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Research paper

Tylosis formation and fungal interactions in an Early Jurassic conifer from northern Victoria Land, Antarctica

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ABSTRACT

Well-preserved fungi occur in permineralized conifer axes from the Lower Jurassic of northern Victoria Land, Antarctica. The fungus is characterized by septate hyphae extending through the vascular ray system via penetration of cross-field pits. Tyloses are present in large numbers and might have been effective as a physical restraint to the spread of the fungus. However, knotted fungal hyphae within and around the tyloses suggest that the fungus was able to surmount the barriers. Hyphae are also present in the secondary phloem. This plant–fungal interaction contributes to a better understanding of the antagonistic relationships that existed between pathogenic fungi and conifers in the Jurassic paleoecosystems of Antarctica, as well as providing evidence of interactions between fungi and tyloses in Mesozoic wood.

1. Introduction

Fungi are an integral part of virtually all modern ecosystems. One of the most recognized and important ecological roles fungi perform includes decomposition and nutrient cycling. In extant forest ecosystems, fungi are the primary organisms responsible for the delignification and degradation of wood (Dighton et al., 2005). Some wood-decay fungi may also be effective as parasites and causal agents of mild to severe diseases. Tracheary elements in the heartwood of living plants (i.e., tracheids and/or vessels) are hollow and dead at maturity, and thus do not provide any physiological barrier against the spread of pathogenic fungi. The living outermost wood portion, i.e., sapwood, however, exhibits various types of defense strategies in order to deter or prevent the infestation of wood by pathogenic microorganisms. An initial process includes wood discoloration caused by the accumulation of a variety of extractives (e.g., tannins, dyestuffs, oils, gums, resins, salts of organic acids) that are deposited around an infected area (Pallardy, 2008). When these extractives are overcome by the pathogen, additional defense measures include the production of tyloses (e.g., Barry et al., 2001). Tyloses are suberized structures that develop from ray parenchyma cells and project through pits to occlude the lumina of tracheids and vessels (Pearce, 1996). Tylosis formation is one of the main processes in the compartmentalization of decay in trees (CODIT model, e.g., Shigo, 1984) and serves to slow down or prevent the spread of pathogens. In addition, tyloses can form around wounds to prevent water loss, even in the absence of decay, in the nonfunctional xylem. Morphologically and functionally comparable structures in the sieve cells of phloem are termed tylosoids (Evert, 2006).

An extensive fossil record of tylosis formation demonstrates that the production of these protrusions has been a common process in woody plants since at least the late Paleozoic. The earliest reports of tyloses in fossil plants come from the Carboniferous, and include a progymnosperm (Scheckler and Galtier, 2003) and several ferns (Williamson, 1876; Weiss, 1906; Phillips and Galtier, 2005, 2011). Tyloses or tylosis-like structures have also been described in the Triassic gymnosperm wood, *Protocedroxylon mineense* (Ogura) Nishida et Oishi (Ogura, 1960; Nishida et al., 1977; Nishida and Oishi, 1982), as well as the Jurassic woods *Metacedroxylon scoticum* Holden (Holden, 1915) and *Xenoxylon morrisonense* Medlyn et Tidwell (Medlyn and Tidwell, 1975). Cretaceous and Cenozoic permineralized woods have yielded abundant reports on the presence of tyloses in fossil angiosperms (Jeffrey, 1904; Bancroft, 1935; Spackman, 1948; Brett, 1960; Manchester, 1983; Nishida et al., 1990; Privé-Gill et al., 1999; Castañeda-Posadas et al., 2009). However,

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information on whether tyloses in fossil plants formed specifically in response to infestation with fungi or other pathogens has so far been lacking and thus the evolutionary history of tylosis formation as a particular defense strategy against pathogens remains unresolved.

In this contribution, we present permineralized conifer axes from the Lower Jurassic of Antarctica that contain numerous tyloses in both the wood and bark in association with fungal remains. What is most significant about these fossils is that the tyloses co-occur with fungal hyphae in the tracheids in a pattern suggestive of tylosis formation as a direct response to fungal colonization.

2. Materials and methods

The three permineralized axes used in this study were collected during the Ninth German Antarctic North Victoria Land Expedition (GANOVEX IX 2005/2006) on Suture Bench, a small bench east of the Gair Mesa in northern Victoria Land, Transantarctic Mountains, East Antarctica. At this site, *in situ* tree trunks occur within the early Toarcian (late Early Jurassic) Kirkpatrick lavas of the Ferrar Group (Bomfleur et al., 2011). The specimens were collected from slope debris directly underneath the base of the lava flows. Acetate peels (Galtier and Phillips, 1999) and thin sections were prepared according to standard techniques (Hass and Rowe, 1999). Pieces of the specimens were mounted on microscope slides using a Hillquist epoxy compound and cut with a Buehler Petrothin® thin-sectioning machine to a thickness of ~250 μm. The wafer was subsequently ground down to a thickness of ~65 μm and analyzed using a Leica DM5000B transmitted-light compound microscope. Digital images were taken with a Leica DC500 digital camera attachment and minimally processed using Adobe Photoshop CS4 Version 11.0.2 (1990–2010, Adobe Systems). Multiple micrographs of the same specimen at different focal planes were compiled to produce composite images (e.g., Bercovici et al., 2009). The images were stacked in Adobe Photoshop CS4 and specific areas were erased to reveal the full three-dimensional view that can be seen through the thin sections. Measurements were taken using ImageJ 1.43u software (Abramoff et al., 2004). Specimens and slides are temporarily deposited in the Paleobotanical Collections, Natural History Museum and Biodiversity Institute, University of Kansas, under specimen accession numbers GIX-SB-007; GIX-SB-014; GIX-SB-036, acetate peel slide accession number AP-GIX-SB-007-CT2-01, and thin section slide accession numbers TS-GIX-SB-007-01; TS-GIX-SB-014-01; TS-GIX-SB-036-01; TS-GIX-SB-036-02.

