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Short communication

The cytoskeleton, elongation and the control of elongation

Jean-Pierre Verbelen[*], Jie Le, Kris Vissenberg

Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Wilrijk, Belgium

The epidermis is often considered to be the growth-limiting cell layer in young, growing herbaceous plants (Niklas, 1992). In his classic work, Green (1980) elaborated this idea further for organ development, and attributed a crucial role to the orientation of cellulose fibrils as indicator of mechanical properties. A factual proof for a relation between the mean cellulose orientation and mechanical anisotropy was reported recently (Kerstens et al., 2001).

Cortical microtubules are supposed to guide the cellulose synthesising complexes in the plane of the plasma membrane (Giddings and Staehelin, 1991). Changes in the direction of cell expansion are accompanied by changes in the orientation of the cortical microtubules. A role for microtubule reorientation is also expected during changes in the rate of elongation: microtubules then will guide nascent cellulose microfibrils deposition in the longitudinal direction, which will hamper elongation and facilitate cell expansion in another direction (Taiz and Zeiger, 1998). However, this generally accepted relation between microtubules and microfibrils has also been questioned (e.g. Baskin, 2000; Emons and Mulder, 2000; Sugimoto et al., 2000; Williamson, 1990).

In the elongation zone of *Arabidopsis* roots, microtubules in epidermal cells are transverse to the root axis. Towards the end of elongation, when cells enter the root hair initiation zone, microtubules switch to a slightly oblique orientation in atrichoblasts and to very oblique or longitudinal orientations in trichoblasts.

The rate of elongation can be affected by different means. When roots are exposed to ethylene or ACC, the precursor of ethylene, the elongation rate is quickly and severely reduced, in a dose-dependent way (Le et al., 2001). This is the result of cells stopping elongation at a much reduced size. As soon as elongation of a cell ceases, microtubules change their orientation from transverse to longitudinal. This rearrangement is cell position bound. In the early part of the elongation zone, cell elongation up to a length of 30 μm is not affected and microtubules keep predominantly to a transverse orientation. Osmotic stress induces similar effects on elongation and microtubule reorientation. Experiments with microtubule drugs, demonstrate that microtubules are essential for elongation to go on but reorientation of microtubules is not involved and only concomitant with the fast control of elongation rate. We propose that the switch in microtubule orientation is a mechanism used by the cells to consolidate the shorter cell size and to inhibit further elongation.

In the *Arabidopsis* hypocotyl, elongation starts at the base and proceeds in an acropetal direction. In darkness, elongation proceeds at a much higher rate than in the light. In the lower half of the hypocotyls, cells grow to about 2.5 times the size they reach in the light, while the cells at the top of the hypocotyl become 6–7 times longer. This is accompanied by striking differences in microtubule levels. In darkness, microtubules are quite immobile and neatly transverse in elongating cells. In the light, however, they are extremely mobile and transverse but also a variety of other microtubule orientations were found. However, in all plants studied, cells that have stopped elongation have fewer microtubules and these generally have a longitudinal orientation. Therefore, we propose that when the elongation rate is maximal (darkness) the wall synthesis activity at the cell membrane recruits all available microtubules in transverse arrays. When the rate of cell elongation is much lower (light) only a fraction of the microtubules is recruited and the remainder of the microtubules can freely change orientation. This leads to the variety of orientations seen in the light. When cells have no longer the possibility to elongate (aged cell at the base) the

* Corresponding author. Tel.: +32-3-820-2277; fax: +32-3-820-2271.

microtubules have a longitudinal orientation and are reduced in number.

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