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Review

Application of X-ray and neutron small angle scattering techniques to study the hierarchical structure of plant cell walls: A review

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ABSTRACT

Plant cell walls present an extremely complex structure of hierarchically assembled cellulose microfibrils embedded in a multi-component matrix. The biosynthesis process determines the mechanism of cellulose crystallisation and assembly, as well as the interaction of cellulose with other cell wall components. Thus, a knowledge of cellulose microfibril and bundle architecture, and the structural role of matrix components, is crucial for understanding cell wall functional and technological roles. Small angle scattering techniques, combined with complementary methods, provide an efficient approach to characterise plant cell walls, covering a broad and relevant size range while minimising experimental artefacts derived from sample treatment. Given the system complexity, approaches such as component extraction and the use of plant cell wall analogues are typically employed to enable the interpretation of experimental results. This review summarises the current research status on the characterisation of the hierarchical structure of plant cell walls using small angle scattering techniques.

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Contents

1. Introduction

The plant cell wall is the structural component which covers plant cells, providing protection against diverse stresses and support through the action of turgor pressure, i.e. preventing over-expansion of cells by the entrance of water. Thus, the cell wall is crucial in determining the shape, growth rate, mechanical strength and resistance against external stresses of plants. Generally, plant cell walls are composed of multiple layers which are deposited successively during the plant life cycle. Initially, a middle lamella rich in pectic polysaccharides is often formed. Subsequently, primary cell walls, consisting of thin and flexible layers, are deposited onto the middle lamella as the plant tissue grows. In certain plant species, once the growth process has been completed, a secondary cell wall may be further deposited onto the primary cell wall. This secondary layer is significantly thicker than the primary wall and it is characterised by its high rigidity. Clearly, the primary and the secondary cell walls present different composition and structure, which define

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their distinct behaviour. While primary cell walls are characteristic of growing tissues and, hence, must provide elasticity to enable cell expansion without rupture, secondary cell walls are typically found in woody tissues which have to withstand considerable compressive forces; they must therefore confer high resistance and stiffness. The composition and structure of primary and secondary cell walls are adapted to the requirements of each particular plant tissue, giving rise to an enormous variety of cell wall systems.

Knowledge of the plant cell wall structure is crucial to understand plant growth mechanisms (Braidwood, Breuer, & Sugimoto, 2013; Gorshkova, Mikshina, Gurjanov, & Chemikosova, 2010; Lev-Yadun, 2010), as well as to establish a link between the structure and mechanical properties of different plant systems (Gibson, 2012; Speck & Burgert, 2011). Investigation of the plant cell wall architecture is not only important from a scientific perspective, but it is also vital for many industrial sectors such as the food industry, textiles, wood, pulp and paper, where the main raw materials are based on plant tissue resources. Additionally, due to the increasing interest in the use of natural fillers for the development of sustainable bio-based composite materials, lignocellulosic fibres are attracting a great deal of attention (Johansson et al., 2012). In this context, the composition and structure of lignocellulosic constituents are key factors which determine their gas barrier and mechanical properties (Siqueira, Bras, & Dufresne, 2010). It is also worth noting that the use of lignocellulosic biomass for the production of biofuels as an alternative to the use of fossil fuels is an active area of research, although making the process economically viable is still challenging. Cellulose needs to be chemically or enzymatically digested to monomeric glucose which, in turn, is used as a feedstock in the fermentation processes carried out for the production of biofuels. However, the association of cellulose with some other polysaccharides and lignin hinders considerably the accessibility of chemical compounds or enzymes and thus, several purification steps are required to isolate cellulose. In this context, extensive research is currently being carried out to increase the efficiency of biomass digestion methods by identifying the role of the different biomass components on the availability of cellulose to be digested (Chen & Dixon, 2007; Penttilä, Varnai, Fernandez, et al., 2013; Pingali et al., 2010a; Yuan, Tiller, Al-Ahmad, Stewart, & Stewart, 2008).

