agronomy

Editorial

Advances in Cell Wall Research of Crop Plants

José-Luis Acebes

Área de Fisiología Vegetal, Departamento de Ingeniería y Ciencias Agrarias, Facultad de Ciencias Biológicas y Ambientales, Universidad de León, Campus de Vegazana s/n, E-24071 León, Spain; jl.acebes@unileon.es; Tel.: +34-987-291-492

1. The Relevance of Cell Wall Research in Crop Plants

Much research has been conduct since cell walls were first depicted, when they were considered to be a mere inert material, such as the cement between cells, which only contributed to mechanical support. In recent decades especially, it has emerged with increasing evidence that the cell wall is an integral part of the cell, that it forms a continuum with the rest of the cellular components, and that it plays important roles in cell differentiation, signalling and thus in development processes, as well as in defence against abiotic and biotic stresses. This research highlighted that the composition and structure of the plant cell wall is surprisingly flexible and diverse, not only among plant species but also among types of tissues.

Current investigations have now shown that there are hardly any physiological processes in plants not associated with modifications produced in the walls of the cells (and thus in the tissues and organs) where they occur.

Consequently, critical physiological processes within crop plants, such as seed imbibition and germination, seedling growth and plant development, including flowering, grain filling, fruit thinning and ripening, etc., are determined by modifications in the composition and structure of their cell walls. Moreover, the crop's resilience to diseases and pests usually relies on modifications in the physicochemical properties of their cell walls. In addition, many agronomic techniques are also dependent on the changes that occur in the cell walls. Pruning, for example, must consider the correct healing of the wounds to avoid desiccation or pathogen infection and pest infestation. Likewise, grafting requires a coordinated set of changes in which the cell walls play an important role, firstly in the healing and adhesion of the tissues between the rootstock and the scion, and subsequently for proper vascular continuity to occur.

On the other hand, the arrangement of cell walls greatly influences the organoleptic properties of vegetables and fruits, conditioning their firmness, hardness, crispness and mealiness, and therefore their digestibility and nutritional value. Similarly, forage crops, which are mainly composed of plant cell walls, depend on the fermentation of their components by microorganisms to produce the constituents that will then be metabolised in the digestive tract by catabolic enzymes. Finally, the yield and quality of plant tissues, fibres, biofuel and related crop products and by-products, also depend on the characteristics of the cell walls from which they are derived.

Much progress in understanding the relationship of cell wall changes in proper plant functioning has been made not exclusively with model plants, such as *Arabidopsis thaliana* or *Brachypodium distachyon*, but also with a wide range of crop plants, to such an extent that some of them, such as rice, maize or wheat, have now become proper model plants. These insights have broadened the comprehension of crop plant physiology and have yielded plants that are more resistant to biotic and/or abiotic stresses, as well as to value-added crops, illustrating the significant link between cell wall modifications and improved crop productivity.

Despite the high relevance of cell wall research, many aspects remain to be discovered, and investigations are now progressing along a multitude of paths, including cell wall

check for updates

Citation: Acebes, J.-L. Advances in Cell Wall Research of Crop Plants. *Agronomy* **2022**, *12*, 2430. https://doi.org/10.3390/agronomy12102430

Received: 29 September 2022
Accepted: 30 September 2022
Published: 7 October 2022

omics in crop plants, changes in the cell walls thorough different physiological processes, the expression profile of cell wall-related genes, the synthesis of cell wall components during the various development stages, the role of cell walls and their components in plant defence against pest and pathogens and thus in crop protection, the production of modified cell walls with improved digestibility properties and energy yields, etc.

This Special Issue (SI) aims to explore some of these avenues in order to highlight recent advances made in the fascinating field of crop-related cell wall research.

2. Overview of the SI

This SI compiles one critical review and four original research articles, carried out using the following four crops: two dicotyledonous plants (strawberry and tomato) and two monocotyledonous plants (maize and rice). This fact highlights the variety of the studies conducted, but this diversity is also underlined by other noteworthy features. From a methodological point of view, the articles include both laboratory (rice, tomato and strawberry) and field (maize) experiments, and the research focuses on different organs, such as stems (tomato and maize), leaves (rice) and fruits (strawberry). In addition, a broad array of geographic areas around the world is also covered, since the investigations were carried out by twenty one authors from six countries, including three from the Americas (Chile, Mexico and the USA), two from Europe (Spain and the United Kingdom) and one from Asia (Thailand). Finally, in terms of the physiological processes of the cell and plants studied, the biosynthesis of cell wall components, fruit ripening, resistance to pests and healing under graft conditions stand out, although many other processes are covered in the review.

