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Comparing plant and animal extracellular matrix–cytoskeleton connections – are they alike?

Review article

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Dedicated to Professor Dr. Hartmut K. Lichtenthaler on the occasion of his 60th birthday

Summary. Cell adhesion and communication is one of the most fascinating fields of modern biology. How do cells receive information from the environment and from neighboring cells? How does this information elicit morphogenesis, cell division and migration? The recent identification of the surface molecules involved in these events in animal systems is beginning to disclose that a continuum, extracellular matrix–plasma membrane–cytoskeleton, may be a common structure present in all eukaryotic cells. In this article we compare current knowledge on this complex structure in animal systems to the emerging data on plants. We point out the areas that need additional research to fully understand the role of the cell wall–cytoskeleton continuum in plants.

Keywords: Adhesion; Cell wall; Cytoskeleton; Extracellular matrix; Integrin; Plasma membrane.

Abbreviations: ABP actin-binding protein; AGP arabinogalactan proteins; CTK cytoskeleton; ECM extracellular matrix; FN fibronectin; hFN human fibronectin; HRGP hydroxyproline-rich glycoproteins; hVN human vitronectin; PM plasma membrane; SAM substrate adhesion molecule; VN vitronectin.

Introduction

The development of cell adhesive mechanisms was a key event in the evolution from single cell to multicellular organisms. In spite of the difference between these mechanisms in animal and plant taxa, cell adhesion has a fundamental role in the perception of environmental signals leading to changes in development, morphogenesis and motility. Specialized structures at the cell surface are the principal elements involved in cell adhesion and communication. These structures include plasmodesmata and gap junctions that interconnect the cytoplasm of neighboring cells in plants and animals, respectively, and the continuum, extracellular matrix (ECM)–plasma membrane (PM)–cytoskeleton (CTK). Plasmodesmata allow the flow of intracellular signals (ions, metabolites and macromolecules) within cells of the same tissue. The complex structure that links the ECM to the CTK guarantees traffic of mechanical signals between the cell and the environment, or between cells.

The involvement of the continuum ECM-PM-CTK as mechanochemical transducer in animals is now well established (Ingber 1991, Edelman 1993). Recent evidence shows that plant cells may also have a cell wall–plasmalemma–cytoskeleton continuum that functionally parallels that of animal systems, but albeit with specific plant components (Wyatt and Carpita 1993). Here we will analyze the similarities and differences found in the ECM-PM-CTK complexes from plants and animals (Table 1).

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The extracellular matrix

Animal systems

Animal ECMs are intricate networks of glycoproteins and carbohydrates secreted by the cell (Woessner 1993). The major components of the ECM include: (a) substrate adhesive molecules (SAM) such as fibronectin (FN), vitronectin (VN), laminin and tenascin; (b) structural components, such as collagen and elastin; and (c) proteoglycans, a complex array of proteins with glycosaminoglycan side chains (Table 1).

It is believed that ECMs have evolved as a response to the mechanical forces acting on multicellular organisms and are therefore an integral part of the machinery that regulates cell function. ECMs can act as positive or negative regulators of functional differentiation depending on the cell type, but they exert their regulation of gene expression by mechanisms distinct from those known for soluble transcription factors. ECM molecules interact with each other and with their specific receptors on the plasma membrane. Extracellular signal transduction occurs across the plasma membrane via ECM-receptor triggered by the ligand binding. Mechanical forces, applied directly to cell surface receptors, increase cytoskeletal rigidity (Wang et al. 1993). Changes in these receptors produce a rearrangement of the cytoskeletal network and they generate an intracellular cascade of signals leading to changes in gene expression.

The plant cell wall

In recent years, plant biologists are using ECM as an alternative term to designate the plant cell wall (Roberts 1989, Adair and Mecham 1990). The term ECM, as taken from animal cell biology, intends to underscore that the cell wall is a dynamic structure and not only a static enclosure for the plant cell. However, the term "extracellular" is not appropriate for the plant cell, even if it is on the external side of the plasma membrane. In this review we will use the classical term cell wall (CW) for plants, keeping in mind that the CW is a dynamic structure with some functions that can be equivalent to the animal ECMs.

