

STRUCTURE AND BIOGENESIS OF THE CELL WALLS OF GRASSES

Nicholas C. Carpita

Department of Botany and Plant Pathology, Purdue University, West Lafayette, Indiana
47907

KEY WORDS: cereals, grasses, cell-wall polysaccharides, cell-wall biosynthesis, cell-wall architecture

ABSTRACT

The chemical structures of the primary cell walls of the grasses and their progenitors differ from those of all other flowering plant species. They vary in the complex glycans that interlace and cross-link the cellulose microfibrils to form a strong framework, in the nature of the gel matrix surrounding this framework, and in the types of aromatic substances and structural proteins that covalently cross-link the primary and secondary walls and lock cells into shape. This review focuses on the chemistry of the unique polysaccharides, aromatic substances, and proteins of the grasses and how these structural elements are synthesized and assembled into dynamic and functional cell walls. Despite wide differences in wall composition, the developmental physiology of grasses is similar to that of all flowering plants. Grass cells respond similarly to environmental cues and growth regulators, exhibit the same alterations in physical properties of the wall to allow cell growth, and possess similar patterns of wall biogenesis during the development of specific cell and tissue types. Possible unifying mechanisms of growth are suggested to explain how grasses perform the same wall functions as other plants but with different constituents and architecture.

CONTENTS

INTRODUCTION	446
THE STRUCTURAL ELEMENTS OF THE PRIMARY WALLS OF THE POACEAE	447
<i>Cellulose</i>	447
<i>Glucuronoarabinoxylans</i>	447
<i>The (1→3),(1→4)-β-D-glucans</i>	448

<i>Xyloglucan</i>	450
<i>Other Glycans</i>	450
<i>Pectic Substances</i>	450
<i>Aromatic Substances</i>	451
<i>Structural Proteins</i>	453
<i>Other Cell-Wall Substances</i>	454
CELL-WALL COMPOSITION AS A TAXONOMIC CHARACTER IN THE MONOCOTYLEDONAE	454
ARCHITECTURE	458
STRUCTURAL DYNAMICS DURING CELL ELONGATION	462
CELL-WALL BIOGENESIS IN GRASSES.	465
<i>Biosynthesis of (1→3),(1→4)-β-D-Glucan</i>	466
<i>Biosynthesis of Other Cell-Wall Polysaccharides</i>	467
GENETIC MODELS OF CELL-WALL DEVELOPMENT IN THE GRASSES	467

INTRODUCTION

In the early 1900s, Walter Norman Haworth and Edmund Langley Hirst, founding fathers of modern carbohydrate chemistry, began studies of the pentose constituents of cell walls of plants. Armed with only rudimentary analytical techniques, they and their colleagues defined the cell walls of esparto grass as composed largely of (1→4)-β-D-xylans (58). By 1970, gas chromatography–mass spectrometry (GC-MS) was employed routinely for unequivocal determination of linkage structure of complex cell-wall polysaccharides. Techniques such as ¹H- and ¹³C-nuclear magnetic resonance (NMR) spectroscopy provided anomeric configurations, linkage structures, and some three-dimensional configurations. Sequence-dependent endoglycanases were used to cleave polysaccharides into oligosaccharides that could be completely sequenced. From characteristic repeating unit structures, the sequence and conformation of very large polymers were deduced (20). By such analyses, the major polysaccharides of the walls of a wide range of flowering plants were defined, and the first models of how cell walls are put together emerged. In subsequent years, the dynamic interactions of individual components were reflected in more current models of the architecture of the primary cell wall of flowering plants—a strong framework of cellulose microfibrils intertwined with xyloglucans that is embedded in a gel of uronic-acid-rich pectins and cross-linked with hydroxyproline-rich glycoproteins (20, 101).

When the first conceptual models were proposed about twenty years ago, the differences in wall compositions between monocots and dicots were just beginning to be catalogued (33). Perhaps because of the socioeconomic importance of the cereals, the vast majority of the monocots studied were grasses. Whistler (164) described grasses as rich sources of xylan, and Aspinall (1), in a review of plant cross-linking glycans, noted the enrichment of xylans and mixed-linked glucans in grasses. Wilkie (165) offered the first comprehensive survey of the cross-linking glycans of grasses. More recent

studies of the carbohydrate and aromatic components of cell walls from a broad spectrum of monocots have revealed that the Poales (family Poaceae, formerly the order Graminales, family Gramineae), their progenitors, and related taxonomic orders have primary cell walls completely different from those of other monocots (3, 20, 68). Dahlgren et al (32) proposed phyletical relationships between some two dozen orders of the Monocotyledonae on the basis of several anatomical features and chemical constituents. One of these features, the presence or absence of ferulic acid in the primary walls, is a major distinguishing feature of the Poales and related orders (56). Nonlignified cells of grasses are enriched in aromatic substances, and polymeric forms constitute a second architectural element.

A third type of architectural element is structural protein. The primary walls of the Poales contain substantially less protein than other species, but several classes of proteins are found in elevated amounts in specific cell types during differentiation. Recent reviews (83, 147) note that the grass wall proteins bear reasonable homology to those representing major classes of structural proteins of nongramineous species. In an earlier review (20), structural models for two types of primary walls were provided: the Type I wall, composed of a cellulose-xyloglucan framework embedded in a pectin gel, and the Type II wall, the special wall of the Poales. This review focuses on the Type II wall of the Poales, its composition, architecture, biogenesis, and dynamics during growth.

THE STRUCTURAL ELEMENTS OF THE PRIMARY WALLS OF THE POACEAE

Cellulose

Cellulose microfibrils in all flowering plants are composed of about three dozen linear chains of (1→4)- β -linked D-Glc condensed to form long paracrystalline arrays that spool around each cell (35). Although each chain may be only several thousand units long, they begin and end at different places within a microfibril and make very long microfibrils whose ends are rarely detected.

Glucuronoarabinoxylans

The linkage structure of the grass glucuronoarabinoxylans (GAX) has been known for much of the 20th century. The *t*- α -L-arabinofuranosyl units are attached primarily at the *O*-3 positions along the (1→4)- β -D-xylan backbone, and the *t*- α -D-glucuronic acids are attached to the *O*-2 positions (1, 165). The highly substituted GAXs of the barley aleurone and barley malts contain significant *O*-2- and doubly branched *O*-2, *O*-3-linked arabinosyl units in addition to the abundant *O*-3-linked units (5, 160). Arabinoxylans are widespread in the walls of all flowering plants, but in nongramineous species the polymer