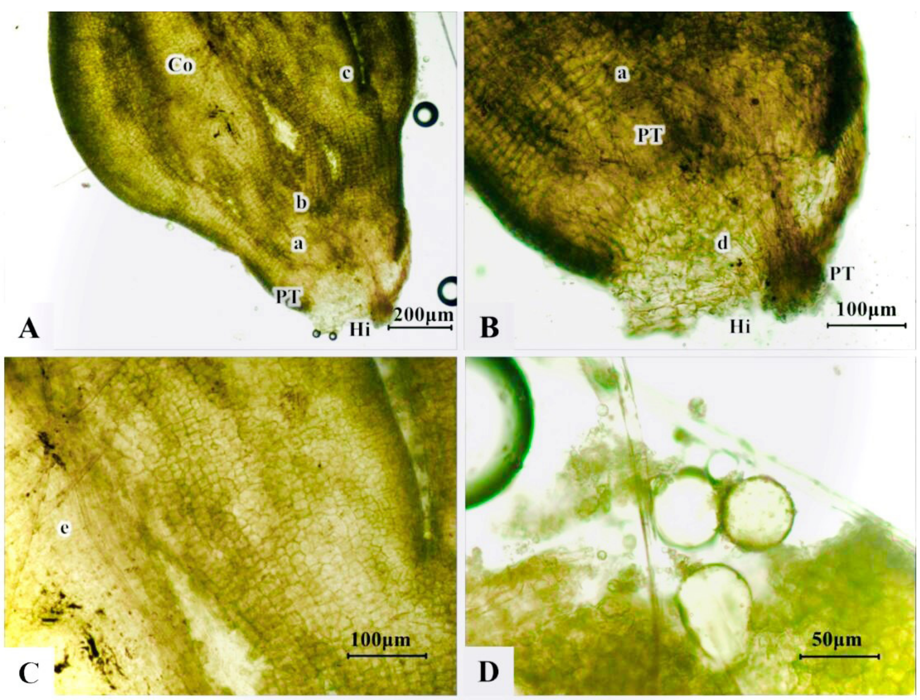

Figure 5. Anatomical characteristics of *Myricaria laxiflora* seeds. (A) Detail of seed squash preparation; (B) Detail of seed squash preparation; (C) Vascular system within the seed; (D) Lipids exuded during squash preparation; Note: a: Palisade-like cells in the radicle zone; b: Meristematic cells of the root apex; c: Shoot apical meristem (chalazal region of the fused cotyledons); d: Large lacuna between the radicle palisade zone and micropyle; e: Vascular system in the cotyledon.