Our understanding of plant CW structure is limited to the chemical nature of the polymers involved. They consist of (a) polysaccharides such as cellulose, xyloglucans, arabinogalactans, and pectins; (b) proteoglycans like arabinogalactan proteins (AGPs); and (c) proteins: hydroxyproline-rich glycoproteins (HRGPs), glycine-rich proteins, proline-rich proteins,

Table 1. Molecules involved in the continuum ECM-PM-CTK in animal and plant systems. The cytoskeleton and the extracellular matrix have been discriminated between the structural elements and the molecules binding such structural elements and the plasma membrane receptors

	Cytoskeleton		Membrane receptors	Extracellular matrix	
	Fiber system	ABPs MAPs		Adhesion molecules	Structural components
Animals	microfilaments	talin vinculin	integrins	vitronectin fibronectin	collagens elastin
	microtubules	α-actinin ankyrin	non-integrin	laminin tenascin	proteoglycans
	intermediate filaments	spectrin distrophin MAPs		collagen V	
Plants	microfilaments	ankyrin motifs	laminin receptor homolog	AGPs	cellulose hemicelluloses
	microtubules	*spectrin*		*vitronectin* *fibronectin*	pectins
	intermediate filaments	*MAPs*	*integrins*	*laminin*	arabinogalactan HRGPs PRPs GRPs

In italics, molecules whose presence has been suggested by indirect evidence, but has not yet been clearly identified in plant tissues
ABPs actin-binding proteins; *MAPs* microtubule-associated proteins

