

Đặc điểm thích nghi về cơ quan sinh dưỡng của một số loài thực vật ven sông sống chủ yếu tại khu vực hạ lưu sông Côn, xã Phước Hòa, huyện Tuy Phước, tỉnh Bình Định

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TÓM TẮT

Hệ thực vật ven sông hạ lưu sông Côn có vai trò rất lớn trong việc điều hòa khí hậu, giữ đất, phòng hộ trong mùa mưa bão và đóng góp vào môi trường sống của các loài thủy sản. Nghiên cứu được tiến hành trên 4 loài thực vật, gồm thân cỏ và thân bụi nhỏ thuộc ngành Ngọc Lan (Magnoliophyta). Các phương pháp hình thái so sánh, vi phẫu, nhuộm kép, đo mẫu và chụp ảnh hiển vi rỗ, thân và lá cây được thực hiện để xác định các đặc điểm thích nghi về cơ quan sinh dưỡng của các đối tượng nghiên cứu. Kết quả nghiên cứu cho thấy, các loài thực vật tại khu vực nghiên cứu thích nghi với điều kiện ánh sáng mạnh: biểu bì lá phân bố nhiều lông che chở và mô giậu phát triển (chiếm đến 56,22% độ dày phiến lá). Mô khuyết phát triển mạnh, có nhiều khoang trống lớn trong rỗ và thân (chiếm đến 63,49% bán kính rỗ), số lượng mạch gỗ ít và đường kính mạch lớn ($25,00 \pm 4,00$ mạch/mm² và đường kính mạch $109,92 \pm 13,15$ μ m ở rỗ thứ cấp, $5,33 \pm 0,33$ mạch/mm² và đường kính mạch $114,83 \pm 20,08$ μ m ở thân sơ cấp) giúp cây thích nghi với điều kiện thiếu oxy và ngập nước trong mùa mưa. Mô cứng bao quanh các bó mạch ở rỗ, tạo thành dải bao quanh thân, rải rác tinh thể oxalate calcium và tế bào đá trong mô mềm thịt lá giúp các đối tượng nghiên cứu chịu được các tác động cơ học (gió, bão).

Từ khóa: Giải phẫu, hình thái, sông Côn, thích nghi, thực vật ven sông.

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Adaptive features of the vegetative organs of some common riparian plants in the lower Con river, Phuoc Hoa commune, Tuy Phuoc district, Binh Dinh province

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ABSTRACT

The riparian vegetation along the lower Con river plays a crucial role in regulating the microclimate, stabilizing soil, providing protection during the rainy and stormy season, and contributing to the aquatic ecosystem. This study was carried out on four herbaceous and undershrub species in Magnoliophyta. Morphological comparison, microsurgery, double-staining, microscopic measurements and imaging of roots, stems, and leaves were applied to identify adaptive features in the vegetative organs of the studied species. The results revealed that the plant species in the study area are adapted to high light conditions, as evidenced by the abundance of trichomes on the leaf epidermis and the well-developed palisade mesophyll (accounting for up to 56.22% of leaf thickness). Aerenchyma tissues were strongly developed, forming large air cavities in both roots and stems (up to 63.49% of root radius). These species also exhibited a low number of xylem vessels with large vessel diameters (25.00 ± 4.00 vessels/mm² and 109.92 ± 13.15 μ m in secondary roots; 5.33 ± 0.33 vessels/mm² and 114.83 ± 20.08 μ m in primary stems), facilitating adaptation to hypoxic and waterlogged conditions during the rainy season. The presence of sclerenchyma surrounding vascular bundles in roots and stems, scattered distribution of calcium oxalate crystals and sclereids in the leaf mesophyll support the species' tolerance to mechanical stress, such as wind and storms.

Keywords: *Anatomy, morphology, Con river, adaptation, riparian vegetation.*

1. INTRODUCTION

The Con river is the largest river in Binh Dinh province, originating from the eastern mountainous region of the Truong Son range, at an elevation of over 1000 meters. In its upper course, the river flows in a northwest-southeast direction; upon reaching Vinh Son, it shifts to a north-south orientation, and at Binh Thanh, it turns west-east before emptying into the Thi Nai lagoon. At Binh Thanh, the Con river bifurcates into two main distributaries: the

