The Evolution of Cell WallBiochemistry in Fossil and Living Plants

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Understanding of vascular cell wall chemistry in living plants as well as their geochemical derivatives, fossils and coal, has begun to be revised dramatically with the capability of submicron-scale resolution of the distribution of biochemical constituents afforded by X-ray imaging techniques. The tracheid cell type of vascular plants serves both as the conduit of water transport and as the primary source of structural support. During the Devonian Era, the evolution of tracheids triggered the large and rapid evolutionary radiation of the vascular plants into a wide variety of growth forms beyond the narrow range available to the morphologically simple, moss-like plants that preceded this radiation. Tracheids are dead and evacuated of cell contents at maturity, so their functional attributes are determined by the detailed structure of their elaborately thickened and pitted cell wall. The primary wall constituents are hydrophilic carbohydrates, such as cellulose, and the hydrophobic polyphenolic compound lignin. The wall is made up of 5 or 6 layers that have varying lignin/carbohydrate ratios and are each less than a micron thick. Investigation of this cell wall layering with Scanning Transmission X-ray Microscopy (STXM) and X-ray absorption near edge spectroscopy (C-XANES), provides the opportunity for testing hypotheses concerning the geochemical preservation of different wall compounds and the study of the evolution of plant physiology in fossil and living plants.

Potential of geochemical preservation of plant biochemistry

Organic matter preserved in cell walls of permineralized plant fossils was analyzed using STXM and XANES at energies near the 1s absorption edge of carbon. Individual tracheid walls of fossils exhibit spatially distinct chemical zoning inherited from original wall biopolymers and cell wall microstructure. This zonation reflects the deposition of lignin and structural polysaccharides in Devonian plants following biochemical and developmental pathways similar to those of living tracheophytes. An important conclusion of this study is that, although chemically transformed, carbon derived from carbohydrate is retained in the fossil, overturning a widely held expectation of the paleontological and geochemical communities that such labile chemical constituents are lost early in diagenesis and that coal has largely been derived only from lignin. This will require a revised understanding of the carbon cycle and new recognition of the potential of a broader range of molecular contributors to the organic burial sink.

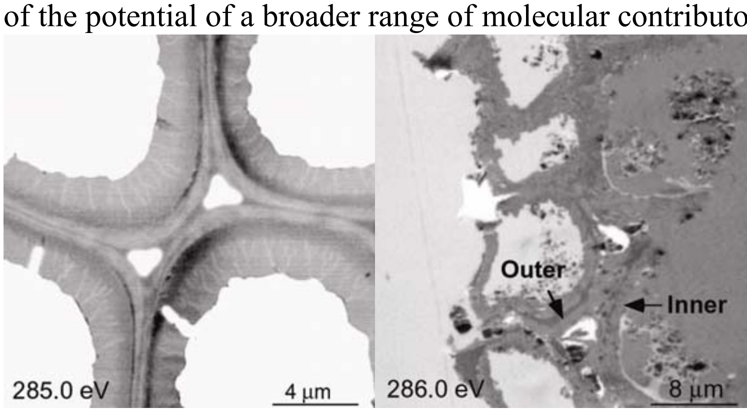

Figure 1: X-ray images of wood at frequencies for which absorption is by aromatic carbon. Differentiation seen in living plants (left) reflects varying lignification of cell wall layers. Persistence of layering in fossils (right) indicates that both lignin and polysaccharides contribute to preserved organic matter. (From Boyce et al. 2002.)

Vascular cell evolution documented in 400 million year old fossils

Anatomically preserved land plant fossils from the Lower Devonian Rhynie Chert contain conducting tissues with cells that range from dark colored, elongated cells without secondary wall thickenings to tracheids similar to those of extant vascular plants. X-ray spectromicroscopy in conjunction with isotope ratio mass spectrometry of Rhynie Chert fossils suggests that the earliest vascular thickenings were probably unlignified and that cell wall lignification may have first appeared in unrelated tissue types. Only later, it seems, was lignin deposited in conducting cells to produce the true tracheids seen today in vascular plants. Therefore, the explosive radiation of vascular plants that completely refigured terrestrial ecosystems was not associated with the initial evolution of the lignin biochemical pathway, but with the novel reconfiguration of characteristics preexisting in much simpler ancestors.

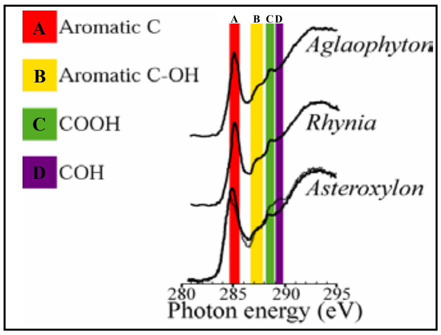

Figure 2: X-ray absorption spectra of Lower Devonian Rhynie Chert fossils. The vascular plant *Asteroxylon* posseses chemically distinct tracheid wall layers similar to those of living plants. This characteristic is lacked by the pre-vascular plant fossil *Aglaophyton* and the intermediate fossil *Rhynia* from the same locality. (From Boyce et al. 2003.)

The link between vascular cell wall biochemistry and physiology in living plants

Lignin imparts water impermeability and strengthens walls by excluding water that would otherwise disrupt hydrogen bonding within cellulose fibers. However, lignin also is metabolically expensive, its hydrophobicity can disrupt other aspects of hydraulic transport, and its presence prevents any further changing of cell size and shape--a problem in growing tissues. Because of these trade offs, the details of the fine-scale distribution of lignin and cellulose within tracheid walls will determine such functional characteristics as the capacity for structural support across different plant architectures, the resistance to water transport (and thereby all modeling of plant hydraulics), and the ability of the plant both to limit the spread of air pockets after the failure of a water stream and to refill tracheids with water after such failures. X-ray microscopy has been used to demonstrate that the fine-scale patterning of lignin deposition in water-conducting cells varies greatly across the vascular plants and in tight correlation with important hydraulic properties (Boyce et al. in review). The evolutionary diversification of vascular cells, thus, reflects biochemical as well as morphological innovations evolved to fulfill opposing cell functions of transport and structural support. More broadly, a detailed understanding of tracheid microstructure across a variety of plant lineages may greatly influence our understanding of the evolutionary and ecological radiation of plants across the immense diversity of environments and growth forms seen in the world today.

References:

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