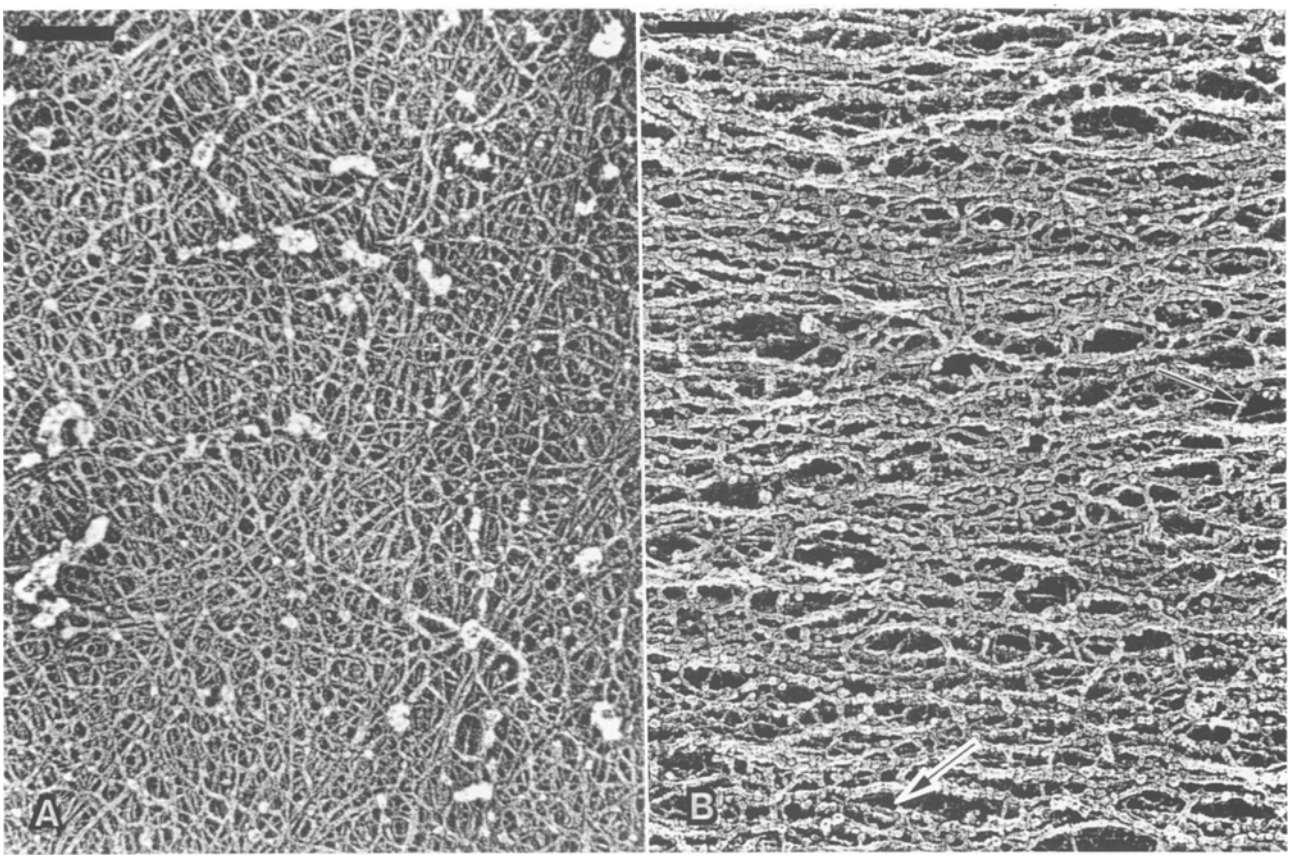

Fig. 1. Micrographs at high resolution electron microscopy of ECM replicas prepared by the quick-freeze, deep-etch, rotatory-shadow replica technique. **A** Fresh unfixed onion cell wall. Bars: 200 nm (McCann and Roberts 1990). **B** Columnar filament layer of the frog otolithic membrane. Bar: 200 nm (Kachar et al. 1990)

and enzymes (Cassab and Varner 1988, Varner and Lin 1989, Keller 1993, Showalter 1993) (Table 1). In spite of the limited available data concerning the supramolecular structure of those components, many published models showing the architectural arrangement of the plant CW are available (Talbott and Ray 1992, Carpita and Gibeaut 1993). Other than the differences in chemical nature of animal and plant ECMs, the plant cell wall is present throughout the life of the cell. Plant cell wall grows and differentiates with the cell, and adapts to changes in environmental conditions as well (Shedletzky et al. 1992, Cosgrove 1993). Finally, unlike animal cells, plant cell adhesion does not result from interactions between the plasmalemma of different cells, but involves the adhesion of neighboring cell walls (Knox 1992).

A shared fibrillar structure

An unexpected fact when comparing plant and animal extracellular matrices is the surprising similarity of their macromolecular structure, when visualized with high resolution electron microscopy. The use of the quick-freeze, deep-etch, rotatory-replication technique developed by Heuser (1981), enables the observation of unfixed, unstained material. The technique preserves the three-dimensional molecular arrangement, and the sample can be observed with high resolution stereomicroscopy. Figure 1 shows the structures of a fresh unfixed onion cell wall (Fig. 1 A) and of a frog otolithic membrane (Fig. 1 B) (McCann et al. 1990, Kachar et al. 1990). ECMs show a particular architectural arrangement that looks like a continuous network. The mechanical properties of the network are probably important, though not the chemical nature of its components. Tomato cell cultures adapted to 2,6-dichlorobenzonitrile (an inhibitor of cellulose synthesis) have functional, coherent walls containing almost exclusively pectins (Shedletzky et al. 1992), clearly demonstrating that molecules can be replaced in the ECM. The shape, strength, and three-dimensional structures of plant

