

## MINIREVIEW

## Adaptations of higher plant cell walls to water loss: drought vs desiccation

John P. Moore<sup>a,\*</sup>, Mäite Vicré-Gibouin<sup>b</sup>, Jill M. Farrant<sup>c</sup> and Azeddine Driouich<sup>b</sup>

<sup>a</sup>Institute for Wine Biotechnology, Faculty of AgriSciences, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

<sup>b</sup>Plate-forme de recherche en imagerie cellulaire de Haute-Normandie, Université de Rouen, 76821 Mont Saint Aignan cedex, France

<sup>c</sup>Department of Molecular and Cellular Biology, University of Cape Town, Private Bag, Rondebosch 7701, South Africa

### Correspondence

\*Corresponding author,  
e-mail: moorej@sun.ac.za

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Water-deficit stress poses unique challenges to plant cells dependent on a hydrostatic skeleton and a polysaccharide-rich cell wall for growth and development. How the plant cell wall is adapted to loss of water is of interest in developing a general understanding of water stress tolerance in plants and of relevance in strategies related to crop improvement. Drought tolerance involves adaptations to growth under reduced water potential and the concomitant restructuring of the cell wall that allow growth processes to occur at lower water contents. Desiccation tolerance, by contrast, is the evolution of cell walls that are capable of losing the majority of cellular water without suffering permanent and irreversible damage to cell wall structure and polymer organization. This minireview highlights common features and differences between these two water-deficit responses observed in plants, emphasizing the role of the cell wall, while suggesting future research avenues that could benefit fundamental understanding in this area.

### Introduction

The sessile nature of plants requires that they tolerate a variety of abiotic stresses present in their environment. One common type of abiotic stress, found in many areas of the world, is water-deficit stress. Drought is defined as the lack of available moisture in a particular region that ultimately results in soil drying (Iljin 1957). A consequence of drought is that most plants growing in drought-prone areas have developed means to evade, avoid or tolerate their water loss. Some plants evade water-deficit stress by undergoing their growth and reproduction cycles when sufficient water is available and so survive the dry periods as drought-tolerant seeds (termed orthodox seeds) or spores (Bewley 1979, Niklas 1997). Succulents and cacti, by contrast, avoid water-deficit stress by storing water in modified tissues (e.g. stems or leaves) during periods of water scarcity (Niklas 1997). Another mechanism of avoiding water stress is illustrated in plants

such as eucalypts, which keep themselves hydrated by mining deepwater sources through their extensive root systems. The strategy of tolerance is one in which vegetative tissues are capable of surviving various degrees of water loss without suffering irreparable damage (Niklas 1997). Various cultivars and genotypes of crop species (e.g. wheat and maize) are capable of displaying varying degrees of drought tolerance in their vegetative tissue through the evolution of mechanisms such as improved water use efficiency and/or osmotic adjustment that mitigate against damage associated with water loss (Clifford et al. 1998, Iljin 1957). This is usually achieved at the expense of crop yield, as energy must be redirected to maintain cellular metabolism during the drought. These drought-tolerant variants can usually only survive a mild degree of water deficit [e.g. tissue water contents of 99–80% relative water content (RWC)] for short periods before irreversible damage sets in (Iljin 1957). A certain

*Abbreviation* – RWC, relative water content.

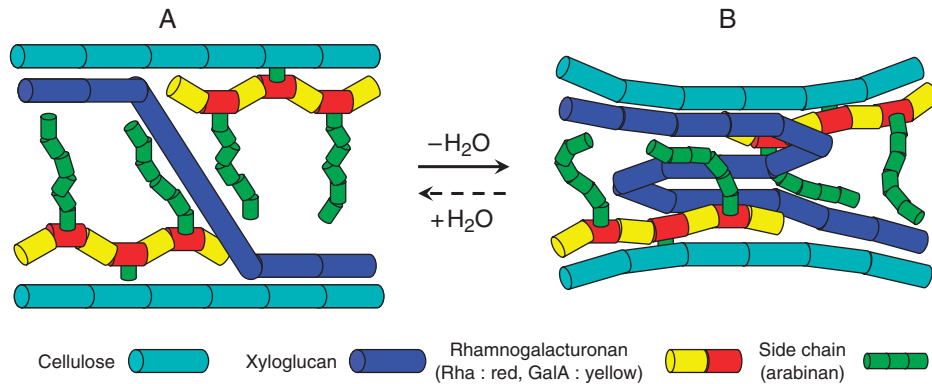
group of plants display the remarkable capacity of being able to survive extreme water loss (down to < 5% RWC) of their vegetative tissues, for prolonged periods, without suffering permanent damage (Gaff 1971). The manner with which they can rehydrate their vegetative organs (roots, leaves and sometimes flowers) and return to a fully hydrated green 'natural' state has earned them the common name 'resurrection plants' (Farrant 2000, Gaff 1971). These resurrection plants, of which many species are found in southern Africa, are truly 'desiccation tolerant' (Gaff 1971). Desiccation as opposed to drought is defined as 'the ability to survive drying to below the absolute water content of  $0.1 \text{ g H}_2\text{O g}^{-1}$  dry mass ( $\text{g g}^{-1}$ ), this being equivalent to air-dryness at 50% relative humidity (RH) and  $20^\circ\text{C}$  and corresponding to a water potential of  $\leq -100 \text{ MPa}$  (Vertucci and Farrant 1995); and so, whereas desiccation-tolerant organisms are also drought tolerant, the opposite is not true. Whereas vegetative desiccation tolerance in angiosperms is rare (Oliver et al. 2000), many lower plant groups such as the bryophytes display such tolerance (Oliver et al. 1998, 2005, Proctor 2001). The focus here is on the recent research on angiosperm resurrection plant cell walls; so, lower plants such as the bryophytes are not discussed. Most higher plants (i.e. angiosperms), to evade drought, produce orthodox seeds that allow survival of the species during periods of extreme environmental stress (drought and freezing) (Bewley 1979). Interestingly, the mechanisms of desiccation tolerance in seeds and vegetative tissues appear very similar (reviewed, inter alia by Berjak et al. 2007, Farrant 2000, Vitré et al. 2004a) and it has been proposed that desiccation tolerance involves the use of the same genes, but that they are under developmental control in the former but environmental control in the latter (Farrant 2007, Illing et al. 2005).

