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***Editorial***

# Microtubules Show their Sensitive Nature

**Geoffrey O. Wasteneys**
*Plant Cell Biology Group, Research School of Biological Sciences, The Australian National University, Canberra ACT, 2601, Australia*

Since their first description in plant cells four decades ago (Ledbetter and Porter 1963), cortical microtubules have been the subject of research that has primarily focussed on the relationship between cortical microtubule orientation and cellulose microfibril alignment during morphogenesis. This research has emphasized microtubules behaving as static elements, with their structural properties put to useful work as scaffolds and barriers. Just how microtubules do this, however, is still a matter of debate, and recent conflicting interpretations (compare, for example, Burk and Ye 2002 and Sugimoto et al. 2003) suggest that we are far away from understanding this phenomenon.

What other functions do plant cortical microtubules have? Their intimate association with the plasma membrane, the major platform for signal perception and transduction (Gilroy and Trewavas 2001, Wasteneys and Galway 2003), suggests that microtubules are targets of various signals and switches. But could the microtubules themselves play an integral role in signalling events that enable plants to adapt to environmental changes?

Microtubules are far more complex than the hollow cylinders that can assemble in vitro from tubulin dimers. Indeed, the microtubule surface is a busy and congested place, covered with protein complexes, motor proteins and structural microtubule-associated proteins, GDP/GTP, regulatory kinases, phosphatases, and ions. But in addition, we now know that microtubules in plant cells are the landing platforms for some things less predicable, like elongation factor 1α (Durso and Cyr 1994) and the signal transduction enzyme phospholipase D (Gardiner et al. 2001). These discoveries suggest that cortical microtubules do much more than just regulate the direction of cell expansion.

Could microtubules act as repositories for signalling enzymes, with their polymer status helping to modulate plant responses to various stresses and signals? In addition to their role in controlling the mechanical properties of cell walls, might cortical microtubules also act as gauges of ambient conditions, such as temperature, or the level of nutrients and toxic substances in the soil? Three articles published in this issue of PCP from the laboratories of Tobias Baskin (University of Missouri), Peter Nick (University of Freiburg) and Jan Marc (University of Sydney) provide glimpses into the behaviour and function of cortical microtubules. These articles suggest that microtubules are not only downstream targets of signalling pathways but also potential agents of signal transduction.

### *Aluminium toxicity responses*

Sivaguru et al. (2003) (pp. 667–675) have uncovered novel features of the aluminium (Al) sensing mechanism in *Arabidopsis* roots. By thoughtful analysis, they demonstrate not only that Al treatment depolymerizes cortical microtubules and depolarizes the plasma membrane (see cover image) but that glutamate receptors are likely to mediate this process. The authors hypothesize that Al stimulates glutamate efflux, which, by activating ionotropic glutamate receptors, drives $Ca^{2+}$ influx. They further suggest that microtubule depolymerization may be integrated with the Al-induced signal transduction cascade that leads to organic acid secretion.

### *Microtubules as thermometers*

Plants that can withstand sub-zero temperatures generally require a period of cool weather in order to adapt, a process known as cold acclimation. Abdrakhamanova et al. (2003) (pp. 676–686) have discovered that transient microtubule disassembly may be an integral feature of cold acclimation. They show that at 4°C, cold-resistant wheat cultivars undergo a rapid but transient disorganization of cortical microtubules in root cortex cells, and that the composition of α-tubulin isotypes also changes during acclimation. In contrast, cold-sensitive cultivars do not respond in this way and microtubules remain intact during unsuccessful attempts at cold acclimation. Remarkably, transient depolymerization of microtubules using the drug pronamide leads to the seedlings of the cold-sensitive cultivar becoming freeze-tolerant. Thus, the transient and partial disassembly of microtubules appears to be sufficient for triggering the adaptive responses that enable wheat seedlings to survive freezing temperatures.

### *Phosphatidic acid signalling*

The second messenger phosphatidic acid (PA) is produced from phospholipids by the enzyme phospholipase D (PLD). PA is emerging as an important signalling molecule in plants (Munnik 2001) and PA produced by PLD has recently been shown to be required for pollen tube growth (Potocký et al. 2003). On pages 687–696, Gardiner et al. (2003) show how 1-butanol, an alternative substrate for PLD, and therefore an inhibitor of PA production, disrupts cortical microtubule organization and impairs anisotropic expansion in *Arabidopsis* seedlings. Their results suggest that microtubule organization is sensitive to changes in PA levels. Previous work by the same group demonstrated that one PLD isozyme associates with microtubules as well as with the plasma membrane (Gardiner et al. 2001). This leads to the interesting question of whether the activity of PLD is somehow linked to microtubule polymer status, and part of a phosphoinositol signalling positive feedback loop involving actin microfilament remodelling.

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