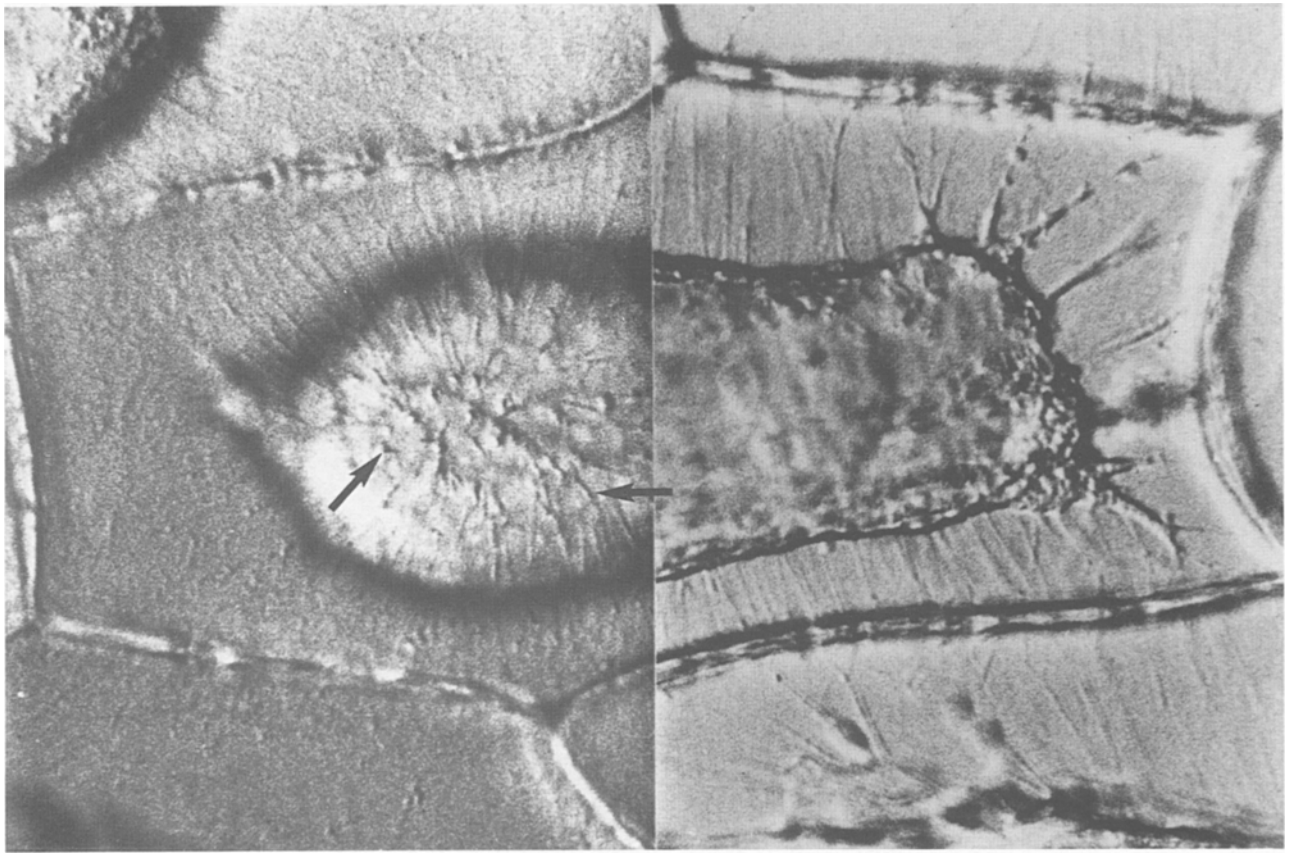

Fig. 2. Epidermal cell of onion bulb scale plasmolyzed in $CaCl_2$ showing Hechtian strands under Hoffman optics. The left half of the picture is taken at a more superficial focal plane showing the strands connecting the plasma membrane to the upper cell wall (arrows). On the right half, the strands connect the plasmalemma with the anticlinal cell wall

and animal ECMs have probably been preserved during evolution, conferring a functional similarity even though the chemical nature of the components is different. This unique fibrillar conformation can be alternatively assembled from polysaccharides (plants) or glycoproteins (animals) maintaining its mechanical properties.

ECM-PM connections

To act as a conductor of the mechanical signals from the environment, the ECM must be physically connected to the plasma membrane. Plant microscopists observed this kind of attachment in the 19th century in plasmolyzed cells (see Oparka 1994, for review). Figure 2 shows a classical view of a plasmolyzed onion epidermal cell observed with Hoffman optics. The strands linking the cell wall to the plasmolyzed plasma membrane were thought to represent plasmodesmata by some authors (Drake et al. 1978, Strasburger et al. 1983), and other considered that those strands were originated from wall sites other than plasmodesmata (Kiermayer 1964, Pont-Lezica et al. 1993 a, Oparka et al. 1994). But, when the microscope focuses the upper part of the collapsed membrane (Fig. 2), the Hechtian strands are seen to be linking the membrane to the upper cell wall. Clearly those strands are not plasmodesmata since no neighboring cells are on the upper part of an epidermal layer. Those sites are thought to be equivalent to adhesion sites in animals and we attempted to identify such sites with antibodies. Since HRGPs resemble primitive collagens that serve as matrix-to-membrane linkers in animal adhesion sites, we used anti-HRGP and fluorescent secondary antibodies on protoplasts and isolated cell walls to identify the sites. Images obtained by computational optical sectioning microscopy showed punctuate loci in the wall and on the protoplast surface, consistent with the existence of discrete adhesion sites (Pont-Lezica et al. 1993 a).