Tan An and Dap Da rivers. The Tan An river subsequently discharges into the Go Boi – Tan An estuary, representing the lower course of the Con river. The ecosystem in this area is highly diverse and is characteristic of riparian ecosystems within the province, with vegetation exhibiting numerous adaptive traits to the local environmental conditions. In addition to its crucial role in climate regulation, participation in essential biological processes, water provision, and serving as a vital habitat for aquatic species, the riparian ecosystem also contributes to

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soil retention and provides natural protection during the rainy and storm seasons.¹ Despite its significant ecological importance, this area has yet to receive adequate research attention and conservation efforts. The vegetation in the study area is primarily composed of shrub and herbaceous plant species. However, the number of species has been severely declining due to the construction of irrigation and civil infrastructure by local communities along the river basin. Given the urgent need to protect the downstream ecosystem of the Con river, it is essential to study the common adaptive characteristics of riparian plant species to establish a scientific basis for proposing effective restoration measures and promoting the sustainable development of the riparian ecosystem in this region.

2. SUBJECTS AND METHODS

2.1. Subjects

The research subjects include four common plant species found in the lower Con river, Binh Dinh province: *Ludwigia octovalvis* (Jacq.) Raven - Onagraceae and *Celosia argentea* L. - Amaranthaceae, both belonging to Eudicots; *Melinis repens* (Willd.) Zizka – Poaceae and *Commelina longifolia* Lam. - Commelinaceae, both belonging to Monocots.

2.2. Methods

2.2.1. Field study methods

The vegetative organs (roots, stems, and leaves) of the studied plant species were observed, described, and measured for morphological characteristics, root length, stem height, and leaf area, and were photographed under natural conditions. Subsequently, the vegetative organs were collected following the botanical survey method,² stored in plastic bags, and transported to the laboratory for preservation and further analysis.

2.2.2. Laboratory study methods

Sample sectioning and double staining method

After collection, the samples were rinsed with water, then fixed and preserved in a FAA

solution comprising ethyl alcohol 96%, acetic acid 40%, formalin, and distilled water.³ Samples were sectioned thinly with a razor blade, subjected to double staining, and prepared as temporary slides. The double-staining technique distinguishes cells with cellulose walls (stained red by carmine) and cells with lignified walls (stained blue by methylene blue).⁴ This method helps identify the presence and distribution of tissue types that enable plant adaptation to specific ecological factors.

Microscopy method

Samples were observed and photographed under a Kruss MBL 2000-T microscope (Germany). Staining allowed identification of lignified cell groups (fibers and sclereids), and collenchyma with cellulose walls which provide mechanical support for plant bodies;⁵ xylem vessels and tracheids also possess lignified secondary walls (stained blue), and the dense distribution of these conductive elements facilitates plant adaptation to drought conditions; the presence of aerenchyma with cellulose-based cell walls (stained red) enables plants to adapt to environments with oxygen deficiency.³

Sampling and Data Processing Methods

For each study species, six mature individuals were collected simultaneously to ensure that the observed samples shared similar size, morphology, and structure at the same developmental stage. Measurements of each vegetative trait were repeated six times across the six individuals of the same species ($n = 6$) to calculate the mean value (\bar{X}) and standard deviation (S) for each parameter.

The dimensions of structural components in roots, stems, and leaves were measured using the measurement tools integrated into the Microscope Manager software. The comparative proportions of these components are related to plant adaptation to environmental conditions. Adaptations to intense light and high temperatures are reflected in the well-developed palisade tissue in leaf blades, the presence of dense trichomes, and protective cutin layers,

while adaptation to oxygen-deficient conditions is indicated by the abundant occurrence of aerenchymatous tissue.³

Measurement data were statistically processed using Microsoft Excel 2016 to determine:

$$\text{Mean value: } \bar{X} = \frac{\sum_{i=1}^n x_i}{n} \quad (n = 6)$$

$$\text{Standard deviation: } S = \sqrt{\frac{\sum_{i=1}^n (x_i - \bar{X})^2}{n-1}} \quad (n < 30)$$

Comparative morphology method

Plant classification was based on morphological characteristics, especially those of reproductive organs, which are less affected by environmental changes compared to vegetative organs.⁶

Scientific identification method

Specimen identification was carried out using the references of Pham and Nguyen.^{7,8}

3. RESULTS AND DISCUSSION

3.1. Morphological adaptations

3.1.1. Roots

Melinis repens (Willd.) Zizka and *Commelina*

longifolia Lam. possess fibrous root systems that exhibit extensive growth, enabling them to effectively compete for water and mineral nutrients with other species by spreading horizontally.⁹ In contrast, *Ludwigia octovalvis* (Jacq.) Raven and *Celosia argentea* L. develop prominent taproot systems (Figure 2). Additionally, the nodes of *C. longifolia* and *L. octovalvis*, particularly along the creeping stems, produce adventitious roots that anchor the plant to the ground and facilitate horizontal expansion, thereby enhancing resistance to mechanical forces such as wind and flooding. Root diameters for *M. repens*, *C. longifolia*, *L. octovalvis*, and *C. argentea* were recorded as 1.72–1.78 mm, 1.84–1.87 mm, 4.28–4.34 mm, and 7.65–7.69 mm, respectively.

