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Plant Vacuoles: from Biogenesis to Function

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Abstract The plant vacuolar system is far more complex than originally expected and multiple sorting pathways leading to various types of vacuoles can be found depending on the cell type and on the stage of development. In addition, the vacuolar system is highly dynamic and can adjust to environmental signals to meet the changing needs of the plant. Some recent advances have been made in the identification of the molecular mechanisms by which such a complex compartmentation develops and evolves over time. In this review, we present an update of the latest results in this exciting field and propose distinct biogenesis models for the formation of vacuoles in vegetative and seed tissues, taking into account some apparently contradictory results.

1 Introduction

The etymology of vacuole derives from *vacuus*, meaning empty. The term refers in fact to the large fluid-filled, seemingly empty compartment originally identified in plant cells when they were first observed under a microscope. The vacuolar content (vacuolar sap) is separated from the embedding cytoplasm by a single membrane called the tonoplast. As early as the 1960s, biologists observed heterogeneity in both size and content of these vacuoles. Under a light microscope, some vacuoles could clearly be seen to contain pigments while others appeared dense in the electron microscope. Presently, after tremendous progress in plant molecular biology and genetics, it is quite exciting to realise that the cellular machinery leading to these vacuolar systems is indeed highly complex. Actually, we are only starting to uncover the pathways generating the different types of vacuoles with their specific functions. In terms of intracellular trafficking, the vacuole is also often described as a "final destination". This idea is no longer up to date since it is now clear that intracellular trafficking can involve all membranes of the secretory pathway, for example vesicle-mediated solute transport from the vacuole to the apoplast (Echeverría 2000), recycling of lipids and some other key factors such as the SNARE proteins involved in specific fusion events between two types of membranes (Bonifacino and Glick 2004). It also does not fit with the novel idea that the vacuolar system may be modified upon various stim-

uli leading for example to controlled fusion events (Jauh et al. 1999) or to a change of the function of a vacuole from lytic to storage vacuole and back (Murphy et al. 2005). Within the last 15 years, numerous publications identified various compartments as vacuoles mostly because they appeared much larger than vesicles (i.e. much larger than the limit of optical resolution). The term provacuole is sometimes preferred for a small vacuole when a larger vacuole can be also detected in the same cell, although the term suggests a precursor compartment in the formation of a larger vacuole. This is usually difficult to appreciate given the time that may be necessary before the fusion of provacuoles to a larger central vacuole. Importantly, a prevacuole (or prevacuolar compartment, PVC) is an entirely different organelle (the equivalent of a late endosome in animal cells, which is also a multi-vesicular body), which is an intermediate sorting compartment where vacuolar receptors release their ligands and from where they are believed to recycle (see Lam et al. 2005). A precise distinction between vacuole, pro- and prevacuole would therefore require long-term dynamic studies of single cells that are technically difficult and therefore these organelles are likely to often be confused in the literature. Our goal is to review some of the latest results since the last excellent reviews made in this area a few years ago (Robinson and Rogers 2000; Sanderfoot and Raikhel 2003). We would like especially to urge to distinguish between biogenesis and function of vacuoles and for example not to conclude, that a target vacuole has a lytic character only because of the involvement of VSR/BP 80 protein.

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Identification of Different Vacuoles

One of the most commonly used dyes to visualise the vacuolar pH is neutral red, which is membrane-permeable in its unprotonated form, and trapped in the protonated form in acidic compartments, colouring acidic vacuoles. The use of various laser lines, usually associated with confocal spectral detection systems now allows us to use a more sophisticated probe, the lysosensor yellow/blue DND-160 with pH-dependent spectral peaks (Swanson et al. 1998; Diwu et al. 1999). It then becomes clear that the vacuolar pH can vary widely within a cell population. Expressed under the same 35S promoter, two different soluble vacuolar GFP markers were targeted by two different types of vacuolar sorting determinants (see below) to label either the acidic or the neutral vacuoles (Di Sansebastiano et al. 1998; Di Sansebastiano et al. 2001). Interestingly, when expressed stably in *Arabidopsis*, these GFP vacuolar markers do not systematically highlight the central vacuole. For example in leaves, the central vacuole of epidermal cells accumulates the acidic vacuolar marker (Aleu-GFP) while in the mesophyll cells the central vacuole accumu-