3. Description

3.1. Wood and secondary phloem

Specimens represent segments of conifer axes with secondary xylem and phloem (Plate I, 1). The most complete and best-preserved specimen is a stem portion with an estimated original diameter of approximately 15 cm. Most of this axis consists of secondary xylem with numerous intercalated rays. Tracheids are polygonal in transverse section and about 20–30 μm in diameter (Plate I, 2). The wood has abundant, evenly distributed uniseriate rays that are 5–8 cells tall (Plate I, 3). Extraxylary tissue is preserved along the outer portion of the axis. Secondary phloem cells are of two principal types: a larger and more prevalent type with diameters up to 75 μm and a smaller, less common type with diameters between 18 and 35 μm (Plate I, 4). The larger cells show distinct concentric layers within the cell wall. The radial walls of the tracheids are further characterized by uniseriate circular-bordered pits with wide borders and narrow apertures (Plate I, 5).

Many of the conifer axes from the Suture Bench locality are *in situ* trunks with well-preserved secondary phloem layers; however, the preservation of the wood is overall very poor. In many sections of the specimen described here, the thick S_2 layer of the tracheid walls appears diffusely degraded and somewhat translucent. The cell walls may further show a separation and detachment of intact S_3 layers, which occur isolated and twisted within the cell lumens (Plate I, 6). In other cases, the boundaries of individual cells are represented by translucent outlines in which it is difficult to determine tracheid wall thickness. Discrete damage structures, such as erosion channels, lysis zones, bore holes, or cavities have not been observed. The ray parenchyma is decomposed to varying degrees; in some areas, the original distribution of rays is recognizable only by opposite pairs of tyloses.

3.2. Tyloses

Abundant tyloses are found along rays in the specimens and are not concentrated in any specific area, e.g., close to ring boundaries. They originate from ray parenchyma cells and each ray cell may produce more than one tylosis; most commonly, tyloses occur in the form of one or more opposite pairs per ray cell (Plate I, 7, 8). One ray parenchyma cell will balloon out through cross-field pits into the adjacent tracheids (Plate I, 9). Tyloses occur in different size ranges (8–25 μm in diameter), and have different morphologies that occlude the tracheid lumen entirely. During development, tyloses are initially small, bulbous protrusions with an undistinguishable base (Plate I, 10). Intermediate stages are

Plate I.

1. Overview of specimen with secondary xylem and phloem cells. Scale bar = 500 μm. AP-GIX-SB-007-CT2-01.
2. Transverse section of secondary xylem in thin section. Due to the relatively poor preservation of the wood, note the difficulty of distinguishing tracheids from rays. Scale bar = 100 μm. TS-GIX-SB-036-02.
3. Tangential section of secondary xylem; note narrow rays. Scale bar = 200 μm. TS-GIX-SB-036-01.
4. Transverse section of preserved phloem in thin section, showing large cells (#) and small cells (*). Note the hypha crossing one of the small cells and the thick, coiled contents of the larger cells. Scale bar = 25 μm. TS-GIX-SB-007-01.
5. Radial section of a tracheid with uniseriate circular-bordered pits. Scale bar = 25 μm. TS-GIX-SB-036-01.
6. Wood in transverse section showing degraded S_1–S_2 layers of the tracheid cell walls. Scale bar = 25 μm. TS-GIX-SB-036-02.
7. Transverse section of wood showing crushed vascular ray (dark line in center), with tyloses in adjacent tracheids. Scale bar = 25 μm. TS-GIX-SB-036-01.
8. Longitudinal section of wood with vascular ray (R) and tyloses in adjacent tracheids. Scale bar = 25 μm. TS-GIX-SB-036-01.
9. Tangential section of tracheids showing a large tylosis (center) ballooning through a cross-field pit into an adjacent tracheid. Scale bar = 25 μm. TS-GIX-SB-036-01.
10. Initial stage of tylosis development. Tyloses at this stage are small, bulbous protrusions with no discernable base. Scale bar = 10 μm. TS-GIX-SB-036-01.
11. Intermediate stage of tylosis development. Tyloses are morphologically similar to initial stage but are large and have a more distinguishable base. Scale bar = 10 μm. TS-GIX-SB-036-01.
12. Final stage of tylosis development. Fully developed tyloses are large bulbous structures that occlude the lumen of the tracheid and have a characteristic narrow base. Scale bar = 10 μm. TS-GIX-SB-036-01.
13. Tylosis with dark, filled lumen. Scale bar = 25 μm. TS-GIX-SB-036-01.
14. Fungal hypha with a right-angled septation. Scale bar = 25 μm. TS-GIX-SB-036-01.
15. Longitudinal section of a tracheid with a hypha extending through its lumen (arrows). Scale bar = 25 μm. TS-GIX-SB-036-01.
16. High degree of hyphal knotting inside a single tylosis. Wall of tylosis indicated by arrows. Scale bar = 10 μm. Note this is a composite image. TS-GIX-SB-036-01.