3.1.2. Stems

M. repens and *C. argentea* possess erect stems, with heights ranging from 77–105 cm and 90–110 cm, respectively. The height of *M. repens* in the present study area is lower than that reported by Corrales-Lerma et al. in Chihuahua, Mexico, likely due to different environmental conditions.¹⁰



Figure 1. Growth forms of the investigated plant species.

a. *Celosia argentea* L., b. *Ludwigia octovalvis* (Jacq.) Raven, c. *Melinis repens* (Willd.) Zizka, d. *Commelina longifolia* Lam.



Figure 2. Morphological characteristics of the investigated plant species.

a. *Celosia argentea*, b. and c. *Ludwigia octovalvis*, d. *Melinis repens*, e. *Commelina longifolia*

L. octovalvis exhibits a mostly erect stem or partially horizontal growth habit, whereas *C. longifolia* features a creeping stem morphology, with recorded heights of 90–130 cm and 22–61 cm, respectively (Figure 1). Most study species grow in dense clumps, with notable stem branching observed in *L. octovalvis*. These morphological characteristics are considered adaptive features that mitigate mechanical stress from environmental factors, such as strong winds and flood-induced water flow.¹¹ Secondary stems of *L. octovalvis* develop cork layers with longitudinal grooves, enhancing gas exchange during inundation seasons and high river water levels.⁵

3.1.3. Leaves

All investigated species exhibit small, elongated leaf blades, an adaptation believed to reduce wind impact during storms.¹² Leaf blade surface areas were recorded as follows: 6.72–11.55 cm² (*C. longifolia*), 9–15.68 cm² (*M. repens*), 7.8–16.8 cm² (*C. argentea*), and 7.82–14.4 cm² (*L. octovalvis*). The leaf area of *C. longifolia* is smaller than that reported by Tran *et al.* in Long An Province (16–30 cm²),¹¹ potentially due to more favorable climatic conditions and reduced storm frequency in that region, which may allow for better growth and larger leaf size.

Leaf thickness values were as follows: 348.37 ± 41.64 μm (*C. longifolia*), 233.27 ± 27.69 μm (*M. repens*), 392.37 ± 75.26 μm (*C. argentea*), and 244.10 ± 18.73 μm (*L. octovalvis*). The outer epidermal surfaces of all species, except *C. argentea*, are covered with protective trichomes, most abundant in *L. octovalvis*, which function to protect leaf tissue from heat stress and reduce water loss through stomatal transpiration.¹³

3.2. Adaptive anatomical characteristics

3.2.1. Roots

The roots of *M. repens* and *C. longifolia* exhibit a primary anatomical structure comprising four main components: epidermis, cortex, stele, and pith. The epidermis consists of 1–2 cell layers, with large cells accounting for 5.98% and 5.11% of the root radius in *M. repens* and *C. longifolia*, respectively (Table 1). The cortex in both species features well-developed aerenchyma (Figure 3), forming numerous large intercellular spaces that account for 63.49% and 62.49% of root radius in *M. repens* and *C. longifolia*, respectively. In *M. repens*, aerenchyma cells are radially arranged from the stele to the epidermis, while in *C. longifolia*, they are uniformly distributed, forming rhomboid-shaped spaces. These air spaces function in gas storage and facilitate

gas exchange under low-oxygen environmental conditions.¹³ In *C. longifolia*, 2–3 layers of lignified cells encircle the cortex region, and the stele in both species is reinforced with multiple layers of sclerenchyma surrounding the xylem vessels, enhancing the mechanical strength of the roots.⁵

