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Intercellular Alignments of the Plant Cytoskeleton

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Abstract

The cytoskeleton orchestrates many processes in plant development, including division and control of the direction of cell expansion, and is therefore central in the coordination of plant growth. There are a number of situations in which there is a precise alignment of the cytoskeleton, in particular microtubules, between neighboring cells. However, it is not known how these intercellular alignments are brought about. We discuss the possibility that the intercellular alignments are due to individual cells each responding in turn to an external orienting vector, without a need for direct communication between cells. Alternatively, there may be information exchange between the cells about the orientation of the cytoskeleton to allow for coordination. This exchange could take place directly via the plasmodesmata or more indirectly through the intervening cell wall. The final possibility, discussed here, is that orientation of the cytoskeleton in neighboring cells is coordinated via direct continuity of the cytoskeleton between neighboring cells, presumably via the plasmodesmata.

Key words: Plant cytoskeleton; Intercellular alignment; Plasmodesmata; Microtubules; Actin; Cell wall

Introduction

The main components of the plant cytoskeleton, microtubules and actin, play a central role in cell division, cell expansion, and intercellular communication in the plant (for review see Kost and others 1999; Meagher and Williamson 1994). The coordination of these processes across tissues and organs is thought to be necessary for correct plant morphogenesis. There are a number of situations in which there is a direct intercellular alignment of the microtubules and sometimes actin in neighboring cells or even across tissues. Here we outline some examples of these intercellular alignments and explore the possible mechanisms involved in orchestrating them.

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Intercellular Alignments of the Cytoskeleton

In plant cells expanding along their entire length, that is, not undergoing tip growth, during interphase the microtubules are arranged in the cortex of the cell in a parallel alignment perpendicular to the axis of expansion (Figure 1A). There is strong evidence that this alignment of microtubules controls the precise alignment of deposition of the cellulose microfibrils in the cell wall (Cyr 1994; Williamson 1991; Wymer and Lloyd 1996) and subsequently the direction of cell expansion. In many tissues, all the cells are expanding in a coordinated fashion so that in longitudinal sections in the plane of expansion the microtubules are seen as transverse arrays across the tissue (Figure 1B). Sections through cell walls show microtubule labeling in a symmetrical pattern on either side of the wall (Figure 1C; Ueda and Mat-

