

## Introduction: plant cell wall proteins

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The cell wall and its underlying plasma membrane represent the dynamic interface between a plant cell and its environment, which includes neighboring cells. Biology texts commonly describe plant cell walls, but rarely acknowledge the existence and importance of cell wall proteins, making them the Rodney Dangerfields of plant biology. This set of multi-author reviews provides the reader with a comprehensive understanding of the major cell wall proteins in plants and attempts to foster respect for these underappreciated and underrecognized components of the plant cell surface.

Plant cell walls are likened to reinforced concrete consisting of cellulose rods (the rebar) impregnated in a matrix of polysaccharides and protein (the cement). This analogy, however, fails to capture the dynamic nature of the wall and its ability to alter its physical composition and properties as cells grow, divide and differentiate. By counting spots on two-dimensional protein gels of cell wall preparations, it is estimated that there may be as many as several hundred proteins in the cell wall. However, the proteins that constitute the majority of this proteinaceous mass are hydroxyproline-, proline- or glycine-rich. These major proteins include the extensins, the proline-rich proteins (PRPs), the arabinogalactan proteins (AGPs), all of which are viewed as hydroxyproline-rich glycoproteins (HRGPs), as well as the glycine-rich proteins (GRPs); they are the subjects of this multi-author review. While these proteins have structural roles, they also appear to function in other equally important and exciting ways which are only now coming to light.

This set of reviews appropriately begins with the contribution of Derek Lampion, the father of the plant HRGP field. Derek was the first to discover hydroxyproline and HRGPs in plant cell walls and provides a humorous historical perspective of how this research area was conceived and has developed. The reader is transported back in time to experience the events surrounding Derek's nervous, exciting discovery of hydroxyproline in the wall. The second part of his review is devoted to defining and discussing function of the HRGPs at the molecular and

ecological levels and everything in between, a formidable undertaking to say the least. He also eloquently reminds the reader that structural roles which these proteins play represent important functions in their own right in addition to other roles which they are likely to have. The idea that HRGPs are important in controlling cell elongation and extension is a paradigm that Derek suggested long ago, as evidenced by his coining the term 'extensins'. This paradigm may now gain further support thanks to the finding that expansins, a group of plant cell wall proteins demonstrated to be involved in cell wall loosening, may be proteases. In any event, I suggest you start this series by pouring yourself a cup of your favorite beverage, grabbing an unabridged dictionary (you will need it for Derek's contribution), and enjoying a wonderful trip down memory lane and into the future of the plant cell wall protein field.

Marcia Kieliszewski, a protégé of Derek's, along with her former graduate student, Elena Shpak, provide another perspective on the HRGPs (i.e. extensins, PRPs and AGPs) and clearly present a theme echoed throughout these reviews, namely that HRGPs are a spectrum or continuum of molecules defined by their peptide periodicity and hydroxyproline-O-glycosylation. They also describe the Hyp-contiguity hypothesis that explains and predicts which hydroxyproline residues get O-glycosylated. But the pièce de résistance of this review is the lucid discussion of their novel approach to studying HRGPs, which involves constructing and expressing synthetic genes encoding various HRGP modules in plant cell cultures in order to answer specific biologically relevant questions. The expression of such women-made modules provides support to the Hyp-contiguity hypothesis and provides a new avenue to explore prolyl hydroxylation, HRGP glycosylation, HRGP cross-linking, HRGP function and even to make designer HRGP modules which may have industrial or commercial uses.

In the next review, I concentrate on the AGPs and provide my views on this particular group of HRGPs. Cloning approaches truly opened up the AGP field and

made it more understandable in terms of its protein structure and diversity and complemented prior work at the (glyco)protein level. The structural organization of AGP sequences is thus compared based upon both protein and DNA information. Next, it was the finding that some AGPs are attached to the plasma membrane by a glycosylphosphatidylinositol (GPI) anchor that further revolutionized the AGP field and stimulated new lines of research. This finding has led to the paradigm that certain AGPs (i.e. the classical AGPs) are attached to the plasma membrane and then processed for release to the cell wall and/or as extracellular secretions. The expression of AGP genes is then considered along with the localization patterns of various AGPs; these data highlight the involvement of AGPs in plant development. Whereas AGPs are likely to have a structural role (e.g. perhaps serving as a cushion between the plasma membrane and cell wall), it is almost certain that they function in other ways, too, including roles in cellular signaling that are only now beginning to be explored. These exploratory studies are discussed and the possible scenarios by which such signaling may occur are presented. Given that AGPs are possibly receiving the most attention of all the cell wall proteins by researchers today, I hope to foster further interest and thoughts on this extraordinary and diverse class of HRGPs.

Alice Cheung, Hen-ming Wu, Barend de Graaf and Celeste Mariani focus their attention on HRGPs found in the reproductive tissues of plants and present their perspective on how these proteins function in the reproductive process. Here the reader is led into the intriguing world of the male and female gametophytes and how the extracellular matrix is involved in their interaction leading to a new sporophyte generation. By focusing on the HRGPs that comprise the stigma, style, ovary and pollen, the reader gains an appreciation for the complexity and importance of the extracellular matrix in these tissues and how it facilitates the reproductive process. Finally, the regulation of one class of these reproductive HRGPs, the TTS (transmitting tissue-specific) proteins, effectively illustrates the way in which synthesis and posttranslational modifications, particularly glycosylation, can serve to control molecular interactions involving the extracellular matrix. Furthermore, the issue of the relationship between *Nicotiana tabacum* and *Nicotiana glauca* TTS proteins is explained in a way

that resolves the apparently conflicting information which has been published on these two species.

Finally, we learn about the only non-hydroxyproline-rich protein class, which serves as a major component of the plant cell wall, the GRPs. Christoph Ringli, Beat Keller and Ueli Ryser provide a guided tour through the DNA and protein sequences of the GRPs, which unlike HRGPs do not appear to be glycosylated. The secondary structure of these molecules appears to be  $\beta$ -pleated sheets. Moreover, some GRPs show susceptibility to collagenase treatment, suggesting a possible connection to animal collagen. The regulation of these various GRPs and their specific localizations to particular cell walls, especially ones in vascular tissue, provide an intriguing account of these unique molecules. Especially novel is the way in which GRPs can move from one cell type (xylem parenchyma cells) to another (protoxylem cells), providing an uncommon illustration of intercellular protein transport in plants.

Hopefully, we have succeeded in our goals to inform readers about the latest thinking on the structure and function of the major cell wall proteins. This tetrad of proteins, the extensins, the PRPs, the AGPs, and the GRPs, all serve as important architectural building blocks of the cell wall and yet appear to have functions that go above and beyond their structural roles. One should keep in mind that these classes are convenient groupings for the human mind, and the HRGPs and GRPs should be viewed as a spectrum of molecules in terms of their protein components and particularly their carbohydrate components, in cases where glycosylation occurs. In some instances, mosaic or chimeric molecules that include portions of these cell wall proteins, as exemplified by potato lectin, exist and illustrate an additional dimension of diversity. In conclusion, the authors of these reviews thank CMLS for providing us with the opportunity to tell our stories and attempt to give some respect to a set of proteins found throughout the plant kingdom that largely 'get no respect' – until now!

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