The secondary roots of *C. argentea* and *L. octovalvis* consist primary components: bark and secondary xylem. Secondary xylem is dominant, comprising 83.88% and 75.15% of the root radius in *C. argentea* and *L. octovalvis*, respectively (Table 2). In *C. argentea*, secondary xylem is clustered and embedded within parenchyma tissue (Figure 4), similar to findings by Rajput on the genus *Celosia*.¹⁴ In *L. octovalvis*, well-developed xylem rays facilitate radial transport.¹² According to the

study by Bedoya and Madriñán on the genus *Ludwigia*, in mature plants, aerenchyma tissue is extensively developed from the phellogen.¹⁵

The xylem vessel density per mm² in the roots of *M. repens*, *C. longifolia*, *C. argentea*, and *L. octovalvis* are 44.33 ± 4.33 , 22.20 ± 1.12 , 23.33 ± 2.33 , and 25.00 ± 4.00 vessels/mm², respectively. These values are lower than those reported by Duong and Phan for species in arid environments - coastal rocky hills, where vessel densities exceed 100 vessels/mm².¹⁶ Vessel diameters in the studied species range from 52–118 µm. According to Thomas, the average vessel diameter in Angiospermatophyta is approximately 40 µm,¹⁷ indicating that the studied species have relatively wide vessels - an adaptive trait suitable for water-abundant environments.

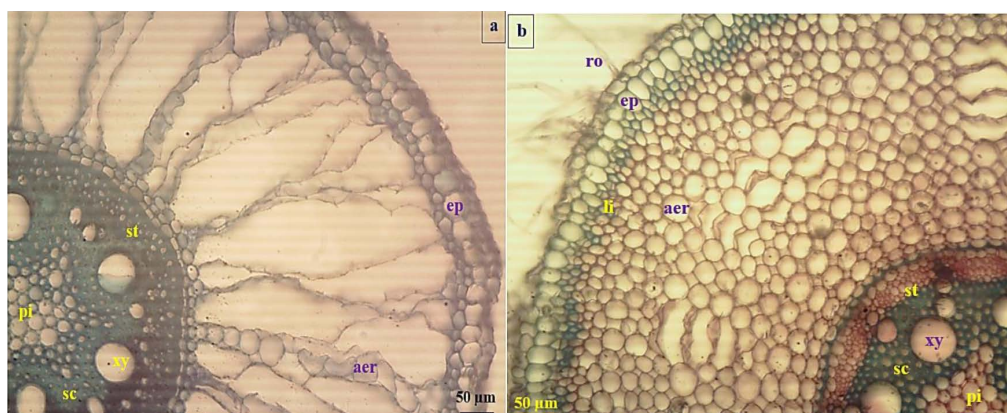


Figure 3. Anatomical features of the primary root structures in the investigated plant species.

a. *Melinis repens*, b. *Commelina longifolia*, ro: root hair, ep: epidermis, li: lignified cell, aer: aerenchyma, st: stele, sc: sclerenchyma, xy: xylem vessel, pi: pith

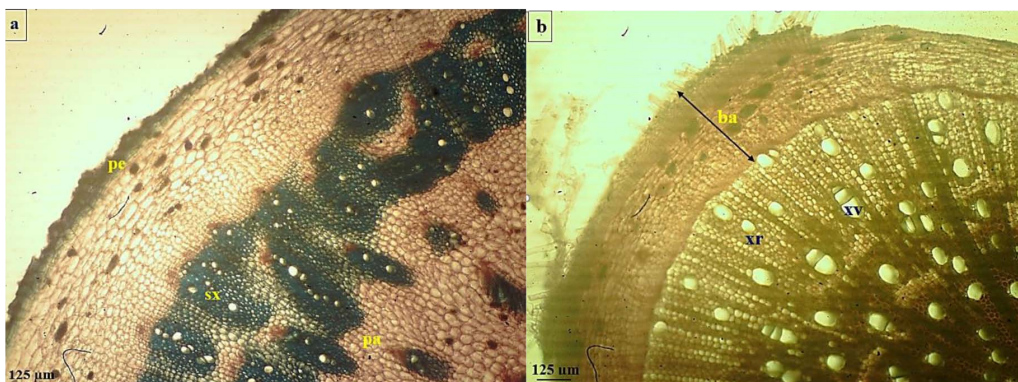


Figure 4. Anatomical features of the secondary root structures in the investigated plant species.

a. *Celosia argentea*, b. *Ludwigia octovalvis*, ba: bark, pe: periderm, sx: secondary xylem, pa: parenchyma, xr: xylem ray, xv: xylem vessel

Table 1. The dimensions of primary root structures in the studied plant species.

