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Cell Expansion: Past, Present and Perspectives

Jean-Pierre Verbelen (✉) · Kris Vissenberg

Biology Dept., Plant Physiology and Morphology, University of Antwerp, Groenenborgerlaan 171, 2020 Antwerp, Belgium
jean-pierre.verbelen@ua.ac.be

Plant size and organ size are dependent both on cell division and cell expansion (Lyndon 1990). Cell division is the process whereby one cell divides into two daughter cells; expansion is the growth in volume beyond the size of the mother cell before mitosis.

Both cell division and cell expansion were correctly defined in the 19th century on the basis of careful microscopic observations. Wilhelm Hofmeister (1867) demonstrated that the nucleus of a mother cell divides and that one half of the contents of the mother cell collects around each of the two daughter nuclei when a new cell wall forms between the daughter nuclei. Julius Sachs (1882) on the other hand clearly depicted the changes in appearance of parenchyma cells during cell expansion in a growing root, with reference to the volume increase of the central vacuole. He further emphasized cell turgor and water uptake as instrumental in causing expansion. He also pointed to the fact that during expansion the existing cell wall was stretched and thinned, but that new material was added keeping wall thickness rather constant (Fig. 1).

In plant organs the peak activities of both events are separated in time or space, a fact also known since the 19th century, as elegantly described and depicted by Sachs (1874). His figures of growing seedling roots gained an immediate popularity and were copied in Strasburger's famous handbook (Strasburger et al. 1894). They remained there as reference illustrations at least up to the 30th edition, published in 1971 (Strasburger et al. 1971).

Since that period of fundamental discoveries the process of mitosis and cytokinesis has been explored intensively and, during the last decades especially, the picture of both aspects has become extremely detailed. It has turned out that the mitotic machinery and its control do resemble that of animal systems but that they are plant-specific and very elaborate (for reviews see Dewitte et al. 2003; De Veylder et al. 2003). The formation of the cell plate, the new cell wall separating the newly formed daughter cells, turns out to be a highly complex cellular activity implying a precise orchestration of cytoskeleton activity, and synthesis and transport of wall components (Otegui and Staehelin 2000a,b; Otegui et al. 2001, and references therein).

Cell expansion has no equivalent in animal systems and progress in the understanding of the process was slow. As mentioned above, from the be-

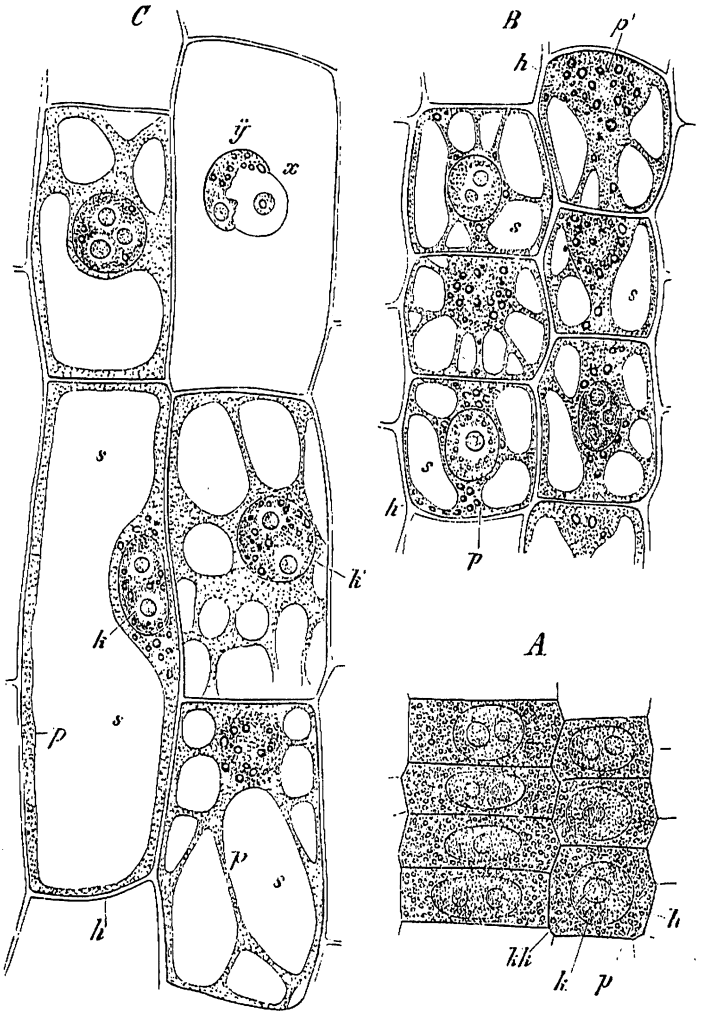

Fig. 352. Parenchymzellen aus der mittleren Schicht der Wurzelrinde von Fritillaria imperialis; Längsschnitte, nach 550maliger Vergrößerung. *A* dicht über der Wurzelspitze liegende, sehr junge Zellen, noch ohne Zellsaft; *B* die gleichnamigen Zellen etwa 2 Millimeter über der Wurzelspitze, der Zellsaft *s* bildet im Protoplasma *p* einzelne Tropfen, zwischen denen Protoplasmawände liegen; *C* die gleichnamigen Zellen etwa 7 — 8 Millimeter über der Wurzelspitze; die beiden Zellen rechts unten sind von der Vorderfläche gesehen, die große Zelle links unten im optischen Durchschnitt gesehen; die Zelle rechts oben durch den Schnitt geöffnet; der Zellkern lässt unter dem Einfluss des eindringenden Wassers eine eigenthümliche Quellungserscheinung wahrnehmen (*x y*).

