Postprint: Anatomical and Barrier Structural Characteristics of Zizania latifolia Adapted to Wetland Environments

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Abstract

Zizania latifolia is a perennial emergent aquatic plant. This study investigated the anatomical structure, histochemistry, and apoplastic barrier permeability physiology of its roots, stems, and leaves. Anatomical and histochemical studies of Z. latifolia were conducted using light microscopy and fluorescence microscopy. The results showed that: (1) The anatomical structure of adventitious roots from outer to inner consisted of epidermis, exodermis, a single-cell-layer sclerenchyma mechanical tissue layer, cortex, endodermis, and vascular cylinder; stem structure from outer to inner consisted of cuticle, epidermis, peripheral sclerenchyma mechanical tissue layer, cortex, vascular bundle-containing sclerenchyma layer, and pith cavity. The leaf sheath possessed epidermis and vascular bundle-containing cortex, while the leaf blade had epidermis, mesophyll, and vascular bundles. (2) Adventitious roots possessed a barrier structure composed of an inner endodermis and its adjacent suberized cells and an outer exodermis; stems possessed a barrier structure composed of an inner sclerenchyma mechanical tissue layer and an outer cuticle and peripheral sclerenchyma mechanical tissue layer. The cell walls of the barrier structures exhibited histochemical characteristics of Casparian strip, suberin, and lignin deposition, and the leaf surface had a cuticle. (3) The aerenchyma of Z. latifolia included root aerenchyma, stem and leaf cortex aerenchyma, and pith cavity. (4) The barrier structures and anatomical features are important characteristics for adaptation to wetland environments; however, the peripheral sclerenchyma layer and sclerenchyma tissue layer in stems are relatively thin, suggesting that while it adapts to wetland environments, its distribution in xeric environments has certain limitations.

Anatomy and Apoplastic Barrier Histochemistry of *Zizania latifolia* Adapted to Wetland Environments

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Abstract

Wild rice (*Zizania latifolia*) is a perennial emergent plant. This study investigated the anatomical structure, histochemistry, and apoplastic barrier permeability physiology of its roots, stems, and leaves using optical and fluorescence microscopy. The results demonstrate four key findings. First, adventitious roots exhibit a distinct anatomical organization from outer to inner layers: epidermis, exodermis, a uniseriate thick-walled mechanical tissue layer, cortex, endodermis, and vascular cylinder. Stem structure comprises, from outside to inside, a cuticle, epidermis, peripheral mechanical tissue ring, cortex, sclerenchyma tissue layer with vascular bundles, and pith cavity. Leaf sheaths possess epidermis and vascular bundle-containing cortex, while leaf blades feature epidermis, mesophyll, and vascular bundles. Second, roots develop a barrier structure consisting of an inner endodermis with adjacent suberized cells and an outer exodermis; stems form barriers through an inner sclerenchyma mechanical tissue layer, outer cuticle, and peripheral mechanical tissue ring. The cell walls of these barrier structures show histochemical characteristics of Casparian bands, suberin, and lignin deposition, while leaf surfaces possess a cuticle. Third, aerenchyma tissue includes root aerenchyma, stem and leaf cortical aerenchyma, and pith cavities. Fourth, these barrier and anatomical structures represent important adaptations to wetland environments. However, the relatively thin peripheral mechanical ring and sclerenchyma tissue layer in stems suggest that while *Z. latifolia* is well-adapted to wetland conditions, its distribution in xeric environments may be limited.

Keywords: *Zizania latifolia*, anatomical structure, apoplastic barriers, histochemistry, permeability

Introduction

Zizania latifolia (wild rice) belongs to the tribe Zizanieae within the subfamily Ehrhartoideae of Poaceae, making it a close relative of cultivated rice (*Oryza sativa*) (Judziewicz & Clark, 2007). This important aquatic plant produces edible grains similar to those of North American wild rice (*Zizania aquatica*) (Sculthorpe, 1967). The species possesses perennial rhizomes, stolons, and aerial culms, with the culms featuring broad leaves. Despite its ecological and economic significance, research on the submerged portions of *Z. latifolia* and their adaptation to wetland environments remains relatively limited. Early studies examined the roots of North American wild rice (Stover, 1928), followed by limited anatomical investigations of roots and stems in *Zizania* species (Stover, 1951; Metcalfe, 1960; Jorgenson et al., 2013; Tateoka, 1969). Leaf anatomy has been more thoroughly documented (Metcalfe, 1960). However, compared to other important herbaceous plants with scaly rhizomes and stolons, rice (*Oryza sativa*) has received far more attention regarding adventitious root anatomy (Tateoka, 1969; Colmer, 2003; Kawai et al., 1998; Kotula et al., 2009), including the presence of a suberized endodermis in rice stems (Metcalfe, 1960).