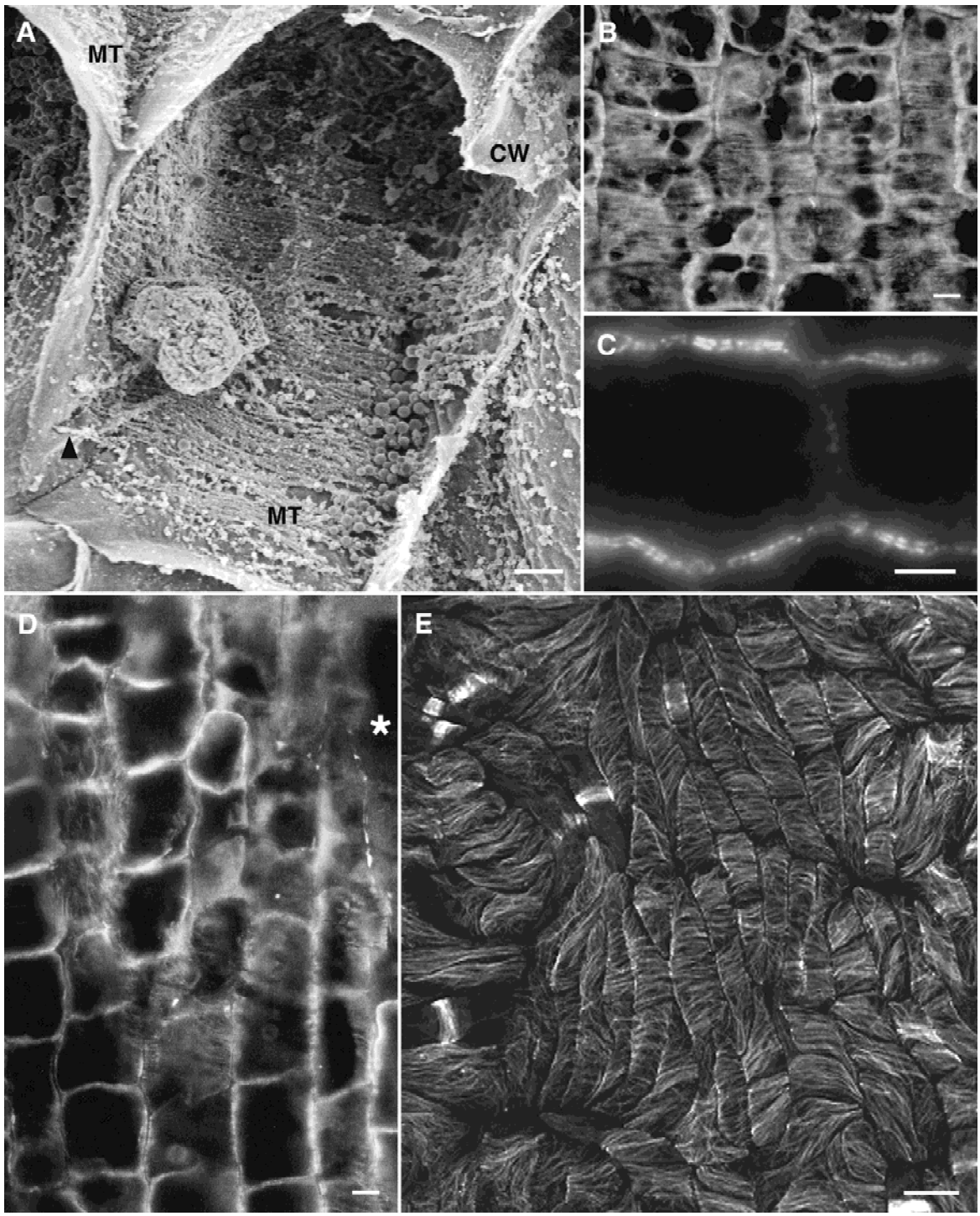

Figure 1. **(A)** High-resolution scanning electron microscope image of a fractured cortical cell in an onion root tip (prepared as described in Vesk and others (2000)). Much of the cell contents and plasma membrane have been lost during preparation but clear transverse arrays of cortical microtubules (MT) remain closely associated with the cell wall (CW). Occasionally, microtubules can be seen terminating at the cell wall (arrowhead). **(B–E)** Immunofluorescent labeling of microtubule arrays. Microtubules form transverse arrays across cortical tissues in pea root tips **(B).** On the side walls of cortical cells in maize roots, there is close alignment of microtubules on opposite sides of the wall **(C).** Following wounding of pea roots, microtubules realign to form arrays parallel to the edge of a wound (asterisk) **(D).** In the epidermal cells of leaf primordia in *tangled 1* mutant of maize, the microtubules in abnormally shaped cells often are co-aligned with those of their neighboring cells **(E).** Scale bars: **(A)** 2 μm, **(B–E)** 10 μm. **(D)** is reprinted with permission from Hush and others (1990), **(C)** was provided by John Gardiner, and **(E)** is reprinted with permission from Cleary and Smith (1998).

suyama 2000), indicating co-alignment of microtubules in parallel arrays in adjoining cells.

The intercellular alignments in tissue undergoing coordinated expansion could simply reflect the fact that the cells have a similar shape and orientation. The intercellular alignments are more striking when the microtubules develop new orientations such as occurs during the establishment of growth axes during the development of leaf primordia (Hardham and others 1980; Marc and Hackett 1989). These microtubules form continuous hoops, transcending cell boundaries, and establishing cellulose microfibril deposition that leads to cylindrical expansion of groups of cells.

Although these examples are programmed developmental changes, unprogrammed changes in the direction of growth, such as occurs following wounding, also are preceded by remarkable reorientations, with the microtubules precisely aligned between cells (Hush and others 1990). In pea roots, microtubules realign parallel to the edge of a puncture by 5 hours after wounding (Figure 1D). The microtubule alignment appears to transcend cell boundaries. Thus, microtubules can change from transverse to oblique or longitudinal depending upon their location relative to the wound. This reorientation establishes a new direction of expansion of the cells surrounding the wound such that they expand inward toward the center of the wound to replace the tissue lost.

