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Review

Organismal view of a plant and a plant cell[★]

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Cell walls are at the basis of a structural, four-dimensional framework of plant form and growth time. Recent rapid progress of cell wall research has led to the situation where the old, long-lasting juxtaposition: "living" protoplast — "dead" cell wall, had to be dropped. Various attempts of re-interpretation cast, however, some doubts over the very nature of plant cell and the status of the walls within such a cell. Following a comparison of exocellular matrices of plants and animals, their position in relation to cells and organisms is analysed. A multitude of perspectives of the biological organisation of living beings is presented with particular attention paid to the cellular and organismal theories. Basic tenets and resulting corollaries of both theories are compared, and evolutionary and developmental implications are considered. Based on these data, "The Plant Body" — an organismal concept of plants and plant cells is described.

When Robert Hooke first observed the cork under microscope and described its structure as composed of small units – "the cells" as he called them [1], he did not realise that in fact he was observing a network of cell walls in a dead tissue. Nevertheless, the idea and the term "cell" persisted and later found its place within the cellular theory of biological organisation. Cell walls (CW) are considered one of the major structural elements that distinguish plant cells from other eukaryotic cells. Taking advantage of the models elaborated for animal systems, and on the basis of recent rapid progress of CW research, it is often suggested

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Abbreviations: CW, cell wall; ECM, exocellular matrix.

that there are functional similarities of plant walls to the animal exocellular matrix (ECM; e.g. [2, 3]). This, however, casts some doubts over the very definition of "plant cell" and the position of cell walls within such a cell.

Cell walls are indispensable elements of plant cells determining their shape and affecting their function. Within a plant they form a structural and functional continuum — the apoplast. On the other hand, CW could be considered as a cellular "organelle" undergoing dynamic changes in response to a plethora of stimuli [4]. In that respect, they could be defined as part of yet another structural and functional continuum, composed of cell walls, plasma membrane, and the cytoskeleton [5–8]. Taken together, CW are at the basis of a structural, three-dimensional or indeed four-dimensional framework of plant form and growth time [9].

EXOCELLULAR MATRICES OF PLANTS AND ANIMALS — A COMPARISON

Plants and animals adopted two different strategies of life and this found a reflection in the properties and behaviour of their cells, and also in the structure and functions of their exocellular matrices. From the chemical point of view, animal ECM is composed mainly of glycoproteins and proteoglycans, while polysaccharides are the major building elements of plant CW with (glyco)proteins and phenolic compounds being minor components. In both cases, the currently used models describe exocellular matrices as complex networks of macromolecules. For example, in plant CW at least three intertwining networks: cellulose/hemicellulose, pectin, protein, and lignin (in some types of walls), could be distinguished [10]. Although chemically different, CW and some types of animal ECM (especially in connective tissue) are relatively similar when their mechanical properties are considered. Both are composite materials with rigid, stretch-resistant rods (cellulose microfibrils or various types of collagen) embedded in an amorphous, compression-resistant, gelatinous matrix [11]. This amorphous gel in plants is formed mainly by pectins and stabilised by (glyco)proteins and phenolics [12]. It should be noted, however, that the occurrence and distribution of exocellular matrices differ in organisms from both Kingdoms, and this reflects their differentiated functionality with respect to the maintenance of internal chemical composition of the cells and the resulting osmotic gradient between cells and their environment. In animal cells, operating systems of active ion transport provide the required osmotic balance [13]. In effect, ECM occurrence is differentiated, depending on the tissue, and within a tissue ECM might be shared by many cells and cell types. In contrast, plant cells are immobilised within the boundaries of their walls, which have to be strong enough to constrain the hydrostatic pressure evoked by osmotic gradients between cells and their milieu. Thus CW forms a structural element which is both an integral part of each cell and a continuum spanning the entire body of the plant [13, 14].

The formation of exocellular matrices is roughly a two-step process, comprising 1) biosynthesis of the building blocks, and 2) assembly of these elements into a functional matrix, with these steps separated spatially and temporally. Due to the differences in chemical composition between CW and ECM, these processes are under different levels of genetic controls. ECM glycoproteins could be regarded as primary products of gene activity and thus transcriptional controls are of primary importance, with some post-translational control. On the other hand, polysaccharides (and phenolics) of plant CW are products of enzyme action. This shifts the weight of biosynthetic controls to the post-translational level. The major difference, however, regards the secretion and assembly of functional matrices. In animal cells, ECM is formed as a result of a co-operative effort of groups of cells. In plants, CW of individual cells are formed only by their respective protoplasts. The process of CW formation is under very precise structural and physiological as well as organismal controls. CW of various tissues, and of different cells within a tissue, and even domains of the walls around individual cells may be formed in different ways, at different speeds and with the use of different components (for review see [9]).

