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Anatomical and histochemical traits of roots and stems of *Artemisia lavandulaefolia* and *A. selengensis* (Asteraceae) in the Jianghan Floodplain, China

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A R T I C L E I N F O

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A B S T R A C T

The present study examined the perennial, rhizomatous *Artemisia lavandulaefolia* and *A. selengensis* (Asteraceae) to determine anatomical and histochemical traits which allow them to be adapted during the seasonal flooding in the Jianghan Floodplain of the Yangtze River in China. Root, rhizome, and aerial stems with leaves of the two *Artemisia* species were obtained from flooded conditions in the Jianghan Floodplain. *Artemisia lavandulaefolia* and *A. selengensis* have generally similar root and stem anatomies, including their barrier layers; endodermis and hypodermal exodermis with Casparian bands and suberin lamellae are present in both organs. The hypodermis becomes multi-layered and peridermal in roots and rhizomes of both species, but aerial stems produce a periderm only in *A. lavandulaefolia*. Leaves lack the barrier layers. *Artemisia lavandulaefolia* roots and stems produce more secondary xylem and phloem than *A. selengensis* at the stages studied. *Artemisia lavandulaefolia* has only schizogenous aerenchyma, whereas *A. selengensis* develops a conspicuous cortical expansi-schizogenous aerenchyma and aerial stem pith cavities. These combinations of traits enable *A. lavandulaefolia* and *A. selengensis* to be well adapted to the seasonal flooding of the Jianghan Floodplain of the Yangtze River in China.

1. Introduction

Unlike the monocot grasses of the Jianghan Floodplain of the Yangtze River, China (Yang et al., 2011, 2014; Zhang et al., 2017), *Artemisia lavandulaefolia* and *A. selengensis* are members of the eudicot family, Asteraceae; they are perennial, rhizomatous plants that can survive seasonal flooding in the floodplain. As noted by Vallés and McArthur (2001), only two species of *Artemisia*, *A. cana* and *A. molinieri*, occur in habitats which can be temporarily inundated. However, as we have observed in the Jianghan Floodplain under various conditions, including flooding, *A. lavandulaefolia* is a difficult to eradicate weed which sprouts in the spring (Xing and Yang, 2004), while *A. selengensis* is a fragrant vegetable which sprouts in the winter (Zheng et al., 2001), that is, they appear differently in the floodplain.

Many structural features of members of the genus, *Artemisia*, have been reported by Milhofer (1933), Obermeyer (1936), Metcalf and Chalk (1950a,b), Noorbakhsh et al. (2008), and Konowalik and Kreitschitz (2012). In drawings, both Obermeyer (1936) and Metcalf and Chalk (1950a,b) reported a stem endodermis in some species, including the non-wetland plants like *A. absinthium*, and Obermeyer (1936) noted leaf endodermis around vascular bundles; photographs of *A. absinthium* by Konowalik and Kreitschitz (2012) did not reveal a stem endodermis. The presence of cork, i.e., periderm, has also been reported (Tetley, 1925; Obermeyer, 1936; Diettert, 1938; Moss, 1940; Metcalfe and Chalk, 1950a,b).

Characteristics of plants which occupy waterlogged or submerged environments include the air spaces and aerenchyma that facilitate oxygen movement and survival (Armstrong et al., 2000, 2006; Colmer et al., 1998; Justin and Armstrong, 1987; Seago et al., 2005). These are usually associated with important cortical apoplastic barriers like endodermis and exodermis, as noted by Abiko et al. (2012), Armstrong et al. (2000), Colmer (2003), Colmer et al. (1998), Enstone et al. (2003), Kotula and Steudle (2009), McManus et al. (2002), Meyer and Peterson (2011), Ranathunge et al. (2003, 2011a,b), Schreiber et al. (2005), Seago et al. (1999, 2000a,b), Soukup et al. (2002, 2007), and Zhang et al. (2017). Furthermore, where some secondary growth occurs, expansion of endodermis and exodermis via dilation (Šottníková and Lux, 2003) and the formation of hypodermal periderm with cork (Lux et al., 2011; Meyer and Peterson, 2011) may be relevant features for evolutionarily derived species and their adaptations to flooding.

