

This Week's Citation Classic

Pate J S. Uptake, assimilation and transport of nitrogen compounds by plants.
Soil Biol. Biochem. 5:109-19, 1973.
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Understanding how plants work internally at the organ and tissue level, and how such activity relates to the assimilation of new raw materials from the environment, has long been regarded as a most worthwhile goal in plant physiology. When applied to plant nitrogen metabolism, fascinating findings emerge, each potentially significant to our appreciation of how different plant species operate, grow, and survive. [The *SCI*® indicates that this paper has been cited in more than 215 publications.]

Unraveling Plant Nitrogen Metabolism

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It is especially good for young scientists to face sustained criticism or even disbelief from senior colleagues. This is what Bill Wallace, my first PhD student, and I endured in the mid-1960s when presenting the Society of Experimental Biology (UK) with evidence that large quantities of amino acids were present in the root xylem bleeding sap of plants and that these compounds were being synthesized in roots from inorganic sources of nitrogen, such as ammonium or nitrate.

The dogma of the time was that roots supplied only water and mineral ions to shoots via xylem, so surely our observations must have resulted from leakage of cut tissues or contamination with microorganisms. However, we persisted in establishing our case to the society over the years, to the extent that one highly respected member was heard to announce with dismay, "Good grief, here's Pate again with his bleeding sap!" At least my Australian colleagues should appreciate the double entendre.

It quickly became apparent that the organic compounds of nitrogen exported from roots, and the ratio of these to free nitrate, were more or less species specific, while also varying with plant age and nutritional status. Our research group, now including Helen Brennan, Jim Greig, Chris Oghoghorie, and Frank R. Minchin, was by

then using assays for nitrate reduction in shoot and root, bleeding sap analyses, and labeling studies using ¹⁴C or ¹⁵N to depict how the exchange of individual solutes between shoot and root impacted upon total nitrogen metabolism.¹ As part of this approach, we also examined the carbon economy of shoot, root, and nodules of N₂-fixing plants,² heralding later work³ in which the carbon and nitrogen relationships of such plants were modeled at whole plant and organ levels.

Based on this approach, we conceived of feedback control of organ growth through complementary exchanges of key solutes in phloem or xylem and the possibility that roots might cycle excess N received from their shoots back to the shoot again through the transpiration stream. These and other aspects were highlighted in our 1973 article in *Soil Biology & Biochemistry*.

In retrospect, the picture presented in the review is embarrassingly incomplete, for it was not until several years later that it became possible to model quantitatively the suspected cycling and remobilization phenomena alongside the plant's measured inputs of carbon and nitrogen.

Despite the political upheavals in Northern Ireland during the 1960s and 1970s, it was an exciting time for botany at Queen's University, especially with the discovery of transfer cells by Brian E.S. Gunning—literally a few doors down the corridor from my laboratory. A cooperative period followed when we puzzled at the functional significance of these unusual cells,^{3,4} especially in relation to the loading and unloading of the long-distance transport systems that we had been studying in respect of nitrogen. It was an enormous pleasure to have someone of Brian's stature as a colleague, and I feel sure that he will be as pleased as I am to see four *Citation Classics* (this plus references 2, 3, and 4) resulting from those days in Belfast.

Frequent citation of the article probably stems from the fact that it addressed concepts that have subsequently featured prominently in research on N metabolism. It has thus served as a benchmark against which the behavior of other plant species can be assessed.

1. Pate J S & Wallace W. Movement of assimilated nitrogen from the root system of the field pea (*Pisum arvensae* L.). *Ann. Bot.* 28:83-99, 1964.
2. Minchin F R & Pate J S. The carbon balance of a legume and the functional economy of its root nodules. *J. Exp. Bot.* 24:259-71, 1973. (Cited 165 times.) [See also: Minchin F R. Citation Classic. (Barrett J T, comp.) *Contemporary classics in plant, animal, and environmental sciences*. Philadelphia: ISI Press, 1986. p. 89.]
3. 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. (Cited 305 times.) [See also: Gunning B E S. Citation Classic. (Barrett J T, comp.) *Contemporary classics in plant, animal, and environmental sciences*. Philadelphia: ISI Press, 1986. p. 14.]
4. Pate J S & Gunning B E S. Transfer cells. *Annu. Rev. Plant Physiol.* 23:173-96, 1972. (Cited 245 times.) [See also: Pate J S. Citation Classic. (Barrett J T, comp.) *Contemporary classics in plant, animal, and environmental sciences*. Philadelphia: ISI Press, 1986. p. 15.]

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