BIOLOGICAL ORGANISATION — A MULTITUDE OF PERSPECTIVES

The discussion on "What is a plant cell?" carried out throughout 1991 in *The Plant Cell* revealed the existence of two opposite ways of thinking about a cell in general and a plant cell in particular. The first one attempts to define the cell as "a basic unit of life" common to all living organisms. This is exemplified by the definition of Alberts *et al.* [3] that cells are "small membrane-bounded compartments filled with a concentrated aqueous solution of chemicals". Hence, everything which is outside the plasma membrane should be considered as a product of the cell, but not a part of the cell. This would mean that CW of plants, fungi or bacteria as well as animal ECM should not be included into the definition of the cell. The opposite approach considers the differentiated organisation of cells as a determinant of diversity observed in organisms belonging to various Kingdoms. In this respect, plant or fungal cell walls constitute a characteristic feature which, when combined with other features, enable us to distinguish a particular type of cell or organism built from such cells as a plant or a fungus. This approach is also more rooted in the traditional understanding of cells, particularly in plant research where the entity enclosed within the plasma membrane is called "a protoplast". As the ability to divide is considered an indispensable feature of a living cell, it is worth to indicate that plant protoplasts are unable to divide before the formation of a functional surrounding wall [15]. Consequently, within this approach cell walls are usually considered to be a part of plant cell. Although in such a definition the exact relationship between the inner protoplast and the outer CW is not precisely identified, historical perspective indicates that CW are the product, but not the partner of the protoplast.

The discussion on the definition of the plant cell is embedded in a much broader controversy over the way of interpreting biological organisation of living organisms. There is a general agreement that the phenomenon of Life originated with the formation of the first cell and that it still is intimately related to the cell (Virchow: "*Omnis cellula e cellula*"). The difficulties appear when attempts to explain the organisation of multicellular organisms are undertaken. Two theories have been proposed, cellular and organismal. The cell theory was originally intended by Matthias Schleiden for describing structural differences between the internal organisation of plants and animals [13]. In 1839 this theory was transformed by Theodor Schwann into a unifying principle that all living things are made up of cells — elementary units of structure, physiology, and organisation [16]. This idea became one of the foundations of modern biology underlying many other concepts aimed at the elucidation of biological phenomena. Basic tenets of this theory state also that each cell is initially an individual of equal morphological rank and that each multicellular organism is an aggregate (a "republic") of cells [14, 17]. At about the same time the organismal theory has been formulated, based on the observations that the cell theory is not well suited to describe plant development (de Bary: "*Die Pflanze bildet Zellen, nicht die Zelle bildet Pflanzen*"; cited after [14]). According to this theory, a living thing is a continuous protoplasmic entity of complex organisation which may or may not be partitioned into smaller units recognised as cells. In any case, such partitioning is a secondary event and if it takes place, the resulting units ("cells") are subordinate parts of the whole [14, 16, 17].

It was rightly pointed out by Korn [16] that both theories originated as, and still are, structural concepts. The development of biology and other contemporary fields of natural sciences allowed other points of view on Life itself or on biological organisation to develop. Well known examples are: the thermodynamic concept defining cell as an open system or the cybernetic one describing cell as a unit of self-control and self-reproduction. It is worth noting, however, that all theories are based to a considerable degree on a qualitative core, while the multitude of life forms and functions is a manifestation of subtle quantitative changes and interactions between various molecules building cells and organisms [18]. Accordingly, none of those perspectives offers a full explanation of such interesting phenomena as the transition of one-dimensional information, carried by genes, into three-dimensional architecture of a living being [9]. Although there have been formulated first modern concepts of the cell and biological organisation (e.g. [16, 19]), for the sake of clarity these two structural theories will be used here to describe the possible extremes of interpretation.

CELLULARITY — EVOLUTIONARY AND DEVELOPMENTAL IMPLICATIONS

Both the cellular and organismal theories attempt to explain the relation between the organism and the cell, between the whole and the part. Their basic tenets as well as corollaries derived from them are formulated in an exclusive manner. This will be illustrated by an analysis of evolutionary and developmental implications. According to the cellular theory, multicellularity arises as a result of the aggregation of individual organisms, the cells. This places the emphasis on the quality of building units, and the properties of the organism would then be viewed as the sum of the properties of many cells [20]. Consequently, developmental processes (ontogeny) would be considered as an effect of the co-operative effort of many cells. On the other hand, the organismal theory views each organism as a protoplasmic unit which might be chambered secondarily into individual parts (subunits) recognised as cells. Accordingly, the theory places the basic developmental controls at the level of the organism and considers ontogenesis as the resolution of the whole into parts. Moreover, as the emphasis is put on the organism as a whole, positional criteria become a primary determinant when analysing relationships between the building subunits [20]. Comparative studies of plants and animals reveal that the cell theory provides the best description of animal development. Here, division of cells involves complete separation of daughter cells enabling their distinct mobility and independence of behaviour. The generation of the final three-dimensional shape of, e.g., a mammalian embryo is a result of cell migration. In contrast, cell division in higher plants involves the insertion of the newly formed cell plate between daughter protoplasts. However, this cell division is incomplete and the cell plate does not fully separate the daughter cells, giving rise to cytoplasmic and endoplasmic system connections through plasmodesmata. And such dynamic structural architecture is best described by the organismal theory (see [9, 13, 14, 17, 21]).