RR: root radius

Species	Primary root									
	Epidermis		Cortex		Stele			Pith		
	$\bar{X} \pm S$ (μm)	% RR	$\bar{X} \pm S$ (μm)	% RR	$\bar{X} \pm S$ (μm)	% RR	Vessel density ($\bar{X} \pm S$) (No. of vessels per mm^2)	Vessel diameter ($\bar{X} \pm S$) (μm)	$\bar{X} \pm S$ (μm)	% RR
<i>Melinis repens</i> (Willd.) Zizka	52.37 ± 1.12	5.98	555.70 ± 36.27	63.49	158.27 ± 16.96	18.08	44.33 ± 4.33	88.00 ± 1.00	108.93 ± 24.86	12.45
<i>Commelina longifolia</i> Lam.	47.27 ± 1.49	5.11	577.77 ± 27.26	62.49	192.17 ± 27.02	20.78	22.20 ± 1.12	72.13 ± 1.05	107.43 ± 16.96	11.62

Table 2. The dimensions of secondary root structures in the studied plant species.

RR: root radius

Species	Secondary root							
	Bark				Secondary xylem			
	Cork		Secondary phloem					
	$\bar{X} \pm S$ (μm)	% RR	$\bar{X} \pm S$ (μm)	% RR	$\bar{X} \pm S$ (μm)	% RR	Vessel density ($\bar{X} \pm S$) (No. of vessels per mm^2)	Vessel diameter ($\bar{X} \pm S$) (μm)
<i>Celosia argentea</i> L.	116.17 ± 15.08	3.03	502.08 ± 42.15	13.09	3217.50 ± 131.25	83.88	23.33 ± 2.33	51.92 ± 2.77
<i>Ludwigia octovalvis</i> (Jacq.) Raven	157.75 ± 16.00	7.32	377.92 ± 25.52	17.53	1620.33 ± 113.02	75.15	25.00 ± 4.00	109.92 ± 13.15

3.2.2. Stems

The primary stems of *M. repens* and *C. longifolia* exhibit aerenchyma development: 4–5 layers of aerenchymatous cells below the epidermis in *M. repens*, and throughout the stem in *C. longifolia*, forming large gas cavities (Figure 5) that enhance gas exchange.¹¹ A similar observation was made by Nguyen in *Panicum repens* L. (Poaceae), which also exhibits abundant

intercellular spaces.¹⁸ Inside the 4–5 layers of cortical parenchyma cells, a continuous band of sclerenchyma tissue is formed encircling the stem. Sclerenchyma also surrounds the vascular bundles, consistent with the findings of Wahua on *Commelina erecta* L..¹⁹ Oval-shaped calcium oxalate crystals are scattered within the aerenchyma of *C. longifolia* stem, collectively contributing to the mechanical reinforcement of the primary stems.⁵

C. argentea and *L. octovalvis* possess secondary stem structures. The cork layer is thin, accounting for 1.41% and 4.3% of the stem radius in *C. argentea* and *L. octovalvis*, respectively (Table 4), compared to herbaceous species living in coastal rocky areas.¹⁶ This is completely consistent with plant species adapted to moist environments. In *C. argentea*, the secondary xylem appears in clusters interspersed with parenchyma. In contrast, a study by Rajut on *Aerva sanguinolenta* (L.), a species belonging to the same family Amaranthaceae, reported that its secondary xylem forms a continuous ring.²⁰ In *L. octovalvis*, secondary xylem develops continuously below the vascular cambium and features abundant fibers, enhancing mechanical

strength, a pattern consistent with Scremin-Dias et al.²¹ Prominent xylem rays support radial transport of nutrients and gases (Figure 6), aiding adaptation to hypoxic conditions during seasonal flooding.³

Xylem vessel density in stems ranges from 5 to 32 vessels/mm², and vessel diameters range from 55 to 117 μ m (Table 3 and 4). Compared to the study by Duong and Phan on herbaceous species in mangrove swamps,²² the studied species have wider vessel diameters. This is consistent with their freshwater riparian habitat, whereas smaller vessel diameters in mangrove species may promote faster flow and limit salt toxicity.

