

This Week's Citation Classic

Gunning B E S & Pate J S. "Transfer cells": plant cells with wall ingrowths, specialized in relation to short distance transport of solutes—their occurrence, structure, and development. *Protoplasma* 68:107-33, 1969.
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Plant cells with plasmalemma surface areas augmented by cell wall ingrowths were shown to be widespread. The term 'transfer cell' was coined in recognition of proposed general functions in transferring solutes between interconnected protoplasts (symplast) and nonliving spaces (apoplast) in or surrounding the plant. [The SC¹® indicates that this paper has been cited in over 220 publications since 1969.]

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"Transfer cells were not a new discovery in 1969. The literature of plant anatomy includes sporadic illustrations of cells with wall ingrowths, back to at least 1903, and when John Pate and I started our work, electron microscopists had published about 20 examples. Our other, more specialised, papers on transfer cells presented much more original research, but the 1969 article did provide a general synthesis by collating a scattered literature and adding new observations.

"The ingrowths of cell wall material, together with the plasmalemma that lines them, were viewed as a module with general functions in intensive short-distance transport of solutes in plants. Because the module can occur in many cell types, in many anatomical locations, and in all major taxa, we thought it useful to have a convenient term for cells that possess it, and hence used 'transfer cell' in a more general way than in our earlier paper¹ on the subject.

"Our backgrounds helped us to interpret and exploit our first observations. I had learned electron microscopy in K.R. Porter's laboratory at Harvard University a few years before, when Bill Philpott was studying surface area amplifications in chloride cells. After returning home to Belfast, I helped start a cell biology course, which included lectures on transporting epithelia in animal tissues. Pate had worked for many years on transport of solutes, particularly in legumes, and was able to provide the physiological insights upon which the whole synthesis rested.

"Nevertheless, when I saw my first wall ingrowths, I was sufficiently baffled to consign the micrograph to a box and get on with more interesting things. My second view, a year later, was again accidental. Pate was supervising an honours student research project on pea leaves, and I had agreed to take pictures of mesophyll cells. However, a minor vein in the sections revealed companion cells with mitochondria nestling between wall ingrowths. I recall referring to the cells as botanical kidney. Pictures from that block appeared in our first publication,¹ in which the term 'transfer cell' was used to convey a role in transferring solutes from one compartment in the leaf (the apoplast) to another (the symplast) prior to exporting them in the sieve tubes.

"We started searching for other examples. Leah Green patiently cut thousands of sections of legume nodules, leaf veins, stem nodes, and numerous other materials (including an *Azolla* root from Pate's father's tropical fish aquarium, thereby triggering my research on this beautiful object, started years later in Australia). It emerged that cells with wall ingrowths were more widespread than had been realised. The idea of writing a general article, and of applying 'transfer cells' in a more general context, followed naturally. The terminology and the structure-function interpretations were evidently acceptable, and the 1969 article now joins a subsequent review,² also highly cited. Perhaps cytologists have cited *Protoplasma* and physiologists, *Annual Review of Plant Physiology*! Reference 3 is the most recent comprehensive review."

1. Gunning B E S, Pate J S & Briarty L G. Specialized "transfer cells" in minor veins of leaves and their possible significance in phloem translocation. *J. Cell Biol.* 37:C7-12, 1968. (Cited 75 times since 1968.)
2. Pate J S & Gunning B E S. Transfer cells. *Annu. Rev. Plant Physiol.* 23:173-96, 1972. (Cited 170 times since 1972.)
3. Gunning B E S. Transfer cells and their roles in transport of solutes in plants. *Sci. Progr. London* 64:539-68, 1977.