The following lines briefly outline the various works included in the SI.

2.1. Elucidating the Role of Phenolic Acids in Crop Cell Walls

Phenolic acids, notably *p*-coumaric acid and ferulic acid, are minor but important components linked to hemicelluloses and/or lignin in the cell walls of grasses and other monocots (usually referred to as type II cell walls). Their incorporation into cell walls, known as feryloylation and *p*-coumaroylation, respectively, often has profound effects on cell walls.

Buanafina and Morris [1] in their review stated that cell wall feruloylation is a significant process implied in cell adhesion, and thus in plant growth, resistance to pests and pathogens, as well as in cell wall degradability. Feruloylation frequently leads to cell wall strengthening, as it promotes a lower rate of enzymatic hydrolysis of polysaccharides, resulting in a decrease in feed utilisation by ruminants as well as a lower conversion to ethanol. Therefore, the understanding and subsequent manipulation of cell wall feruloylation will allow for an efficient use of crop cell walls, especially in agriculture, but also in the food and biofuel industries, improving the deconstruction of lignocellulose biomass and thus the energy yield for bioethanol production, as well as improving the nutritional value of forage crops.

In relation to pest resilience, the accumulation of phenolic acids has been postulated as a possible defence mechanism, due to their effect on the stiffening and fortification of plant cell walls. In this context, López Malvar et al. [2] studied the relationship between maize resistance to corn borers (the most significant pest attacking this crop) and the composition of its cell walls, particularly in relation to cell wall-bound phenolic acids. For this purpose, they used Recombinant Inbred Lines (RILs) from the same genetic background (developed from a Multiparent Advanced Generation Intercross—MAGIC—with a population of eight parents) that displayed contrasting behaviour towards the corn borer injury. They showed that corn borer-resistant lines exhibited a higher concentration of *p*-coumaric acid than susceptible ones, pointing to a potential role of this phenolic acid in maize resistance to corn borers. The role of *p*-coumaric acid in maize resistance might be linked to both the lignin content and its composition and microstructure.

2.2. Deepening the Cell Walls Changes Related to Fruit Ripening

Typically, the ripening of fleshy fruits is accompanied by a profound restructuring of their cell walls, leading to huge changes in their texture. These modifications come from the softening of the pulp, which occurs as a consequence of the disassembly of the cell wall structure, due to the coordinate activity of a group of enzymes and other proteins. In this SI, Castro et al. [3] conducted a thermogravimetric analysis to explore the involvement of cell wall constituents in strawberry ripening. Previously, this Chilean group reported that the degree of thermal stability of fruit samples was correlated with the stability and compactness of their cell walls, as soft ripe strawberries were characterized by lower thermal stability compared to green stages of the same cultivar [4]. In the current study, they used two strawberry cultivars with contrasting fruit softening characteristics and detected, as expected, that the fruits of the softer cultivar showed a degree of depolymerisation inversely correlated with the thermal stability of the cell walls; the green stage had the highest thermal stability, whereas the ripe stage showed a lower thermal stability linked to its degree of depolymerisation and partial disassembly of the hemicellulose-cellulose matrix, as revealed by scanning electron microscopy images. However, this clear correlation between depolymerisation and thermal stability could not be established in the fruits of the firmer cultivar.

2.3. Connecting the Synthesis of Ascorbic Acid and the Composition of the Cell Wall

Some cell wall components are also involved in the synthesis of other biologically important molecules. This is the case for the formation of ascorbic acid, which is synthesized via L-galactose. A necessary step for the biosynthesis of mannose, galactose and ascorbic acid is the formation of GDP-D-mannose, which is catalysed by the enzyme GDP-D-mannose pyrophosphorylase (GMP or VTC1). Three homologues of the gene encoding VTC1 have been described in rice, with *OsVTC1-1* being implied in ascorbic acid production in leaves. To further investigate the function of the *OsVTC1-1* gene, Lamanchai et al. [5] studied three rice RNAi lines with lowered expression levels of this gene, and showed that the ascorbic acid content of their leaves was drastically reduced, pointing to a role of *VTC1-1* in ascorbic acid synthesis. In addition, both mannose and galactose contents were reduced in these RNAi lines, as were a set of cell wall-related proteins, concluding that the *OsVTC1-1* gene takes part in ascorbic acid biosynthesis as well as in a set of cell wall-related processes in rice leaves.