In our analyses presented here, we find that adventitious roots, rhizomes, and aerial stems form barrier layers in *A. lavandulaefolia* and

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Fig. 1. *Artemisia* species in habitat settings. Scale bars = 10 cm.
1A. *Artemisia lavandulaefolia*.
1B. *Artemisia selengensis*.

Table 1
The comparative structures and histochemistry of *Artemisia lavandulaefolia* and *A. selengensis*.

Organ samples	*Artemisia lavandulaefolia*	*A. selengensis*
adventitious roots	vascular cylinder has primary and secondary structures; schizogenous aerenchyma in cortex; dilation endodermis and exodermis; endodermis, uniseriate exodermis, and periderm with Casparian bands, suberin lamellae, and lignin	vascular cylinder have primary and less secondary structure; large schizogenous aerenchyma in cortex; dilation endodermis and exodermis; endodermis, uniseriate exodermis, and periderm with Casparian bands, suberin lamellae, and lignin
rhizomes	pith; vascular bundles have primary and secondary structures; small schizogenous aerenchyma in cortex; dilation endodermis and exodermis; endodermis, multiseriate exodermis, and periderm with Casparian bands, suberin lamellae, and lignin; cuticle	pith; vascular bundles have primary and less secondary structures; expansi-schizogenous aerenchyma in cortex; dilation endodermis and exodermis; endodermis, multiseriate exodermis, and periderm with Casparian bands, suberin lamellae, and lignin; cuticle
aerial stems	pith with pith cavity; vascular bundles have primary and secondary structures; schizogenous aerenchyma in cortex; endodermis, uniseriate exodermis and periderm with Casparian bands, suberin lamellae, and lignin; cuticle	pith with pith cavity; vascular bundles have primary and less secondary structures; schizogenous aerenchyma in cortex; endodermis, uniseriate exodermis with Casparian bands, suberin lamellae, and lignin; no periderm; cuticle
leaves	lignified xylem and phloem fibers, parenchyma, mesophyll, cuticle	lignified xylem and phloem (in large cluster) fibers, parenchyma, mesophyll, cuticle

A. selengensis under moderate, early season wetland conditions, but leaves do not. Our understanding of endodermis and exodermis and their possible roles in structure and function in these plants is enhanced by apoplastic permeability tests. These features show their adaptabilities to the Jianghan Floodplain of the Yangtze River.

2. Materials and methods

Artemisia lavandulaefolia (Fig. 1A) and *A. selengensis* (Fig. 1B) specimens were obtained from mature plants in wetland growth conditions during May from the Jianghan Floodplain, China, but mature leaves were collected in late season, October.

2.1. Anatomy and histochemistry

Roots, rhizomes, and leafy aerial stems (or stems) were studied as follows: for representative sections of root tips, distal sections of roots were sectioned within 50 mm (10–50 mm) of the root tips and proximal sections were 70–90 mm behind the tips of 90–180 mm long adventitious roots. For the 80–750 mm long rhizomes, distal sections were within 10–20 mm of the rhizome tip and proximal sections were beyond 30 mm from the tip. For 80–360 mm long stems, distal sections came from 10 to 20 mm of the stem tips and proximal sections from greater than 30 mm from their tips. Leaves were sectioned at the distal petiole or at the point of connection of petiole to blade, and in middle regions of a blade. The specimens were processed fresh or fixed in FAA, rinsed in deionized water, and stored in 70% ethanol preparatory to sectioning (Jensen, 1962).

Roots, rhizomes, stems, and leaves of *A. lavandulaefolia* and *A. selengensis* samples were cut freehand with two-sided blade under a stereoscope. Sections were left unstained or were stained with toluidine blue O (TBO) or Sudan III, berberine hemisulfate–aniline blue (BAB) for Casparian bands and thickened cell walls and lignin (Brundrett et al., 1988; Seago et al., 1999), Sudan red 7 B (SR7B) for suberin lamellae (Brundrett et al., 1991), and phloroglucinol–HCl (Pg) for lignin (Jensen, 1962). Samples were observed under light and/or epifluorescence microscopy and photographed as described by Yang et al. (2011).