Attempts to understand the control of cell division and morphogenesis have focused on mutants in which these processes have been disrupted. One such mutant is *tangled 1*, in which the spatial control of cell division in maize leaf development is disrupted (Smith and others 1996). Although this leads to abnormally shaped cells, the mutant leaves still have a normal shape. The microtubules in these abnormally shaped cells are often co-aligned with those of their neighboring cells (Figure 1E). It has been suggested that there is a regional exchange of information between cells that helps to orient the expansion of these abnormally shaped cells to produce a normal leaf (Cleary and Smith 1998). The maize mutant *warty-1*, which has abnormal division and cell expansion in the leaf epidermis, has also been hypothesized to have regional communication between neighboring cells (Reynolds and others 1998).

Some form of regional communication may well be involved in the positioning of the preprophase bands of microtubules that establish the site of cell plate fusion with parent walls. Four-way junctions of cell walls are generally avoided (for example, Flanders and others 1990). One exception is in the unusual case of wound regeneration in which the new cell walls are inserted side by side parallel to the edge of the wound (for review see Gunning 1982).

Kennard and Cleary (1997) have suggested that there is an unknown signal that emanates from the guard mother cell to influence polarization and mitosis in the surrounding subsidiary mother cells. The guard mother cell appears to control the organization of the cortical actin (Cleary and Mathesius 1996), cytoplasmic actin (Kennard and Cleary 1997), and cortical microtubules (Pickett-Heaps and Northcote 1966) in the surrounding subsidiary mother cells.

Our knowledge about intercellular alignment of actin is not as strong as that for microtubules, probably because actin is notoriously difficult to preserve. However, there is evidence of co-alignment of cortical actin and microtubules as well as suggested roles for actin in establishing and maintaining the microtubule orientations (for review see Kost and others 1999) so that an intercellular alignment of actin could be expected. Indeed, Goodbody and Lloyd (1990) demonstrated precise realignments of cortical actin that transcended cell boundaries in the epidermis of *Tradescantia* leaf following a wound.

These examples of intercellular coordination in cytoskeletal orientations suggest that intercellular signaling is taking place. However, it should be noted that there are also situations in which neighboring cells have no coordination in cytoskeletal alignment. One notable example of this is the azuki bean epicotyl epidermis in which microtubule alignment alternates among transverse, oblique, and longitudinal in individual cells, but is not coordinated between neighboring cells (Takesue and Shibaoka 1998). It may be that this tissue is able to turn off the communication pathway that is normally in operation. There are also sites of discontinuities in microtubule alignment at the apical meristem as the leaf primordia are initiated (Marc and Hackett 1989).

How Is Intercellular Alignment Brought About?

Cells May Respond to a Common Gradient

The co-alignment of microtubules in neighboring cells may simply reflect the fact that the individual cells are responding to a common gradient (for review see Hush and Overall 1996) generated at the level of the whole plant or tissue.

The minute electrical fields that are generated around plant tissues (for review see Nuccitelli 1990) are an attractive candidate as an orienting signal for microtubules. The precise realignment of microtu-

bules parallel to the edge of a wound in pea roots (Hush and others 1990) may well be mediated by the electric gradients generated in tissue by wound currents (Hush and Overall 1989). Indeed, small applied electric fields orient microtubules perpendicular to the field in plant organs (Hush and Overall 1991), cells (White and others 1990), and callus (Blackman and Overall 1995). In the case of the callus, microtubules realign to the electric field, irrespective of cell orientation and shape. Eventually, this new alignment generates coordinated cell expansion within the callus.

Mechanical vectors generated by turgor pressure, growth, and shape of the organ are also present in plants. The orientation of microtubules appears to be sensitive to the mechanical environment of the cell (Cleary and Hardham 1993; Fischer and Schopfer 1998; Hush and Overall, 1991; Wymer and others 1996). In addition, isolated plant cells are able to determine a shear-free orientation for insertion of new walls (Lynch and Lintilhac 1997), presumably preceded by a pre-prophase band of microtubules. The intercellular alignment of microtubules may involve microtubules responding to a tissue-wide mechanical environment (for review see Hejnowicz and others 2000). Alternatively, it may be that individual cells exert physical forces on their neighbors and that the mechanical signals for coordination of cytoskeletal alignment could be quite localized. Localized pressure on an individual cell causes nuclear migration to the site of pressure (Kennard and Cleary 1997). The precisely orchestrated actin-based migrations of nuclei during guard cell formation has been suggested to involve a physical signal from the guard mother cell to the subsidiary cells (Kennard and Cleary 1997).