A critical feature of wetland herbaceous plants is the presence of apoplastic barriers, including root endodermis, exodermis, and epidermis (Armstrong et al., 2006; Seago et al., 1999; Soukup et al., 2007; Armstrong et al., 2000), as well as sclerenchyma mechanical tissue layers (SCR) and peripheral mechanical rings (PMR) in stems and leaves. Species such as bermudagrass (*Cynodon dactylon*) and knotgrass (*Paspalum distichum*) possess lignified and suberized SCR and PMR layers along with cuticles, which function as protective tissues controlling water, ion, and oxygen diffusion between the plant interior and environment (Yang et al., 2013; Enstone et al., 2002). For instance, rice grown in stagnant solution exhibits accelerated and enhanced deposition of suberin and lignin in root endodermal and exodermal cell walls, more effectively blocking ion permeation (Ranathunge et al., 2011). These wetland plants also develop extensive aerenchyma tissue that provides oxygen under flooded conditions, including root aerenchyma (Seago et al., 2005; Jung et al., 2008) and pith cavities with cortical aerenchyma in stems (Armstrong et al., 2006).

Beyond the genus *Oryza*, research on structural adaptations to wetland environments in other Ehrhartoideae species remains scarce. *Zizania latifolia* thrives in and widely distributes across wetland habitats, yet unlike bermudagrass and knotgrass, it cannot tolerate xeric conditions (Yang et al., 2011). The species holds significant value for restoring agriculturally polluted environments in the Jianghan Plain and degraded wetlands in the Three Gorges Reservoir region. Therefore, we conducted a comprehensive investigation of the anatomical and histochemical characteristics of *Z. latifolia* roots, stems, and leaves, along with permeability of apoplastic barriers, to elucidate the structural features underlying its wetland adaptation and distribution limitations.

Materials and Methods

During summer 2017, wild *Z. latifolia* plants were collected from wetlands in the Jianghan Plain of Hubei Province. After washing with tap water, adventitious roots were excised and fixed in FAA solution (Jensen, 1962). Fresh roots and rhizomes were used for apoplastic permeability tests. Hand sections were prepared using double-edged blades at specific positions: adventitious roots at 5, 10, 30, 50, 70, and 90 mm from the tip; stolons, rhizomes, and leaves at both young and mature regions. Young stems were taken from newly elongating internodes, while old stems were sampled from internodes with pith cavities after removing leaf sheaths and blades. Sections were stained with Sudan Red 7B (SR7B) for suberin (Brundrett et al., 1991), berberine hemisulfate-aniline blue (BAB) for Casparian bands and lignified walls (Seago et al., 1999; Brundrett et al., 1988), phloroglucinol-HCl (PG) for lignin (Jensen, 1962), and toluidine blue O (TBO) for general cell structure observation. Microphotographs were captured using compound optical and fluorescence microscopes.

For apoplastic permeability testing of adventitious roots and rhizomes, 30–40 mm root segments were excised, dried with tissue paper, and sealed at both ends with molten paraffin wax. Rhizome samples were prepared as internode segments with nodes at both ends, which remained unsealed. Five segments each of roots and rhizomes were subjected to berberine tracer assays. Segments were first stained with 0.05% berberine sulfate for 1 h, followed by treatment with 4.85×10^{3} g • mL^{1} potassium thiocyanate solution for another 1 h. Hand sections were then examined under fluorescence microscopy (Seago et al., 1999; Meyer et al., 2009; Meyer & Peterson, 2011).

Results

2.1 Adventitious Root Structure and Histochemistry At 5 mm from the root tip, adventitious root anatomy consisted of, from outer to inner layers: epidermis, a bilayered hypodermis, an outer cell ring, developing schizolysigenous aerenchyma, cortex, endodermis, and vascular cylinder with differentiating protoxylem and metaxylem (Fig. 1 [Figure 1: see original paper]A). By 10 mm from the tip, weak Casparian bands appeared in the radial walls of the uniseriate exodermis, accompanied by the emergence of a subepidermal sclerenchyma layer (SC) composed of small lignified cells and protoxylem elements (Fig. 1B). At 30 mm, exodermal cells enlarged and formed suberin lamellae, endodermal Casparian bands became evident, and both adjacent cortical cells and the subepidermal sclerenchyma layer began lignifying and suberizing (Fig. 1C, D). At 50 mm, endodermal Casparian bands remained weak (Fig. 1E), while both the subepidermal sclerenchyma layer and exodermal cell walls underwent lignification and suberization thickening. By 70 mm, endodermal Casparian bands were fully developed with suberin lamellae formation (Fig. 1D, F, H), followed by deposition of lignified secondary walls (Fig. 1H).