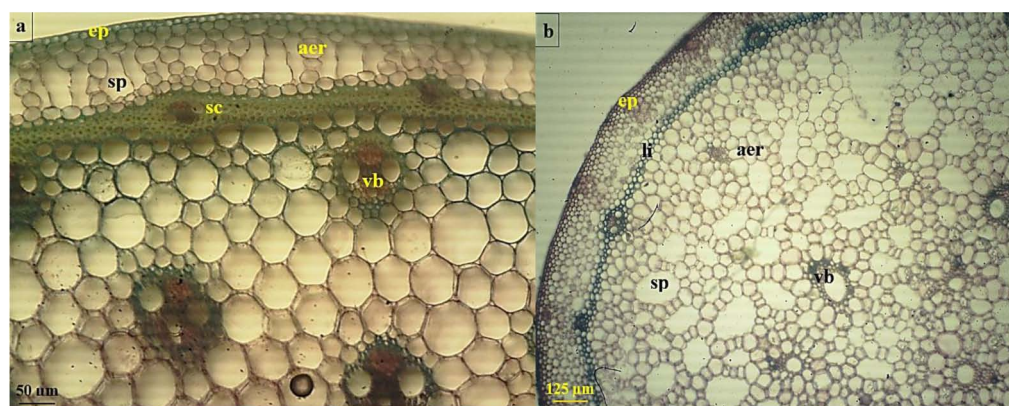


Figure 5. Anatomical features of the primary stem structures in the investigated plant species.

a. *Melinis repens* and b. *Commelina longifolia*, ep: epidermis, aer: aerenchyma, sp: intercellular space, sc: sclerenchyma ring, vb: vascular bundle, li: lignified cell

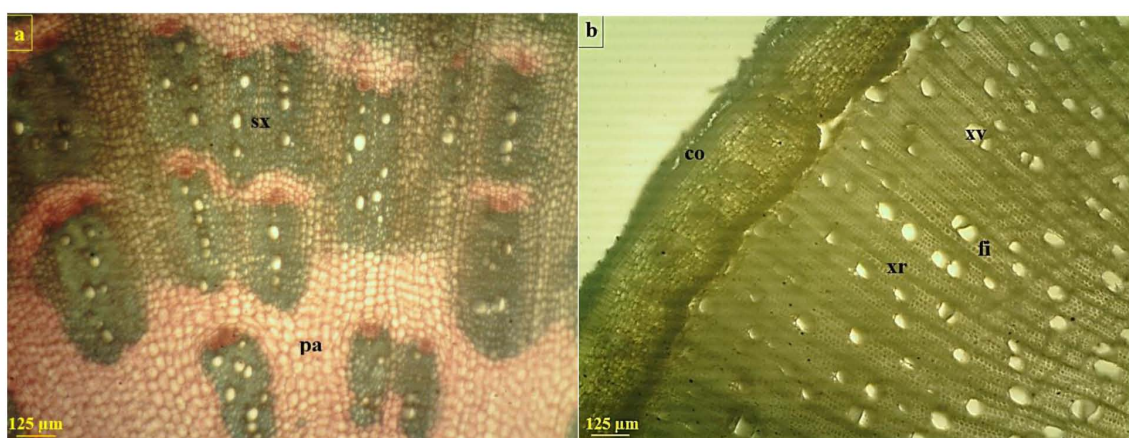


Figure 6. Transverse section through the secondary xylem of the secondary stem of *Celosia argentea* (a) and the secondary stem of *Ludwigia octovalvis* (b), sx: secondary xylem, pa: parenchyma, co: cork, xr: xylem ray, xv: xylem vessel, fi: fiber

Table 3. The dimensions of primary stem structures in the studied plant species.

SR: stem radius, "-": absent

Species	Primary stem							
	Epidermis		Parenchyma and vascular bundles				Pith cavity	
	$\bar{X} \pm S$ (μm)	% SR	$\bar{X} \pm S$ (μm)	% SR	Vessel density ($\bar{X} \pm S$) (No. of vessels per mm^2)	Vessel diameter ($\bar{X} \pm S$)	$\bar{X} \pm S$ (μm)	% SR
<i>Melinis repens</i> (Willd.) Zizka	12.58 ± 0.27	0.60	1365.00 ± 81.25	64.69	28.67 ± 4.33	55.42 ± 3.65	732.50 ± 25.00	34.71
<i>Commelina</i> <i>longifolia</i> Lam.	21.17 ± 1.08	1.02	2053.33 ± 109.90	98.98	5.33 ± 0.33	114.83 ± 20.08	-	-

Table 4. The dimensions of secondary stem structures in the studied plant species.