Plant hormones can affect microtubule orientation (for review see Hush and Overall 1996). Thus, intercellular alignments may reflect a particular concentration of a hormone in a group of cells. However, it is difficult to understand how the precise realignments of microtubules around a pea root wound (Hush and others 1990) could be generated by the distribution of a hormone.

Signals May Pass Between Cells Via the Plasmodesmata

The cytoplasm and endoplasmic reticulum (ER) of adjoining cells are continuous via the connecting cylindrical membrane-lined channels known as plasmodesmata (Figure 2A–D) (for review see Overall 1999). The size of molecules that can pass through plasmodesmata depends upon the species, tissue, and developmental and physiological state of the tissue (for review see van Bel and others 1999). This size ranges from small molecules around 600Da (Robards and Lucas 1990) to GFP fusion proteins in the order of 50kDa (Crawford and Zambryski 2000; Oparka and others 1999). In plants, positional information, rather than cell lineage, determines the fate of cells (Szymkowiak and Sussex 1992; van den Berg and others 1995). There is an expanding body of evidence that developmental signals such as the KNOTTED 1 protein (Jackson and others 1994; Lucas and others 1995) and LEAFY protein (Sessions and others 2000) pass from cell to cell via plasmodesmata. Given this, it is possible that an as yet unidentified signal passes through plasmodesmata to either control cytoskeletal orientation or provide information about the orientation in neighboring cells.

There is currently no direct evidence to support this suggestion but there are some examples in which changes in the cytoskeleton in adjacent cells are associated with changes in intercellular communication. For example, wholesale realignment of cortical microtubules in tobacco thin cell layers (Wilms and Derksen 1988) is accompanied by an increase in the level of intercellular communication (Cantrill pers. comm.). In some tissues, cells that are dividing synchronously remain in communication whereas asynchronous divisions involve communication isolation (Ehlers and Kollman 2000; Kwiatkowska and Maszewski 1986).

Signals May Pass Between Cells Via the Cell Wall

The plant cell wall is also a pathway for developmental signals (Brand and others 2000; Fletcher and Meyerowitz 2000) and signals that elicit a defense response (Chappell and others 1997). The signaling molecules may involve cell wall components such as arabinogalactan proteins or oligosaccharides (for review see Wojtaszek 2000). This opens the possibility that signals that orchestrate the co-alignment of microtubules in adjacent cells could move through the cell wall.

However, the one-to-one alignment of the cytoskeleton in neighboring cells, as illustrated in Figure 1C, suggests that some form of short-range signaling is taking place. The cortical microtubules and actin appear to be closely anchored to the cell membrane and possibly through to the cell wall (Figure 2E,F). The cytoskeleton may be anchored via integrin-like molecules (Wayne and others 1992) or microtubule-associated proteins such as the 90kDa protein identified by Marc and others (1996). The strength of the plasma membrane attachment to the cell wall