At 5 mm from the tip, root cortex exhibited schizolysigenous aerenchyma (Fig. 1A), which developed into radial lysigenous aerenchyma by 50 mm (Fig. 1F, G). The stele contained 8-12 protoxylem vessels and 2-3 metaxylem vessels (Fig. 1A, D, F, G, H). In mature roots, nearly all vascular cylinder cells had lignified into sclerenchyma tissue (Fig. 1G).

2.2 Structure and Histochemistry of Aerial Culms, Stolons, and Rhizomes Rhizomes, stolons, and aerial culms all possessed a peripheral mechanical ring (PMR) and an inner sclerenchyma ring (SCR) composed of lignified thick-walled cells, with the latter typically enclosing vascular bundles and separating cortex from the central cylinder (Fig. 2 [Figure 2: see original paper]A-H). The outer layer of the PMR contained suberin but lacked Casparian bands (Fig. 2A, B). The anatomical and aerenchyma structures of aerial culms, stolons, and adventitious roots showed similar patterns.

Young culms exhibited a thick epidermal cuticle (Fig. 2A), with numerous cells in the cortex, central cylinder, vascular bundles, sclerenchyma ring, and PMR showing suberization (Schreiber & Franke, 2011) (Fig. 2C). In mature aerial culms (Fig. 2C) and stolons (Fig. 2E), the sclerenchyma ring, vascular bundles, PMR (Fig. 2D, F), and thickened cuticle (Fig. 2B, C) all contained suberin. In mature rhizomes, both vascular bundle and PMR cells were suberized (Fig. 2G) and lignified (Fig. 2H).

Aerial culms (Fig. 2B, C) and stolons (Fig. 2E, F) developed schizolysigenous aerenchyma in the pith cavity, cortex, and within the sclerenchyma ring. Rhizome aerenchyma comprised pith cavities and cortical schizolysigenous aerenchyma (Fig. 2G, H). Both leaf sheath and blade surfaces possessed thickened cuticles on adaxial and abaxial sides (Fig. 2I, J), with vascular bundles surrounded by sclerenchyma sheaths and schizolysigenous aerenchyma. However, sclerenchyma layer cells in leaves were not suberized.

2.3 Permeability of Apoplastic Barriers in Adventitious Roots and Rhizomes Berberine tracer assays revealed barrier permeability characteristics. Under UV illumination, from outer to inner tissues, root epidermis, hypodermis, endodermis with adjacent cortex, stele, and rhizome PMR exhibited weak autofluorescence (Fig. 3 [Figure 3: see original paper]A, B).

In segments treated with berberine alone, endodermal cell walls and hypodermal layers in roots, and epidermis and PMR in stems showed weak brown autofluorescence. Berberine thiocyanate crystals attached to root exodermal cell walls, while the subepidermal sclerenchyma layer emitted strong yellow fluorescence (Fig. 3C, D).

Following treatment with both berberine and potassium thiocyanate, endodermal and sclerenchyma layer cell walls in roots and epidermal cells in rhizomes showed intense orange fluorescence due to strong berberine absorption (Fig. 3E, F). Unstained aerenchyma revealed berberine thiocyanate crystals within ruptured exodermis (Fig. 3E). After dual treatment, ruptured exodermis in both roots and rhizome internodes contained berberine thiocyanate crystals emitting strong yellow fluorescence (Fig. 3G, H), with central sclerenchyma in roots showing strong yellow autofluorescence (Fig. 3E, G). These results demonstrate that root exodermis and sclerenchyma layers, along with rhizome epidermis and outer cortex, effectively absorb and block ion entry into inner tissues.

Discussion

Our investigation of *Zizania latifolia* anatomical and histochemical characteristics builds upon previous research on wetland and amphibious plants in the Jianghan Plain, including bermudagrass (*Cynodon dactylon*), knotgrass (*Paspalum paspaloides*), centipedegrass (*Eremochloa ophiuroides*), limpograss (*Hemarthria altissima*), and cogon grass (*Imperata cylindrica*) (Yang et al., 2015; Yang and Zhang, 2013; Zhang et al., 2013). International studies have similarly examined root and rhizome anatomy in rice (*Oryza sativa*), mannagrass (*Glyceria maxima*), pickerelweed (*Pontederia cordata*), common reed (*Phragmites australis*), silvergrass (*Triarrhena sacchariflora*), and cattail (*Typha orientalis*) (Soukup et al., 2007; Seago et al., 1999; McManus et al., 2002; Watanabe et al., 2006).