Fig. 1 Parenchyma cells from the cortex of the root of *Fritillaria imperialis* in a longitudinal section of fresh material. *A* cells immediately above the root tip without vacuoles. *B* cells about 2 mm above the root tip with small developing vacuoles. *C* cells 7–8 mm away from the root tip with large vacuoles

ginning botanists knew that during cell expansion it was mainly the vacuole that grew considerably in volume and also that the existing cell wall became thinner as it was stretched but "reinforced" by addition of new wall material. A crucial step for the understanding of the physiology behind expansion was made by the discovery that auxin affects elongation and its control (Went and Thimann 1937). Most of the research, however, only refined the existing descriptive knowledge (Avery and Burkholder 1936; Erickson and Sax 1956). Interest within the scientific community was indeed very moderate, as witnessed by the limited attention to cell expansion in notorious handbooks (Esau 1960; Clowes and Juniper 1968; Wareing and Philips 1973; Fahn 1974; Bidwell 1979).

A reliable view on the state of the art in the early 1960s can be found in the *Encyclopedia of Plant Physiology, vol XIV* on growth and growth substances (Ruhland 1961). It clearly depicts the nascent interest in the process of cell expansion. Cell expansion receives little attention in the anatomy chapter (one sentence) but is treated in detail in the chapters "Cell expansion and metabolism (Ziegler H)", "Physics of cell elongation (Burström H)" and "The growth of the cell wall (Preston RD)". These chapters contain detailed information on in vitro extensibility of cell wall preparations and on changes in cell wall composition (cellulose, hemicelluloses, pectin and proteins) in elongating coleoptiles and hypocotyls.

Around that time, the attempts to understand cell expansion shifted into a new gear. On the theoretical side, Lockhart (1965) summarized a lot of experimental data on wall extensibility in a formula that was readily comprehensible for the whole scientific community and that continued life as the "Lockhart equation":

$$r = \Phi(P - Y)$$

where r is growth rate, Φ is extensibility of the cell wall, P is turgor pressure (i.e. the source of cell wall stress) and Y is yield threshold (i.e. the minimum pressure required for growth).

This simple equation clearly states that the rate of cell expansion is a product of the imbalance between turgor pressure and the mechanical properties of the cell wall, emphasizing that the principal players are thus to be found in the symplast as well as in the apoplast.

Since then, detailed data were gathered on the composition and the interaction of the primary cell wall and its then-known components: cellulose, hemicelluloses, pectins and proteins. Cellulose was found to be synthesized by cellulose synthases (Arioli et al. 1998) that are organized in cellulose synthase complexes (Kimura et al. 1999). Fluorescent labelling of these rosettes pointed to the role of the cytoskeleton in the orientation of the cellulose microfibrils in the wall (Paredez et al. 2006). The acid growth theory was substantiated by the discovery of expansins (McQueen-Mason et al. 1992), while many other proteins and processes with putative roles in cell wall loosening

were described (Cosgrove 2005). Mechanisms emerged that counteract the loosening of the cell wall and so arrest cell expansion (Cooper and Varner 1984). Aquaporins were described as universal facilitators of water transport through vacuolar membranes (Crispeels and Maurel 1994). The mode of action of auxins and of the other plant growth regulators became much clearer (e.g. Weijers and Jurgens 2004). These are the scene and the actors that make the content of this volume. Most of the recently published reviews focus on or are limited to the cell wall. As stated above, the Lockhart equation indicates that both apoplastic and symplastic players are involved in cell elongation. This volume therefore combines actual state-of-the-art papers on the different aspects of the cell's biology involved in expansion and its control. Nuclear ploidy is often related to cell expansion (Nagl 1979). As this is only the case in about half of the plant species, endoreduplication does not seem fundamental for expansion. It will therefore not be treated. It also needs to be mentioned that cell expansion includes diffuse expansion (in most cells) and tip growth (in certain specific cells). The latter method of cell growth will not be treated as it has been covered by Rui Malhó in another volume of this series (Malhó 2006).

During cell expansion, the cell wall clearly is a centre of activity. Up to now, however, an adequate model of the cell wall structure and how this structure permits both an increase in surface and the incorporation of new wall material still remains elusive. Using wall microscopy, selective extraction of components followed by structural analysis and in situ spectroscopic approaches, several artificial models have been proposed. Cosgrove (2000) mentions and discusses three models that differ only in the types of interaction and spacing of the different components. These specific associations and locations of the components need to be further elaborated to fully understand the mechanism of cell wall enlargement.

At the onset, during, and at the end of cell expansion, undoubtedly different sets of genes and proteins are expressed and active/inactive. Several of these crucial genes and proteins are starting to emerge, but the complete picture is far from clear. The combination of the knowledge on the three-dimensional architecture (e.g. of the *Arabidopsis* root, which is well-described) and cell type-specific expression profiling as performed by Birnbaum et al. (2005) could eventually provide the complete transcriptome of single cells in the root apex. This information could then provide all of the changes in gene expression that occur when a cell switches from a meristematic to an expanding cell or when a cell responds to environmental and hormonal stimuli. Similar proteomic approaches could give complementary information on protein involvement in the cell's crucial developmental processes and switches.

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