The acceptance of either theory influences also our views on the evolution of multicellularity. As the cellular theory is deeply implicated in the concepts of modern biology, it offers a familiar perspective known from many textbooks. This theory views unicellular organisms as primitive ("elementary") forms of life and multicellular organisms as advanced ones. In this way, phylogeny appears as a relatively straightforward process leading from unicellular organisms, through a colonial stage, to multicellular organisms characterised by specialisation and independence of their building cells. The organismal theory suggests another explanation. As each living thing is a protoplasmic whole, unicellular and multicellular organisms are of the same rank, and they shall be considered as nonseptate and septate individuals, respectively. In the course of evolution, eventual chambering (cellularization) of the protoplasmic unit enabled the division of labour among various subunits. In particular, the utilisation of mechanical benefits resulting from the inclusion of CW into their bodies permitted plants to successfully colonise land (or more properly, air) [14, 22, 23].

The present state of knowledge indicates that multicellularity evolved independently in a few evolutionary lineages. Both plants and animals started with the same cellular toolkit as their last common ancestor, most probably a unicellular eukaryote containing a mitochondrial endosymbiont and functional elements of the cytoskeleton [24]. They diverged however, about one billion years before they became multicellular organisms [25]. As multicellularity presents a clear evolutionary advantage [22], it emerged in both lineages but the mechanisms by which this was achieved appear to be lineage-specific. The different life styles of plants and animals seem to be the consequence of the solutions utilised in both Kingdoms to solve the problem: how to maintain the chemical composition of cells and enable cell-to-cell communication and exchange of materials at the same time? In animals, active ion transport system, controlling chemical gradients across plasma membranes, has been employed [13]. Direct physical contact between neighbouring cells is achieved in one of three nonexclusive ways: tight junctions, desmosomes, and gap junctions [22]. Only the latter two enable the exchange of solutes containing small metabolites and ions. It should be noted, however, that due to the complete separation of daughter cells, all forms of intercellular contacts between animal cells are formed *de novo*, often following migration of cells. Thus, animals are truly multicellular in the sense given by the cellular theory. In plants, osmotically driven water influx creates intracellular hydrostatic pressure (turgor) which is counteracted by mechanically and structurally stable cell walls. The acquisition of such a regulatory mechanism has important evolutionary consequences reflected in plants' life styles. As summarised by Peters *et al.* [13], these could be listed as follows: 1) the hydrostatic pressure across the plasma membrane exceeding 2 MPa could be used for mechanical stabilisation of plant bodies, 2) functional cell walls become indispensable elements of plant cells, 3) protoplasts surrounded by the walls are unable to move, and thus plants have to be sessile, 4) the presence of a hermetic matrix around protoplasts limits the possibilities of energy and nutrient acquisition, and thus fungi are saprophytic and plants are autotrophic, and 5) the existence of the walls fixes the position of each cell in relation to its neighbours [13]. These constraints have been to some extent overcome, however, by a new mechanism of cell division leading to the formation of the cell plate and the development of a new type of intercellular communication through plasmodesmata [26]. The effect was a true symplasmic continuity between plant cells, enabling them to exchange not only low molecular mass solutes, but also proteins and informational macromolecules. As the number and location of plasmodesmatal connections could be actively regulated, this allowed for the exertion of a new, supracellular control of gene expression in symplastic domains during plant development [27].

"THE PLANT BODY" — AN ORGANISMAL CONCEPT OF PLANTS AND PLANT CELLS

The fundamentally different tenets and resulting corollaries of both theories seem to preclude the application of models elaborated in animal systems for the explanation of, e.g., plant development. The same is true for the respective exocellular matrices. Although some of the mechanical and functional characteristics of ECM and CW seem to be similar (see above), in general they appear to be noncomparable, and the mechanisms by which plants and animals interact with the outside world seem also to be quite different [28]. The relations between plant cells and their walls are much easier to comprehend in terms of the organismal theory which views CW as a means for chambering plants into smaller subunits recognised as cells [23]. Thus, CW could be defined both in relation to the protoplasts that produce them, and in relation to the whole plant. Consequently, CW are indispensable features of plant cells, not only products, but also partners of plant protoplasts. As they are both chambering devices and determinants of the boundary of the organism, their biosynthesis and function are also underorganismic control [9].