The differentiation of tracheary elements in *Zinnia* cell cultures provides another example of wall-to-membrane links in plants, where it induces the formation of secondary wall with a typical xylem cell pattern. Plasmolysis of the *Zinnia* cells during differentiation shows adhesion zones between the plasma membrane and the ECM (Roberts and Haigler 1989). Physical connections between the plant CW and the plasmalemma exist that are independent of the plasmodesmata. Which are the molecules involved in such connections? Arabinogalactan proteins (AGPs) are a group of plant molecules localized at the interface plasma membrane-CW. The role of AGPs is not yet clear but it is believed that they are involved in membrane-to-wall connections. The study of AGPs in plant development will provide valuable information concerning the role of proteoglycans in cell structure and communication (Pennell et al. 1989, Roberts 1990, Knox et al. 1991, Knox 1992).

Adhesion molecules

Immunological and functional evidence indicate that plants may share adhesion molecules similar to those of animal systems. The first evidence suggesting that plants have molecules homologous to animal SAMs came from studies of a soybean seed polypeptide which contains the motif Arg-Gly-Asp (RGD) in a fibronectin-like portion of its sequence (Odani et al. 1987). This short amino acid sequence is present in most of the SAMs and is recognized by the integrins, a family of integral membrane receptors. In addition, as judged by cross reactivity with anti-human vitronectin (hVN) sera, Sanders et al. (1991) found that several higher plants contain a 55 kDa homolog to hVN, mainly in cells surrounding the stylar duct. VN-like molecules facilitate the movement of the pollen tube to the ovule in the style (Sanders and Lord 1989). Nucleic acid hybridization shows that VN-like DNA and mRNA sequences are present in higher plants (Sanders et al. 1991, Wang et al. 1994). A VN-like protein (62 kDa) has been purified from zygotes and two-celled embryos of *Fucus*. The algal homolog shows specific cross-reactivity to polyclonal antibodies to hVN, and possesses affinities for glass and heparin identical to those of hVN. It is first localized in the cytoplasm of the zygote, followed by the polar transportation to the cell wall of the elongating rhizoid tip (Wagner et al. 1992). In addition, the ECM linkers (60 and 66 kDa) connecting the epidermal cells of the onion plasma membrane to the cell wall are not HRGPs, but VN-like molecules, as determined by immunological cross-reactivity, amino acid analysis, and affinity to glass beads (Pont-Lezica et al. 1993 a, Gens et al. 1993 a, Hocquette and Pont-Lezica 1993).

Proteins immunologically related to hVN (55 kDa) and human fibronectin (hFN) (59 kDa) have been found in the cell walls of tobacco cell cultures. Salt-adapted cultures show higher levels of VN- and FN-like proteins than non-adapted ones (Zhu et al. 1993). Recently, Zhu et al. (1994) purified and sequenced the putative VN-like protein from tobacco salt-adapted cells. The surprise is that the protein appears highly homologous to a translation elongation factor-1α (EF-1α). Unlike other EF-1α, the tobacco homolog seems localized in the cell walls of style transmitting tract cells as shown by immunolocalization. There have been several reports associating EF-1α to activities unrelated to protein elongation factors (Rils et al. 1990), the cell wall EF-1α adds one element more to the puzzle.

Other approaches add evidences to the involvement of SAM homologs in plant cell adhesion. First, the use of animal SAMs, or their antibodies, to inhibit the recognition between microorganisms and a plant host. The adhesion of the fungi *Phytophtora megasperma* to the host cell wall can be completely inhibited by antibodies against collagen, FN, laminin and VN (Hohl et al. 1992). *Agrobacterium tumefaciens*–carrot cell binding is also inhibited by hVN and anti-hVN antibodies (Wagner and Matthysse 1992). Secondly, peptides containing the sequence RGD, present in animal SAMs and recognized by the membrane receptors inhibit adhesion between plant cells. RGD-containing peptides block the perception of gravity by the algae *Chara*, whereas similar sequences like DGR or RGE do not interfere with gravity sensing (Wayne et al. 1992). Protoplasts from tobacco cells adapted to high salt concentrations agglutinate strongly, while those isolated from unadapted cells do not. Peptides containing the RGD sequence inhibit this adhesion (Zhu et al. 1993).