Despite this knowledge, there are limited publications concerning the details of the plant cell wall hierarchical structure and many questions still remain open. The great complexity of the system, in which diverse components interact at different structural levels, together with the heterogeneous range of structures found in different species and plant tissues, have complicated considerably research within this field. Plant cell walls have been most typically characterised using microscopy techniques. However, these methods may provide limited information and conclusions should be drawn carefully, as the sample preparation processes, which often involve specimen drying, may alter the structure of the native material. In this sense, small angle scattering techniques, which require minimal sample preparation, are envisaged as a powerful tool to characterise intact plant cell walls in their hydrated state. Thus, the combination of microscopy with spectroscopic and scattering techniques is probably the most efficient approach to study the plant cell wall structure in its native state, covering the size range extending from the molecular to the microstructural level. On the other hand, several strategies such as sequential component extraction in model systems like celery and spruce wood, or the use of cell wall analogues based on bacterial cellulose to mimic the biosynthesis process, have been suggested in order to limit the complexity derived from the presence of multiple components in plant cell walls.

This review summarises advances with regards to the characterisation of the hierarchically assembled structure of plant cell walls by using small angle neutron (SANS) and X-ray (SAXS) scattering techniques, covering a broad size range and thus structural hierarchy, i.e. from the arrangement of cellulose molecules into crystalline and amorphous domains to the association of different components into composite bundles or microfibril aggregates, as well as connecting the structural arrangement of these components to their biological function in plant cell walls.

2. X-ray and neutron small angle scattering techniques

Scattering techniques are based on the analysis of the scattered radiation produced after a source, such as X-rays and neutrons, interacts with the particles present in a sample. These techniques are powerful tools to obtain information about the size, shape and orientation of components in systems that do not necessarily need to have long-range or crystalline order. In scattering experiments, the radiation scattered by the sample of interest is typically measured on a two-dimensional detector; in the event of isotropic scatterers, after being radially averaged, the intensity is plotted versus the magnitude of the scattering vector q, which describes the relationship between the incident and the scattered wave vectors and is defined as:

$$q = \frac{4\pi}{\lambda} \sin\theta \quad (1)$$

where θ is half the angle through which the radiation is scattered and λ is the wavelength of the incident radiation. Anisotropic scattering is typically managed using a similar approach based on the selection of angular sectors and comparing the average scattering parallel and perpendicular to a particular orienting direction; the latter may arise due to, for example, tensile forces.

By combining Eq. (1) with the Bragg's law ($\lambda = 2d\sin\theta$), one can determine the real-space dimension of the scattering object, through the relationship:

$$d = \frac{2\pi}{q} \quad (2)$$

According to this, scattering methods are classified into wide angle and small angle scattering techniques depending on the range of scattering angles (and corresponding length scales) covered. Thus, whereas wide angle scattering techniques are used to probe sub-nanometer dimensions, small angle scattering techniques, i.e. small angle neutron (SANS) and X-ray (SAXS) scattering, are able to cover a size range from 1 nm to several hundreds of nanometres. To study larger structures, small angle may be coupled with ultra-small angle scattering techniques (USANS and USAXS), hence extending the size range up to ca. 10 μm.

Selection of the proper source of radiation should be made on the basis of the sample composition and structural features to be probed. While X-rays are scattered by the electrons present in an atom, neutrons are scattered by the atomic nuclei; thus SAXS is sensitive to variations in electron density, while SANS depends on the nuclear structure of the atom. Hence, whereas heavier elements present greater X-ray scattering intensity scaling linearly with atomic number, in the case of neutron scattering, different isotopes of an element may present significantly different scattering intensity. At the molecular level, the scattering length density (SLD) quantifies the scattering power of a molecule by considering its physical density and the scattering length of its component atoms. Thus, the source of radiation should be strategically selected in order to enhance the SLD contrast between the sample and the surrounding material or between different sample components. In the particular case of SANS, the scattering length difference existing between hydrogen (-0.3742×10^{-12} cm) and its heavier isotope, deuterium (0.6671×10^{-12} cm), is the basis of the contrast variation method. This is an extremely valuable approach used to enhance

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