The adventitious root anatomy of *Z. latifolia* follows a consistent pattern from outer to inner layers: epidermis, exodermis, sclerenchyma mechanical tissue layer, cortex, endodermis, and vascular cylinder. The barrier structure comprises an inner endodermis with adjacent suberized cells and an outer exodermis, identical to reported wetland plants including bermudagrass, knotgrass, cogon grass, rice, and common reed (Yang et al., 2011; Zhang et al., 2013; Watanabe et al., 2006; Simone et al., 2003). The endodermis represents a typical feature among herbaceous plant roots (Yang et al., 2011). The exodermis resembles that of mannagrass (Soukup et al., 2007), though mannagrass lacks the thick-walled mechanical tissue layer despite having thickened secondary walls. The predominantly radial lysigenous aerenchyma in *Z. latifolia* roots characterizes many wetland species (Seago et al., 2005; Jung et al., 2008; Sangster, 1985), indicating similar barrier structures across wetland and drought-adapted plants.

Stem anatomy (including stolons, rhizomes, and aerial culms) progresses from outer to inner layers as: cuticle, epidermis, PMR, cortex, SCR, and pith cavity. Aerenchyma includes cortical aerenchyma and pith cavities. The stem barrier structure consists of an inner sclerenchyma mechanical tissue layer, outer cuticle, and PMR, with cell walls exhibiting Casparian bands, suberin, and lignin deposition. *Zizania* stems differ from those of bermudagrass, knotgrass, limpograss, and centipedegrass in two key aspects. First, while *Z. latifolia* possesses lignified and suberized PMR layers—common in herbaceous stems and leaves (Fahn, 1990; Evert et al., 1996)—its vascular bundle cells are both lignified and suberized, unlike the exclusively lignified bundles in the comparative species. However, the

PMR and SCR in *Z. latifolia* stems contain fewer cell layers than in bermudagrass and knotgrass, suggesting that while the species is hygrophytic and can tolerate brief water deficits, it cannot survive xeric conditions. The relatively thin sclerenchyma layers lead to excessive water loss and cellular desiccation under prolonged drought.

Second, *Z. latifolia* aerial culms and stolons possess both lignified and distinctly suberized sclerenchyma rings, whereas bermudagrass, centipedegrass, knotgrass, and limpograss exhibit only lignified sclerenchyma layers (Yang et al., 2011). Unlike other Poaceae such as mannagrass (Metcalfe, 1960), *Zizania* stems contain sclerenchyma layers connecting the inner vascular bundle ring. Cattail lacks exodermis and endodermis with Casparian bands (Yang et al., 2011). *Zizania* stolon epidermal cells resemble those of other stoloniferous grasses like cattail and bermudagrass (Yang et al., 2011; McManus et al., 2002) in having thickened cuticles, but differ in showing minimal epidermal suberization (Schreiber & Franke, 2011).

The aerenchyma system of *Z. latifolia*, comprising root aerenchyma, stem cortical aerenchyma, and pith cavities, parallels that of bermudagrass, centipedegrass, limpograss, and silvergrass (Seago et al., 2005; Jung et al., 2008; Yang et al., 2011; Sangster, 1985). The schizolysigenous aerenchyma dissolution in stems and leaves represents a normal developmental process. These continuously forming air spaces (Kawai et al., 1998) facilitate oxygen storage and transport to other organs under hypoxic conditions (Armstrong et al., 2006; Vartapetian & Jackson, 1997), representing an effective wetland adaptation.

Apoplastic barriers in *Z. latifolia* primarily reside in the root exodermis and endodermis, and in the stem PMR. These barriers show many similarities to typical wetland plants such as bermudagrass, centipedegrass, limpograss, common reed, knotgrass, and cattail. However, the PMR contains fewer cell layers compared to bermudagrass, and the inner mechanical tissue layer is less developed. We hypothesize that under xeric conditions, these protective tissues provide limited defense, leading to rapid water loss and inability to maintain turgor and structural integrity (Meyer et al., 2009; McManus et al., 2002; Tan et al., 2009; Yang et al., 2011; Wang et al., 2008). In wetland environments, these barrier structures effectively restrict uncontrolled diffusion of oxygen and ions between the plant and its surroundings (Meyer et al., 2011; Krishnamurthy et al., 2011).

In summary, our investigation of *Z. latifolia* anatomical and histochemical features, compared with other wetland and amphibious plants adapted to aquatic and terrestrial habitats, reveals that the relatively thin peripheral mechanical and sclerenchyma layers in stems predispose the species to water loss under xeric conditions, preventing maintenance of cellular turgor and drought tolerance. This clarifies the limitations of its distribution to wetland environments. These findings on vegetative anatomy provide valuable insights for the effective utilization of wetland plant resources and the restoration of vegetation in the Three Gorges Reservoir drawdown zone and degraded wetlands of the Jianghan

Plain.

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