The plasma membrane

The plasma membrane plays a central role in the exchange of information between the cell and the environment. It directs the transport of ions and molecules via channels and transporters and allows for the transmission of extracellular and intracellular information. The PM appears as a complex structure that

enables the physical interlink of the extracellular matrix and the intracellular cytoskeleton. Signals may be transmitted bidirectionally, that is from the ECM to the CTK and vice versa. Most of the connections of the continuum ECM-PM-CTK in animal cells occur via specific proteins at focal adhesion zones, at adherent junctions (Luna and Hitt 1992), through interaction with membrane lipids (Aderem 1992), or at other scattered interaction sites. Membrane receptors functionally and structurally link cells and SAMs on the external side to the internal CTK in focal contacts.

Integrins

The most universal and versatile animal ECM receptors are the integrins (Albelda and Buch 1990, Ingber 1991). Integrins are clustered at focal adhesion sites and fixed to the CTK through actin-binding proteins (talin, vinculin, α-actinin) (Table 1). Other receptors like selectins or cadherins also can mediate force transmission, but integrins are the best known receptors connecting ECM to the cytoskeleton (Luna and Hitt 1992). Integrins are perhaps the most sophisticated of the transmembrane receptor families, both in terms of versatility in ligand recognition and ability to transmit information in both directions across the membrane. They are heterodimers that span the plasma membrane. The integrin family has at least 20 members based on the expression of 14 α- and 8 β-subunits (Ruoslahti 1991, Hynes 1992). Multiple divalent cation binding domains and a transmembrane sequence with a cytoplasmic tail characterize the α-subunit, generally the larger of the two (approximately 1100 amino acids). The β-subunit (approximately 750 amino acids) contains a Cys-rich domain in which the positions of the cysteine residues are strictly conserved. The β chain has its own transmembrane/cytoplasmic domain, thought to be responsible for the interaction with the CTK (Springer 1990, Sastry and Horwith 1993). Recent studies indicate that adhesion of integrins to their ligands is not constitutive but is dynamically regulated by intracellular signal transduction pathways (Diamond and Springer 1994).

There are few examples of integrin homologs in plants. Shindler et al. (1989) detected an integrin-like molecule in soybean cells using antibodies against a human VN-receptor. This protein (72 kDa) was purified on a RGD-affinity matrix and was recognized by antibodies against the human β_3 subunit of the receptor. In addition, antibodies raised against an external epitope of the β_1 integrin from chicken bind to onion protoplasts (Gens et al. 1993 b). Most of the experiments involving interactions with RGD-containing peptides in plants point to the presence of homologous receptors to SAMs that recognize an identical sequence as compared to animal integrins.

Non-integrin membrane receptors

An *Arabidopsis* clone encoding for a protein homologous to a high-affinity laminin receptor has recently been identified (Axelos et al. 1993). This molecule is not a member of the integrin family of receptors. In the deduced sequence (298 amino acids) and 200 residues of the N-terminal region show a strong homology (up to 80%) with the high affinity laminin receptor sequences from other species: human, mouse, *Drosophila*, yeast, hydra. The carboxy-terminal region (amino acids 223 to 298) do not present any significant homology (Pont-Lezica et al. 1993 b). The receptor function of this molecule has not yet been confirmed in plants. It is difficult to predict the role of this putative receptor since so far no laminin-like protein has been identified in plants. However, a cDNA clone showing little homology to animal lamininns has been identified in the *Arabidopsis* database. The isolation and characterization of plant membrane receptors to ECM molecules is imperative to explain the nature of the plant ECM-CTK continuum.

Ion channels

Besides the ECM-receptors, other PM proteins can be involved in mechanochemical signal transduction. Ion channels are important components of the system and some of them are mechanosensitive. Such channels are widespread in microbes and animals (Sachs 1988, Morris 1990, Martinac 1993) as well as in plants (Falke et al. 1988, Schroeder and Hedrich 1990, Schroeder and Hagiwara 1990, Cosgrove and Hendrich 1991, Sentenac et al. 1992, Thuelau et al. 1993). For example, the presence of stretch-activated Ca^{2+} channels in onion epidermal cells has been reported (Ding and Pickard 1993 a, b). Pickard and Ding (1993) proposed recently an interesting model for a cluster of regulatory plasmalemmal proteins and cytoskeletal elements grouped around a set of wall-to-membrane and transmembrane linkers: it is the plasmalemmal control center.