ST: stem radius, "-": absent

Species	Bark				Secondary xylem				Pith parenchyma	
	Cork		Secondary phloem							
	$\bar{X} \pm S$ (μm)	% SR	$\bar{X} \pm S$ (μm)	% SR	$\bar{X} \pm S$ (μm)	% SR	Vessel density ($\bar{X} \pm S$) (No. of vessels per mm^2)	Vessel diameter ($\bar{X} \pm S$) (μm)	$\bar{X} \pm S$ (μm)	% SR
<i>Celosia</i> <i>argentea</i> L.	137.17 ± 40.90	1.41	1440.83 ± 127.08	14.80	8159.42 ± 742.90	83.79	15.33 ± 2.33	82.75 ± 1.31	-	-
<i>Ludwigia</i> <i>octovalvis</i> (Jacq.) Raven	265.58 ± 21.65	4.30	366.17 ± 34.08	5.93	3901.42 ± 372.90	63.18	32.67 ± 4.33	117.75 ± 18.81	1642.08 ± 113.02	26.59

3.2.3. Leaves

The leaf blades of *M. repens* and *C. longifolia* are characteristic of monocots. In *C. longifolia*, the epidermal cells are large, occupying 23.31%

(upper) and 15.07% (lower) of total leaf thickness (Table 5). These results are generally consistent with the findings of Tran *et al.*¹¹

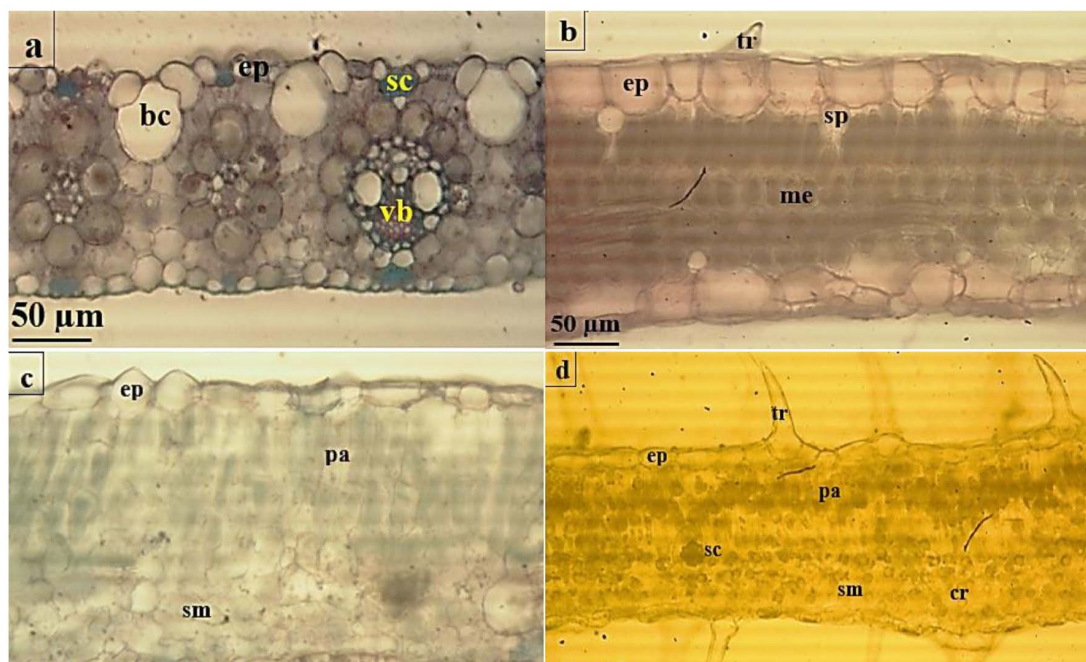


Figure 7. Anatomical features of the leaf blade structures in the investigated plant species.

a. *Melinis repens*, b. *Commelina longifolia*, c. *Celosia argentea*, d. *Ludwigia octovalvis*, tr: trichome, ep: epidermis, bc: bulliform cell, sc: sclerenchyma, vb: vascular bundle, sp: intercellular space, me: mesophyll, pa: palisade mesophyll, sm: spongy mesophyll, cr: crystal