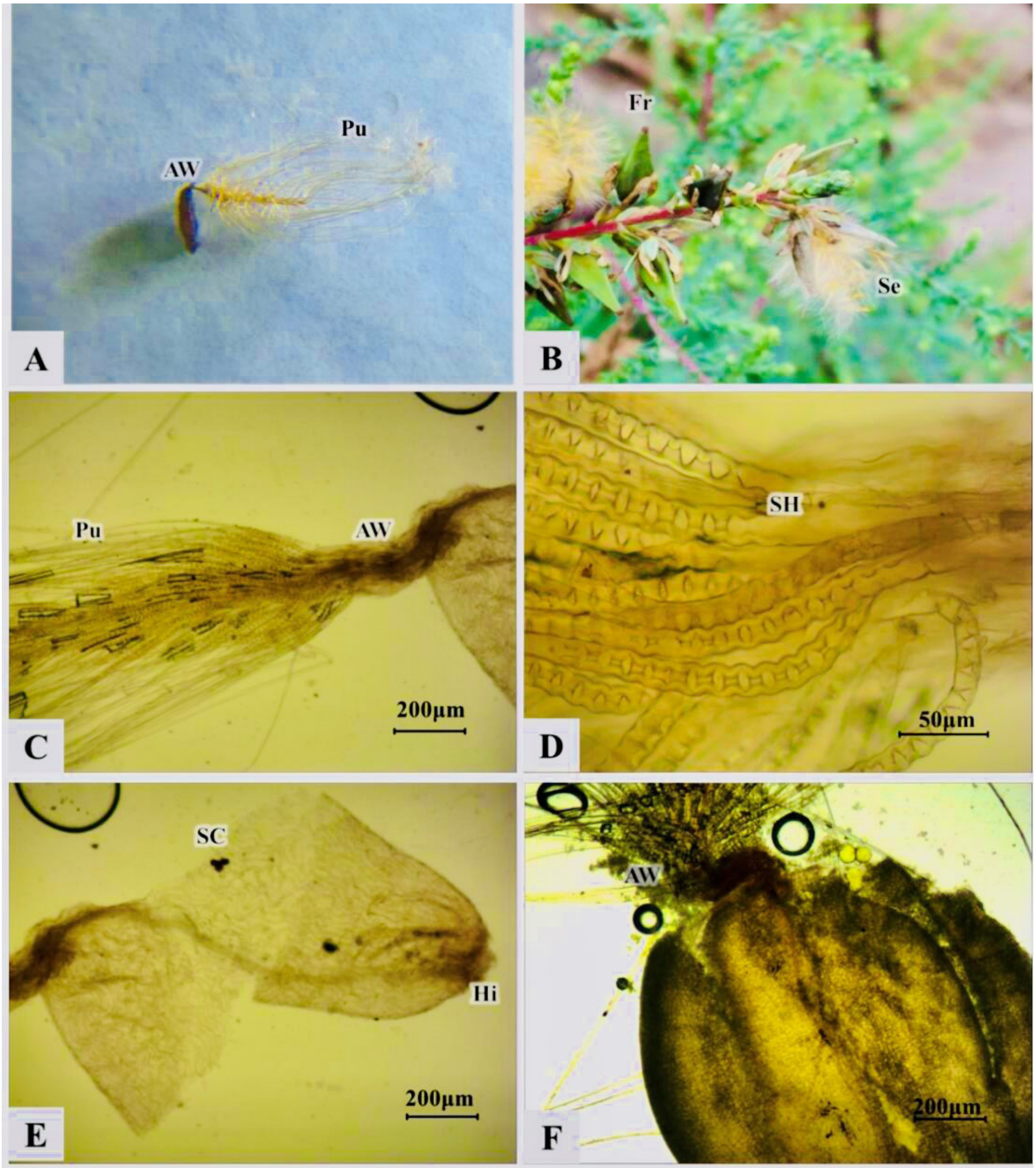

Figure 6. Seeds and seed appendages of *Myricaria laxiflora*. (A) Seed; (B) Fruit (capsule); (C) Seed awn column with pubescence; (D) Detail of seed pubescence; (E) Seed coat; (F) Awn column; Note: AW: Awn column; Pu: Pubescence emerging from the awn column; Fr: Fruit; Se: Seed; HS: Helical base (of trichomes); SC: Seed coat; Hi: Hilum.

Discussion

Myricaria laxiflora develops a strong and extensive root system that firmly anchors it in sand and gravel. Its perennial roots possess thick periderm with tightly arranged cork layer cells. The xylem occupies approximately one-third of the root cross-sectional area, containing numerous large diameter vessels and abundant wood fibers, which indicates enhanced water transport capacity under moisture stress. The thickened periderm substitutes the cortex and epidermis as a barrier against the external environment (Wang, et al. 2015), thereby restricting the free movement of water and ions. This not only reduces stress under adverse conditions but also minimizes oxygen and nutrient ion leakage from roots, preserving physiological functions. Aerenchyma in the root cortex provides channels for O_2 transport from leaves to roots and facilitates upward movement of ethanol and CO_2, alleviating stress damage and improving survival during flooding (Vartapetian and Jackson 1997). Like many wetland plants, *M. laxiflora* experiences hypoxia during summer floods (Jackson and Colmer, 2005, Colmer, et al. 1998), relying on aerenchyma and barrier structures to store oxygen under anoxic conditions and to regulate water-solute exchange (Kotula, et al. 2009, Enstone, et al. 2003).