The cytoskeleton

The cortical cytoskeleton underlies the plasma membrane in animal cells and gives mechanical support to the membrane. It also provides specific attachment

sites for cytoskeletal components and facilitates the organization into domains of some integral membrane proteins. The CTK contains microfilaments (polymerized actin), intermediate filaments and microtubules (polymerized tubulin) (Table 1). It is linked to the PM in different ways: either directly (cadherins, annexins) or through specific proteins such as actin-binding proteins (ABP). There are around 70 forms of actin-binding proteins, defined by their function with respect to the assembly of actin monomers (Aderem 1992, Bretscher 1991). The membrane skeleton of erythrocytes is the best known, but a model of a general spectrin-based membrane skeleton has been recently proposed for animal systems (Pumplin and Bloch 1993). In this model, the spectrin family of proteins is the major component, bound to integral membrane proteins by intermediary linkers (ankyrin), and connected to the internal CTK (actin filaments, microtubules, intermediate filaments) and to the ECM through a transmembrane complex.

In plants, the presence and role of actin and tubulin, two main components of the internal CTK, is well established (Staiger and Schliwa 1987, Steer 1990). The importance of the nucleus in the organization of microtubules is being actively studied (Lambert 1993). Microtubule-associated proteins are being characterized, and their role in the regulation of microtubule assembly is being established (Schelenbaum et al. 1993). Several experiments suggest the interaction of microtubules with the CW (Simmonds 1992). Treatment of tobacco protoplasts with HRGPs protects the cortical microtubules from disruption by cold temperature, a protection similar to the one conferred by the cell wall (Akashi et al. 1990). Protease treatment of protoplasts with many cortical microtubules produces a partial disruption of their cortical array, increasing protoplast sensitivity to cold (Akashi and Shibakoa 1991). Tight adhesion of the PM to the cell wall in subapical region of *Adiantum* protonemal cells is disturbed by the disruption of the microtubules (Kagawa et al. 1992). The presence of intermediate filaments in plants has been suggested by immunological studies (Shaw et al. 1991). Antibodies against acidic and basic animal keratins recognize several polypeptides from plants. These polypeptides assemble in vitro into filaments that are indistinguishable from the native filaments in the plant cell (Yang et al. 1992).

Notwithstanding, the existence of a membrane skeleton in plants has not yet been demonstrated. Antibodies raised against animal spectrin detect proteins immunologically-related to spectrin in several plants (Faraday and Spanswick 1993, de Ruijter and Emmons 1993). Actin-binding proteins have as yet not been clearly characterized in plants (McCurdy and Williamson 1991). However, a potassium channel cloned from *Arabidopsis thaliana* contains a 33-amino-acid repeat present 6 times at the cystolic C-terminal region (amino acids 517–712). This sequence shows homology to erythrocyte ankyrin (Sentenac et al. 1992).

Conclusions

There is a body of evidence suggesting that the plant CW might bind directly to the plasma membrane and to cytoskeletal elements. This continuum appears to play an important role in several plant responses to the environment such as gravity sensing, adaptation to salt- or cold-related stress, pollen tube migration, polarity and embryogenesis. This CW-CTK continuum parallels the best known ECM-CTK from animal systems. How similar are these two structures? Functionally it seems clear that both share an important role: the perception and transduction of environmental signals. The involvement of homologous molecules in the ECM-CTK structures from plants and animals seems a possibility. But much work remains to be done since most of the evidence comes from the cross-reactivity between plant proteins and antibodies raised against animal proteins from the continuum ECM-PM-CTK. The actual knowledge seems to predict that the molecules involved in plant and animal cytoskeleton are functionally and structurally well conserved. On the other hand, we should expect the major differences at the other end of the ECM-CTK complex. The chemical nature of the animal ECM and the plant CW are very different. However, the structural resemblance of these fibrillar structures and the equivalence of many of their functions are remarkable. We may expect to find that adhesion molecules from plant and animals are quite divergent. Animal glycosaminoglycans and plant AGPs are chemically very different, but they may play equivalent roles. The same is valid for animal collagens and plant HRGPs. We may be surprised to find that maybe some members of the cell wall proteins without a known function today (PRPs, GRPs, HRGPs) have short domains that are conserved in animals SAMs, like the RGD or laminin-like motifs.

The proteins involved in the CW-PM-CTK continu-

um need to be purified and characterized in order to have a clear vision of the similarities and differences of this complex structure in plants. Understanding the structure and role of the plant cell surface in the perception and transduction of environmental signals, and comparing the plant and animal models, will be a tremendous and fascinating advancement in the comprehension of evolution from single cells to multicellular organisms.

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