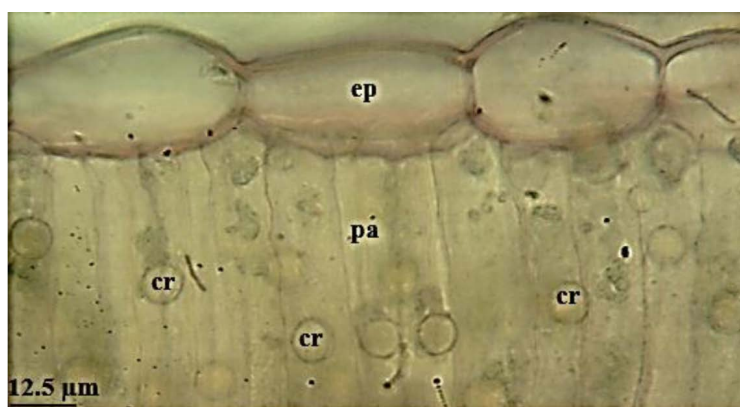


Figure 8. Transverse section through the palisade mesophyll of *Ludwigia octovalvis* leaf blade.

ep: epidermis, pa: palisade mesophyll, cr: crystal

The upper epidermis of both species possesses trichomes, with scattered intercellular spaces observed in the leaves of *C. longifolia* (Figure 7), which facilitate gas exchange.¹⁸ In the leaf blade of *M. repens*, the upper epidermis contains bulliform cells that enable the lamina to roll, thereby reducing water loss through stomata under hot or drought conditions.⁵ Sclerenchyma clusters beneath the epidermis in *M. repens* increase mechanical strength, the vascular bundles exhibit a Kranz anatomy.²³

In contrast, the leaf blades of *C. argentea* and *L. octovalvis* exhibit the anatomical structure characteristic of eudicots. The epidermis of *L. octovalvis* is densely covered with protective trichomes (Figure 7), and stomata are distributed on both surfaces of the leaf blade, though more abundantly on the abaxial side.²⁴ In the upper epidermis of *C. argentea*, epidermal cells exhibit considerable variation in size, whereas the lower epidermal layer is thinner and possesses an undulating surface.²⁵ In *C.*

argentea, the palisade and spongy mesophyll comprise 44.18% and 39.18% of the total leaf thickness, respectively (Table 5). Spherical crystals and sclereids are scattered throughout the mesophyll of *L. octovalvis* leaves (Figure 8),

consistent with findings by Scremin-Dias et al. in *Ludwigia grandiflora*,²¹ and contribute to increased mechanical resistance against wind and storm damage.

Table 5. The dimensions of leaf blade structures in the studied plant species.

TLT: total leaf thickness

Species	Leaf blade								
	TLT (µm)	Upper epidermis (µm)	% TLT	Lower epidermis (µm)	% TLT	Palisade mesophyll (µm)	% TLT	Spongy mesophyll (µm)	% TLT
	$\bar{X} \pm S$	$\bar{X} \pm S$		$\bar{X} \pm S$		$\bar{X} \pm S$		$\bar{X} \pm S$	
<i>Celosia argentea</i> L.	392.37 ± 75.26	42.23 ± 3.06	10.76	23.07 ± 1.21	5.88	173.33 ± 10.29	44.18	153.73 ± 12.41	39.18
<i>Ludwigia octovalvis</i> (Jacq.) Raven	244.10 ± 18.73	26.47 ± 2.12	10.84	15.53 ± 0.82	6.36	137.23 ± 23.12	56.22	64.87 ± 2.24	26.58
<i>Melinis repens</i> (Willd.) Zizka	233.27 ± 27.69	16.13 ± 1.22	6.92	22.13 ± 1.10	9.49	Mesophyll		% TLT	
						195.00 ± 12.96		83.60	
<i>Commelina longifolia</i> Lam.	348.37 ± 41.64	81.20 ± 4.21	23.31	52.50 ± 4.99	15.07	214.67 ± 25.33		61.62	

4. CONCLUSION

Riparian plant species are heliophilous, with features such as protective trichomes on the outer epidermis and highly developed palisade tissue (up to 56.22% of total leaf thickness).

These species are adapted to water-abundant, low-oxygen environments, as evidenced by low xylem vessel densities (lowest in *C. longifolia*: 22.20 ± 1.12 vessels/mm² in roots and 5.33 ± 0.33 vessels/mm² in stems) and wide vessel diameters (widest in *L. octovalvis*: 109.92 ± 13.15 µm in roots and 117.75 ± 18.81 µm in stems). Aerenchyma is well-developed in roots and stems (up to 63.49% of root radius in *M. repens*), and intercellular spaces are scattered throughout the leaves.

These species also exhibit adaptations to mechanical stress from wind and flooding:

growth in dense clumps, adventitious rooting from prostrate stems, presence of sclerenchyma bands or clusters surrounding xylem vessels or stems, and scattered calcium oxalate crystals in stem and leaf parenchyma.

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