Water stress poses significant challenges to plant cells surrounded by a relatively rigid polysaccharide-rich cell wall. The cell wall, of fundamental importance in growth and development, also makes the plant cell susceptible to plasmolysis because of osmotic imbalances, which in turn can damage cellular protoplasm (Brett and Waldron 1996). The pressure exerted by the protoplasmic fluid on the cell wall (turgor pressure) is critical to the mechanism used by the plant cell to grow and divide (Brett and Waldron 1996). The plant cell wall is a composite structure consisting of a cellulose-hemicellulose framework embedded within a matrix of pectin and proteins, which allows it to respond to stresses and strains imposed upon it from many directions (Carpita and Gibeaut 1993). The wall responds to turgor pressure by initiating elastic (reversible stretching) and plastic (irreversible/viscous stretching), which results in cell growth (termed viscoelastic growth) (Brett and Waldron 1996). In addition, the

polysaccharide-rich wall is bathed in an aqueous solution (termed apoplastic fluid), which functions in relation to cell adhesion, general wall biosynthesis and intercellular signaling (Brett and Waldron 1996). This viscoelastic semi-solid composite is therefore dependent on the buffering capacity of its watery matrix. Loss of water from the wall matrix can result in serious disruption to polymer organization. One obvious effect of water removal is that polymers usually well separated in the hydrated wall are brought in close proximity to each other, thus causing polymer adhesion. Polysaccharides form non-covalent bonds commonly through hydrogen bonding and in the absence of water, this bonding is greatly enhanced to the extent that water loss is likely to cause irreversible bonding between polymers resulting in altered wall biophysical properties and severely impaired growth. A model illustrating the effect of water loss on cell wall polymers clearly indicates the disruptive effect on wall organization (Fig. 1). Investigating the relationship between water loss and the cell wall is not only fundamental to understand how plants adjust to water deficit as well as being related to the development of drought-tolerant crop species through genetic modification strategies but should also advance fundamental understanding in plant growth and development. This minireview highlights the role of the cell wall in the tolerance of higher plants to water loss, examining the common and unique responses observed under drought and desiccation stresses, respectively.

### **Physiological and molecular responses of the cell wall to drought stress**

Water loss in plant tissues controls turgor pressure and so directly affects the extensibility of the plant cell wall. The cell has been shown to respond to changes in turgor pressure by either relaxing or tightening the wall. These responses are believed to be mediated at physiological as well as biochemical and genetic levels. Drought tolerance appears to result in both tightening and loosening of cell walls. Tissues that are essential to maintain in a growth 'ready' state are loosened, whereas non-essential tissue is tightened (made inextensible) thereby allowing important growing points, such as apices, to continue to grow at lower turgor pressures (Wu and Cosgrove 2000). It is likely that the threshold turgor pressure in these growing regions is modified to permit wall growth. The mathematical and biophysical relationships between wall growth and water deficit have been reviewed previously (Neumann 1995), and so, the focus here is on the molecular changes that have been shown to occur in the wall upon water loss. We provide a number of models summarizing the major effects of and responses to