2.4. Setting Cell Wall Changes in the Course of Grafting

Grafting is a very useful and widespread agronomic technique for many crops, in which the cell walls of the rootstock-scion union play a fundamental role. The dynamics of cell wall modifications can be followed over the course of the grafting process. At first, there is a phase of tissue damage, where some polysaccharides (pectins) are actively deposited in the necrotic layer. This is followed by the formation of new shared cell walls within the cohesion phase and subsequently, during vascular reconnection, the production and deposition of a new cell wall is needed [6]. Grafting success is limited by the production of unfunctional grafts, which decreases the benefits achieved, and thus it is highly desirable to elucidate the factors behind graft unfunctionality. In this Special Issue, Frey et al. [7] analysed graft failure in tomato plants, focusing on cell wall defence reactions and histological modifications. Unfunctional grafts revealed the lack of vascular reconnections and the absence of adhesion between rootstock and scion, although clusters of callus cells and the differentiation of new vasculature occurred. In addition, the cell walls of unfunctional grafts showed the following three types of deposits: callose, lignin and suberin, with the coupled accumulation of lignin and suberin being frequent. These cell wall deposits appear to be one of the main causes of graft failure as they apparently prevent adhesion.

3. Conclusions

The works collected in this Special Issue are proof that cell wall research related to crop plants is in good health. They show recent success stories that illustrate a wide range of objectives achieved in this fascinating field. These works also illustrate the usefulness of using different approaches and techniques to carry our cell wall research, showing that thermogravimetry, microscopy, molecular biology approaches and biochemical analyses, together with statistical methods can be used to characterize cell walls, analyse their components, and monitor their modifications. Finally, this set of reports opens the way for further research and indicates that much work needs to be conducted to extend this research to other areas in order to learn the secrets of cell walls and to achieve crops with cell walls that are better adapted to environmental conditions and human demand.

Funding: This research received no external funding.

Acknowledgments: The Editor would like to thank all the contributions to the present SI, the authors for investing their time, as well as the anonymous reviewers and editorial managers who have contributed to the development of the articles in this SI.

Conflicts of Interest: The author declares no conflict of interest.

References

1. Buanafina, M.M.d.O.; Morris, P. The impact of cell wall feruloylation on plant growth, responses to environmental stress, plant pathogens and cell wall degradability. *Agronomy* **2022**, *12*, 1847. [CrossRef]
2. López-Malvar, A.; Reséndiz, Z.; Santiago, R.; Jiménez-Galindo, J.C.; Malvar, R.A. Relationships between stalk resistance and corn borers, agronomic traits, and cell wall hydroxycinnamates in a set of recombinant inbred lines from a maize MAGIC population. *Agronomy* **2021**, *11*, 1132. [CrossRef]
3. Castro, R.I.; Muñoz-Vera, M.; Morales-Quintana, L. Evaluation of cell wall modification in two strawberry cultivars with contrasted softness. *Agronomy* **2021**, *11*, 1100. [CrossRef]
4. Castro, R.I.; Muñoz-Vera, M.; Parra-Palma, C.; Valenzuela-Riffo, F.; Figueroa, C.R.; Morales-Quintana, L. Characterization of cell wall modification through thermogravimetric analysis during ripening of Chilean strawberry (*Fragaria chiloensis*) fruit. *Cellulose* **2021**, *28*, 4611–4623. [CrossRef]
5. Lamanchai, K.; Salmon, D.L.; Smirnoff, N.; Sutthinon, P.; Roytrakul, S.; Leetanasaksakul, K.; Kittisenachai, S.; Jantasuriyarat, C. *OsVTC1-1* RNAi mutant with reduction of ascorbic acid synthesis alters cell wall sugar composition and cell wall-associated proteins. *Agronomy* **2022**, *12*, 1272. [CrossRef]
6. Frey, C.; Manga-Robles, A.; Acebes, J.L.; Encina, A. The graft framework: Quantitative changes in cell wall matrix polysaccharides throughout the tomato graft union formation. *Carbohydr. Polym.* **2022**, *276*, 118781. [CrossRef] [PubMed]
7. Frey, C.; Álvarez, R.; Encina, A.; Acebes, J.L. Tomato graft union failure is associated with alterations in tissue development and the onset of cell wall defense responses. *Agronomy* **2021**, *11*, 1197. [CrossRef]