Zhang and Tan, 2003 proposed *M. laxiflora* as a hygrophyte with low drought susceptibility, yet field surveys have revealed arid post-flood conditions in some habitats. Stem anatomy reveals a single-layered epidermis with a thick cuticle (3-4 μm) in annual stems, flattened phellem cells with thickened walls, and abundant solid inclusions in cortical sclerenchyma and pith cells. Liu's research indicates that such inclusions enhance drought adaptability (Khaleghi, et al. 2019), suggesting that they may improve water retention and cold tolerance in arid environments. Additionally, developed xylem and phloem fibers optimize water/nutrient conduction while maintaining stem mechanical strength against flood scouring.

Leaves exhibit typical xeromorphic traits: small size, bilayered palisade tissue, thick cuticle (3-4 μm), and transparent epidermis (common in Tamaricaceae), indicating drought adaptation. Both leaf surfaces are covered by thick cuticle, and robust phloem in veins enhances cold resistance and water absorption. As the primary interface with environmental factors, leaves evolve structural adjustments under prolonged cold, conferring heritable ecological adaptations. Being the only evergreen *Myricaria* species in winter, *M. laxiflora's* leaf architecture serves as a reliable indicator of cold resistance. Palisade tissue development (up to 50 μm thick) is a key evaluative metric-highly developed palisade cells enhance leaf compactness, providing a "protective barrier effect" under extreme cold. Qiu, et al. 2022 noted that increased palisade ratio improves cold resistance (2022). Its isolateral leaf structure (with palisade tissues on both surfaces) withstands harsh winters. Under strong light, dense palisade tissues prevent mesophyll scalding; thicker, smaller, tightly packed cells increase solar energy efficiency (Khaleghi, et al. 2019). Small thick leaves, thickened cuticle, slightly thickened epidermal walls, hypodermis, and elongated palisade cells represent adaptations to high-light riparian habitats.

The sustainability of riparian plants is profoundly influenced by their habitat niche specificity and ecological adaptations. M. laxiflora's adaptations include rapid winter growth, high seed yield, efficient wind/water dispersal, and clonal propagation in alluvial sands. Seed reproduction requires dispersal *via* gravity, wind, or mechanical forces. Seed shape and volume-key environmental adaptation factors-determine dispersal distance and area, with external (e.g., awn column) and internal structures (e.g., radicle-hilum lacuna) co-adapted to dispersal modes. Long-term evolution derives habitat-specialized structures to counter multiple stressors. Although seed germination faces drought and flood stresses (Chen and Xie, 2007), high reproductive output-small, lightweight seeds and high yield-compensates for low seedling survival.

As in most wetland species that produce buoyant seeds, hydrochory (secondary dispersal) is a common mechanism of seed dispersal. Endemic to the Three Gorges fluctuating zone, *M. laxiflora* seeds primarily disperse by wind or secondarily by water. The awn column is adapted to windy banks, with dense pubescence that facilitates long-distance anemochory. Awn hairs absorb water *via* capillarity to accelerate imbibition, while hair buoyancy aids floating during hydrochory (Zhou, et al. 2021). A hydrophobic lipid coating extends the duration of water flotation. The radicle-hilum lacuna serves three functions: (1) enhancing buoyancy and improving hydrochory efficiency; (2) acting as an oxygen reservoir that supports the oxygen-demanding germination process; and (3) forming air bubbles ahead of the radicle apex to prevent water intrusion during drift (Yang, et al. 2025), thereby transiently protecting meristematic cells from inundation.

Conclusion

In summary, *Myricaria laxiflora* exhibits the typical characteristics of amphibious plants. Key adaptive features include a thickened periderm, large root vessels and well-developed aerenchyma, densely developed phloem and xylem fibers and a thick cuticle in stems, highly differentiated palisade tissue, phloem networks, and cuticular layers in leaves, along with specialized seed structures such as awn columns and hydrophobic lipid coatings. These integrated traits collectively facilitate survival in post-flood, arid environments during autumn and winter, while sustaining a high reproductive capacity. This study provides an anatomical interpretation of *M. laxiflora's* adaptive features to amphibious habitats, establishing a scientific framework for understanding its taxonomy, evolutionary trajectory, phylogeny within the genus *Myricaria*, and conservation strategies for this endangered species.

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