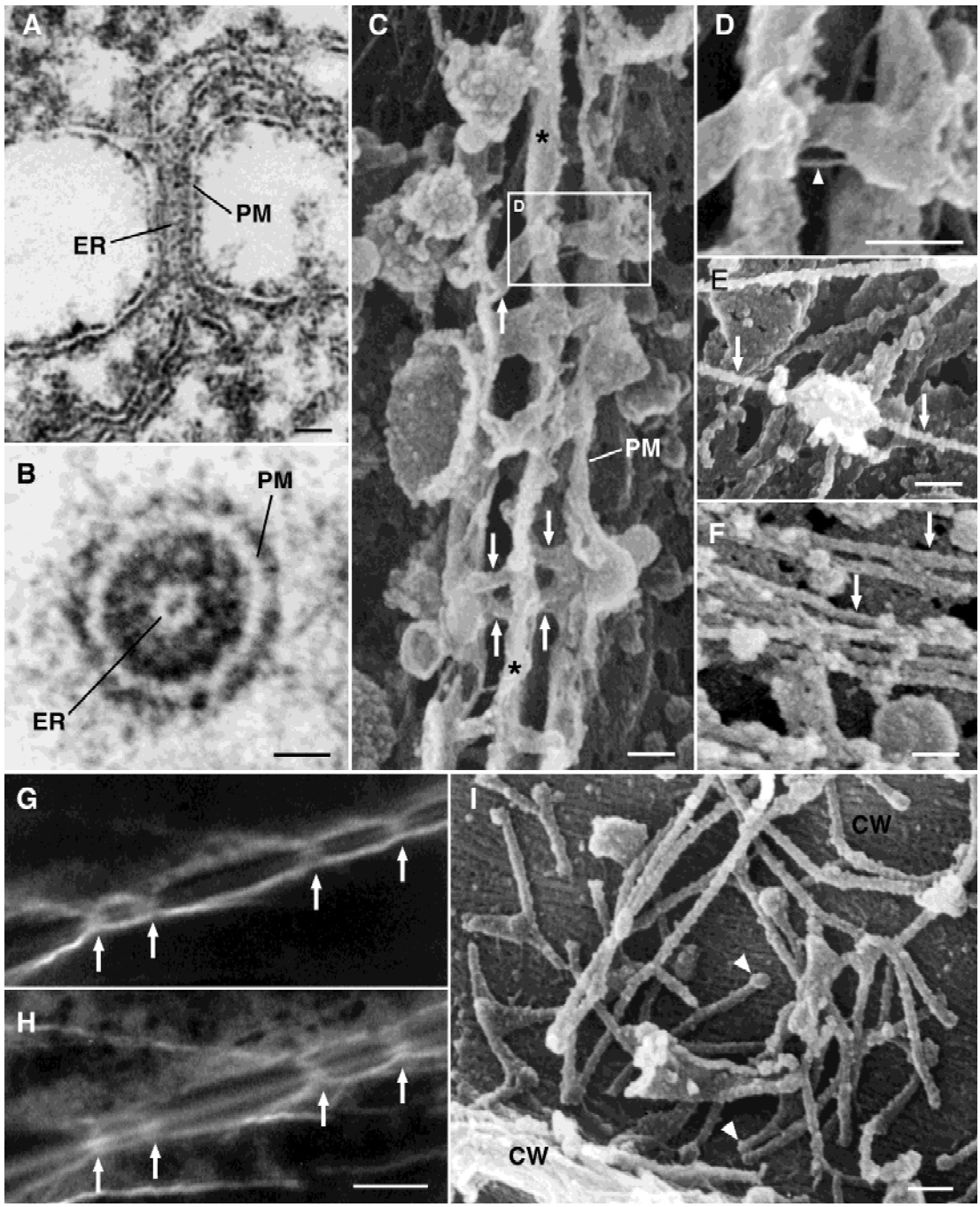

Figure 2. **(A,B)** Transmission electron micrographs of plasmodesmata from *Azolla* root tips. In the longitudinal view, **(A),** the plasma membrane (PM) surrounding the plasmodesma can be seen to be continuous between neighboring cells. The endoplasmic reticulum (ER) in the neighboring cells is continuous through the plasmodesma. **(B),** a transverse image shows the cell membrane clearly delimiting the plasmodesma; the ER forms a tightly furled cylinder. There is a mottled layer between the ER and the plasma membrane. **(C–F)** and **(I)** are high-resolution scanning electron microscope images of cortical cells in onion root tips (prepared as described by Vesk and others (2000)). **(C)** Figure shows a fracture through the cell wall (asterisks), several plasmodesmata (arrows) joining the two adjacent cells, and the plasma membrane (PM). **(D)** A higher magnification of the box in **(C)** showing fine connections between cells (arrowhead). Actin microfilaments (arrows) **(E)** and microtubules (arrows) **(F)** remain closely associated with the plasma membrane and the underlying cell wall. **(G,H)** Adjacent confocal laser scanning microscope optical sections of inner epidermal peels of *Hordeum vulgare* stained with rhodamine-phalloidin, showing actin filaments and fluorescent pit fields (arrows). **(I)** Sites of attachment (arrowheads) of Hechtian strands to the cell wall (CW) in plasmolyzed cells. Scale bars: **(A)** 25 nm, **(B)** 10 nm, **(C–F, I)** 100 nm, **(G,H)** 5 μm. **(A,B)** Reprinted with permission from Overall and others (1982), **(C)** reprinted with permission from Vesk and others (2000) and **(G,H)** reprinted with permission from White and others (1994).

