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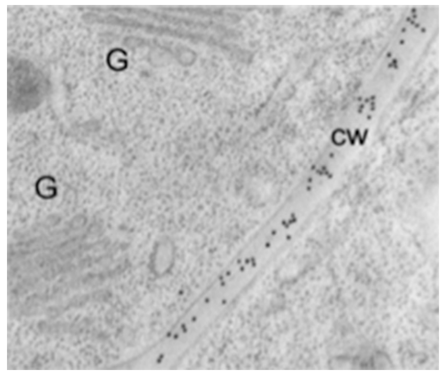
IN BRIEF

Uncovering the Unexpected Site of Biosynthesis of a Major Cell Wall Component in Grasses

Plant cell walls, like the walls in your room, offer protection, stability, and structure. Unlike the walls around you, however, plant cell walls aren't rigid and static; they are, in fact, "smart" walls! While cell walls are tough enough to handle strong osmotic pressure from within, as well as an onslaught of biotic and abiotic stresses, they are also wonderfully dynamic and complex, altering their structures throughout cell division, expansion, and differentiation. Cell walls are primarily composed of rigid cellulose microfibrils embedded within a gel-like matrix of polysaccharides and glycoproteins, which vary among plant species. Whereas the polysaccharides pectin and xyloglucan are abundant in the cell walls of most land plants, the cell walls of noncommelinoid monocots such as grasses (Poaceae) are rich in (1,3; 1,4)-β-D-glucans, also known as mixed-linkage glucans (MLGs), which likely form a gel-like matrix during cellular expansion (Kiemle et al., 2014). The biosynthesis of cell wall polysaccharides takes place via the action of two classes of enzymes: polysaccharide synthases (enzymes of the carbohydrate active enzymes [CAZy] family GT2, with multiple membrane-spanning domains that reside in the plasma membrane or Golgi) and type II glycosyltransferases (which reside in the Golgi). Among the many polysaccharide synthase genes, cellulose synthase-like (*CSLA-K*) genes encode the backbones of a wide range of polysaccharides. For example, *CSLF6* is responsible for most MLG biosynthesis in grasses, although *CSLH1* may play a minor role in this process (Doblin et al., 2009). Based on large amounts of biochemical and immunochemical data, cell wall matrix polysaccharides are synthesized and assembled in the Golgi, although whether this is the case for MLG has long been a matter of controversy. A study by **Wilson et al. (2015)** helps settle this issue, providing compelling evidence that MLGs, unlike other cell wall matrix polysaccharides, are primarily synthesized and assembled at the plasma membrane rather than in the Golgi.



Revealing the subcellular location of MLG in grass tissues. MLG is found abundantly along the cell wall (CW) in barley root tip cells but is absent over nearby Golgi (G). (*Reprinted from Wilson et al. [2015], Figure 1A.*)

Pinpointing the site of MLG biosynthesis is no small task, as standard chemical fixation techniques used to visualize the site of enzyme function destroy the integrity of the subcellular ultrastructure. Therefore, the authors subjected various grass tissues to cryofixation using high-pressure freezing to maintain cell ultrastructure and protein antigenicity. They then probed these tissues with anti-MLG antibodies, revealing that MLG is abundant in the cell wall but absent in the Golgi (see figure). The next step was to determine whether CSLF6 is present at the plasma membrane, which they did using anti-CSLF6 antibodies. When cryofixed sections of various grass tissues were labeled with anti-CSLF6, labeling was detected at the plasma membrane as well as intracellular membranes. This finding suggests that the dogma that all noncellulosic polysaccharides are synthesized and assembled in the Golgi is incorrect. By contrast, labeling with anti-CSLH localized CSLH1 to the endoplasmic reticulum, Golgi, and secretory vesicles, demonstrating the conventionally accepted localization of this minor player in MLG biosynthesis. The locations of CSLF6 and CSLH1 were confirmed using biochemical approaches, as well as functional analysis of fluorescently labeled CSLF6 and CSLH1 in transiently transformed wild tobacco (*Nicotiana benthamiana*) cells.

While this study strongly suggests that CSLF6 synthesizes MLG at the plasma membrane, the mode of action and possible interacting partners of CSLF6 have yet to be identified. Indeed, although technical hurdles remain, this study brings us one step closer to understanding the molecular mechanisms underlying biosynthesis of the plant cell wall, a structure infinitely more complex than the walls around you.

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