Cell walls seem to be one of the critical factors affecting cellular fate and development. Plant protoplasts require a surrounding, functional CW (or other matrix) in order to divide at all [15], and the composition of such matrix determines the fate of the embedded protoplasts (e.g. [29]). The same is true for, e.g., a newly formed naked *Fucus* zygote, where the first cellular event is the formation of the walls. These CW are then required for the fixation of the polarised cell axis and next function as a reservoir of morphogenic information which can be actively delivered back to the protoplast to direct its further development [30]. In plant cells, through the continuum of cell walls – plasma membrane – cytoskeleton, CW provide an anchor stabilising the “tensegrally” organised cytoskeletal network [31–33] thus providing the scaffolding onto which the cellular structures could be attached [8, 34, 35]. In this way, the continuum constitutes a major source of architectural biological information and an environment for a part of the biochemical machinery [32].

At the higher level of organisation, the structural and functional CW continuum forms an architectural framework ensuring the developmental integrity of plants. It provides the means and the route for inter- and intracellular signalling events. Changes in wall mechanics and/or changes in turgor pressure will physically affect the geometry of cells [36] leading to changes in the fate of individual cells. Experiments with calluses and cells cultured *in vitro* indicate that the physical environment found *in planta* is crucial for normal plant development [37, 38]. Moreover, they demonstrate also that such mechanical stimuli are decisive for the proper organisation of cellular metabolic networks [39], reflected in CW composition as well [40]. On the other hand, changes in biomechanical propertiesof the walls are important for cell growth and for organ generation [41]. Localised expansin-dependent weakening of cell walls induces the formation of root hairs [42], while localised application of expansins onto the stem apical meristem induces generation of leaf-like outgrowths and reversal of the direction of phyllotaxis [43]. When combined with the developmental control of symplasmic continuity through the regulation of the extent of plasmodesmatal communication [26], these mechanisms provide the basis of plant morphogenesis.

This particular duality of cell wall functioning in relation to the whole organism and its parts – the cells, seems to be a unique feature of plants. It also provides the strongest argument for the organismal nature of plants [17]. Using this point of view, cell walls, although external to protoplasts, become integral parts of plant cells. These cells, however, lose their individuality and are treated as subordinate parts of the organism, the plant. Nevertheless, the walls function as the determinants of not only cellular, but also organismic boundaries. The particular mechanism of cell division, used for internal chambering, does not disrupt the protoplasmic continuity of a plant giving rise to two continua, recognised early by plant biologists: the symplast and the apoplast. “The Plant Body” concept [9] treats thus a plant as a unit filled with several intertwining “networks” with cell walls providing a living architectural scaffolding. These networks include: (1) the symplast understood as a cytoplasmic continuity of plant body lined with a continuous plasma membrane, (2) the endomembrane system, (3) the cytoskeletal continuum, (4) communication contact points provided by the cell wall – plasma membrane – cytoskeleton continuum [9]. Several models of the organisation of plant cells, such as the plasmalemmal control centre [44], the endomembrane sheath [45], and the cell body and the cell periphery complex [8, 46], have been proposed recently. They were accompanied by two other models indicating the possible supracellular nature of plants due to the intercellular communication through plasmodesmata [27] or the existence of a mobile endoplasmic network spanning the whole plant [47]. All these concepts are rooted in the cellular theory of biological organisation. The latter two models could, however, be treated as a means for overcoming serious difficulties in interpreting some experimental data concerning plants when using this theoretical basis. Moreover, in all those concepts cell walls are not present. In that respect, the proposed idea of “The Plant Body” provides a broader perspective of biological organisation and includes the unique duality of cell wall functioning in plants.

As it was mentioned before, both the cellular and the organismal theory originated as structural ideas, and now they provide probably the most extreme ways of interpreting data concerning biological organisation of living beings. At the present state of knowledge, each of the theories appears to be most suitable to describe organisms belonging to different Kingdoms: the cellular theory for animals, and the organismal theory for plants and most probably also fungi. Both theories, however, have their own limitations and Life itself seems to be more complicated. For example, plants are able to determine the size and shape of their organs, and they regulate accordingly the number and positions of cell divisions. This phenomenon could be easily explained by the organismal theory. However, such processes are also observed during animal development which indicates that at least some level of organismal control exists also in these multicellular organisms [48]. Thus, there is still a need for much more general unifying concept(s) which would be able to embrace the tenets and the resulting corollaries of both theories. Based on the rapid progress of modern biology, these concept(s) would most probably originate as cellular [19] or informational [16] ideas explaining the wonderful multitude of Life forms.

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