

Endocytic Uptake of Nutrients, Cell Wall Molecules and Fluidized Cell Wall Portions into Heterotrophic Plant Cells

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Abstract After arrival at the surface of heterotrophic cells, nutrients are taken up by these cells via endocytosis to sustain metabolic processes. Recent advances in plant endocytosis reveal that this is true for their heterotrophic cells, either cultivated in suspension cultures or for intact root apices. Importantly, sucrose appears to act as a specific stimulus for fluid-phase endocytosis. Uptake of extracellular nutrients by endocytosis is not in direct conflict with transport through membrane-bound carriers given that cell homeostasis can be better maintained if both these mechanisms operate in parallel. Besides nutrients, plant cells also accomplish internalization of cell wall molecules, such as xyloglucans and boron/calcium cross-linked pectins. Even large portions of apparently fluidized cell wall together with symbiotic bacteria can be internalized into some plant cells, suggesting that they can perform phagocytosis-like tasks despite their robust cell walls. Internalized cell wall molecules allow effective adaptation to osmotic stress, and also may serve for nutritive purposes. Plant endosomes enriched with the internalized cell wall molecules are used for new cell wall formation during plant cytokinesis. Moreover, rapid remodeling of cell walls through endosomal recycling is likely involved in opening/closing movements of stomata, and perhaps also in the formation of wall papillae during pathogen attacks and in recovery of cells from plasmolysis.

1

Introduction

Endocytosis is an inherent feature of all eukaryotic cells. The most notable role of endocytosis, elaborated especially in amebae and *Dictyostelium* cells, is cell nutrition via internalization of extracellular nutritive molecules and solutes (Marsch 2002). While vesicle-mediated nutrient uptake had been demonstrated in other organisms, corresponding studies in plants were derailed by: (i) studies suggesting the possible involvement of ion channels in the uptake of Lucifer Yellow when this fluorochole was actually intended to serve as a fluid phase marker (Cole et al. 1991); and (ii) by the demonstration of sugar transporters at both the plasma membrane (Williams et al. 2000; Lemoine 2000) and the tonoplast (Getz 1991).

Early reports on the engulfment of multilamellar and multivesicular compartments, now known to represent the plant late endosomes (Tanchak and Fowke 1987; Tse et al. 2004), by the central vacuole (Herman and Lamb 1991), as well as on their fusion with the plasma membrane resulting in so-called paramural bodies (Roland 1972), were dismissed as fixation artifacts. Early indications, that endocytosis may participate directly in the trapping, distribution, and sorting of extracellular components, were inherent in several papers published from the seventies up to the early nineties. Unfortunately, these early studies were not accepted by the mainstream plant cell biology community, since the general view was, that the high turgor pressure makes endocytosis in plant cells unfeasible (reviewed by Šamaj et al. 2004, 2005). As a result, the role of endocytosis as an inherent part of the overall mechanism of nutrient uptake into heterotrophic plant cells remained a controversial issue until recently (Echeverría 2000; Baluška et al. 2004; Etxeberria et al. 2005a, 2005b, 2005c).

The concept that dissolved nutrients in the extracellular milieu are potentially carried to the vacuole by an endocytic-related network was revived using a variety of membrane impermeable soluble dyes which eventually appeared in the vacuole, for instance in tobacco cultured cells (Emans et al. 2002; Yamada et al. 2005). Moreover, new studies reported internalization of fluid-phase endocytosis markers into cells of onion and maize root apices (Cholewa and Peterson 2001; Baluška et al. 2004), as well as into tobacco suspension culture cells (Yano et al. 2004). These studies using the fluorescent membrane impermeable dyes Alexa-568, 8-hydroxy-1,3,6-pyrenetrisulphonate, and Lucifer Yellow (LY), helped to overcome previous doubts and put to rest criticisms expressed on early experiments performed with these endocytic tracers (see the chapter by Šamaj, this volume).