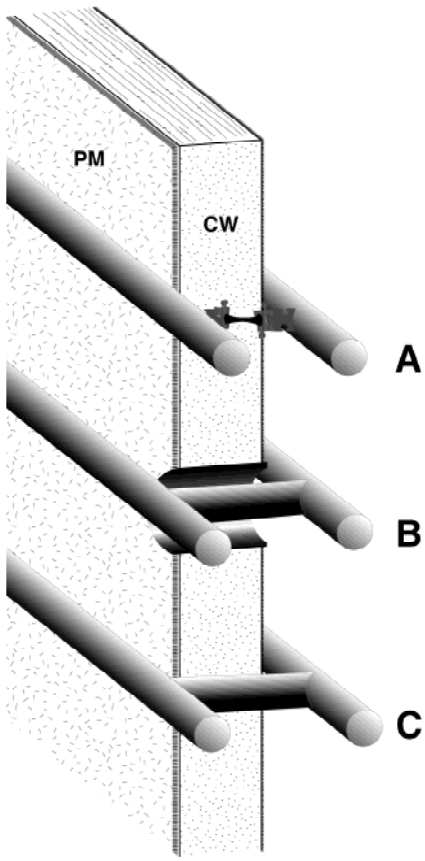

Figure 3. A diagram of possible linkages connecting the cytoskeleton in neighboring cells across the intervening cell wall (CW) and plasma membranes (PM). **(A)** An indirect link via transmembrane proteins and some as yet unidentified connection. **(B)** The cytoskeleton, in particular actin, probably links to that in neighboring cells directly via the plasmodesmata. **(C)** Illustration of the unlikely possibility that the cytoskeleton is continuous between neighboring cells, but not via plasmodesmata. This diagram is not to scale.

at particular sites, not only at plasmodesmata, is evidenced in plasmolyzed cells where Hechtian strands anchor to the cell wall (Figure 2I, Lang-Pauluzzi 1999; Oparka and others 1994). This cytoskeleton-cell membrane-cell wall continuum may even continue between neighboring cells such that the extracellular links to the cytoskeleton may be connected in an unknown way through to similar links on the other side of the wall (Figure 3A). There is no direct evidence for such links but occasionally, in high resolution scanning electron micrographs, fine connections can be seen along with plasmodesmata connecting adjacent cells (Figure 2D).

Cytoskeleton May be Continuous Between Adjacent Cells

The final possibility is that the co-alignment of the cytoskeleton in adjacent cells is orchestrated by the direct continuity of the cytoskeleton between neighboring cells. Actin (Figure 2G,H) and myosin have both been localized to plasmodesmata in the green alga *Chara* and other plants (for review, Overall and others 2000). In models of intercellular movement of tobacco mosaic virus, the movement protein bound to the viral RNA is transported on microtubules to the cell periphery and the plasmodesmata (Reichel and others 1999). Indeed, the movement protein may even co-assemble with tubulin as it has a conserved sequence that shows similarity to the region in tubulin responsible for lateral association of protofilaments (Boyko and others 2000). As this association of the movement protein with the microtubules is critical in the intercellular spread of the viral RNA, there may be some association of the microtubules with the plasmodesmata. However, though tubulin is found in wall extracts containing plasmodesmata but not in extracts lacking plasmodesmata (Blackman and Overall, 1998), there is no specific immunolocalization of tubulin to plasmodesmata. A rather unlikely possibility is that microtubules or actin actually cross the cell wall but not within plasmodesmata (Figure 3C). There is no evidence for elements of the dimensions of actin or tubulin seen crossing between adjacent cells alongside the plasmodesmata (compare Figures 2C-D with Figures 2E-F). For microtubules to show precise co-alignment in sections such as in Figures 1B and D, the microtubules would need to pass into neighboring cells along the edges of the cell. A single microtubule can be seen attached to the cell wall in just this position in Figure 1A, but there is no evidence for intercellular continuity.

Conclusion

Intercellular co-alignment of the cytoskeleton is widespread but our knowledge of how this alignment is orchestrated is limited. The challenge now is to determine if there is a relationship between the level and nature of intercellular communication and the intercellular co-alignment of the cytoskeleton.

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