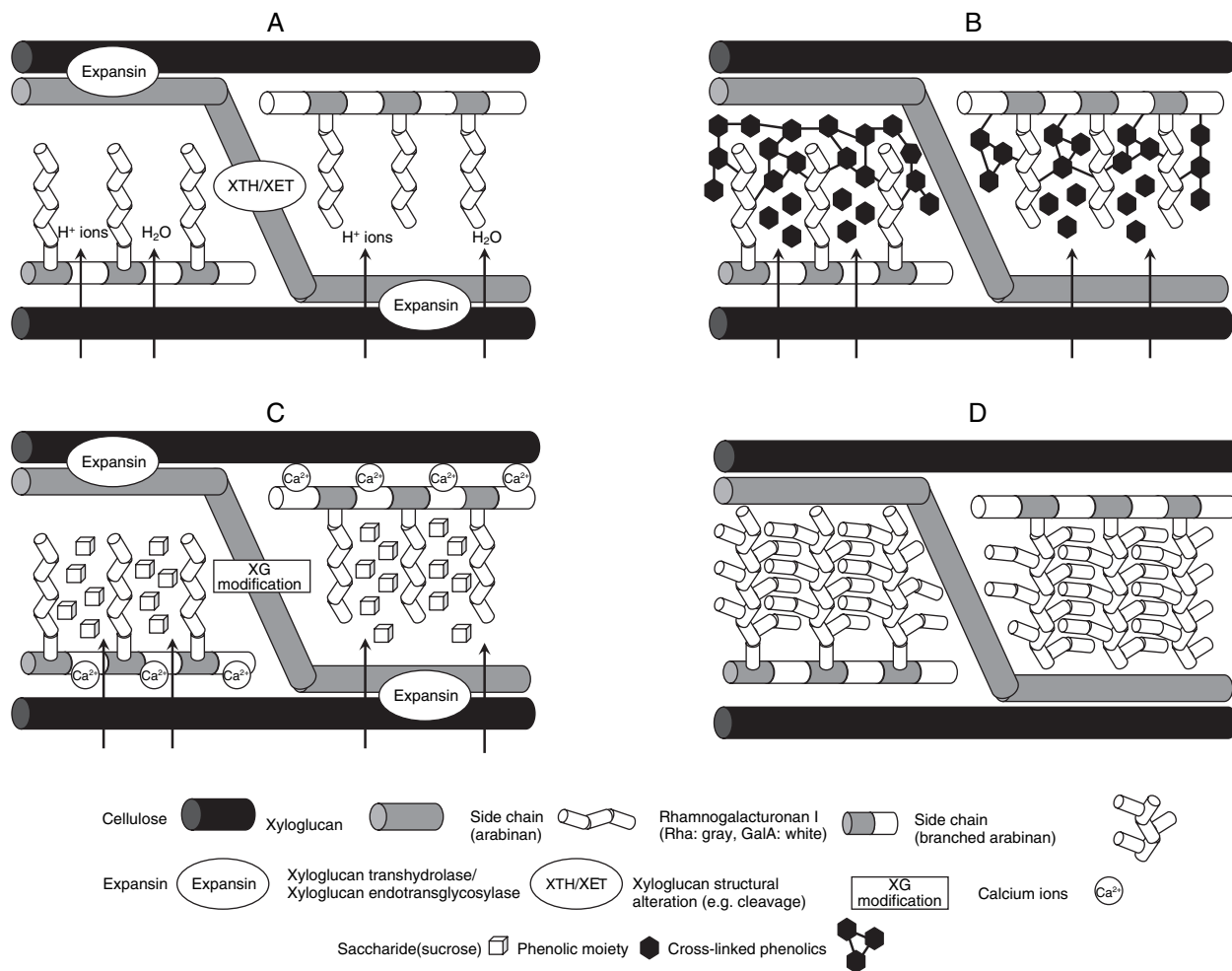


**Fig. 1.** A model representing the effect of water loss on plant cell wall structure. (A) Hydrated plant cell wall and (B) dehydrated cell wall. The solid arrow represents the direction of water loss (this is usually irreversible below water contents of 80% RWC for many plants). The dashed arrow represents the direction of water regain that occurs in a select group of desiccation-tolerant plants termed resurrection plants.

water-deficit stress, contrasting drought and desiccation, in relation to the plant cell wall (Fig. 2). The effect of water deficit on wall structure and properties has been most intensively studied in maize roots exposed to controlled drought causing treatments (Wu and Cosgrove 2000). Maize roots subjected to drought treatments have revealed that the apical region (0–3 mm from the tip) cell walls are maintained in a flexible state and so this tissue continues to grow slowly even at low water potentials (Fan and Neumann 2004, Wu and Cosgrove 2000). In contrast, the elongation region (3–9 mm from the tip) cell walls are made inextensible resulting in a cessation of further growth (Fan et al. 2006). The mechanisms that govern the respective loosening and tightening of these two regions of the maize root appear to be the result of a number of different processes, thus constituting a complex stress response. Models summarizing the wall loosening (Fig. 2A) and tightening (Fig. 2B) phenomena are provided. The wall-associated pH has been shown to vary with drought stress such that a lower pH is associated with growing tip compared with the elongation zone (Bogoslavsky and Neumann 1998, Chazen and Neumann 1994, Fan and Neumann 2004; Fig. 2A). This spatial variation corresponds well with the acid growth hypothesis where proton extrusion into the wall, partly governed by auxin presence, is believed to cause a general loosening through a combination of chemical and biochemical processes which remain unclear at present (Brett and Waldron 1996). Furthermore, water channels have also been implicated in facilitating water transport to the cell walls of the tip, thereby promoting wall loosening (Fig. 2A). These channels were shown to be sensitive to the addition of mercury that inhibited the growth phenomenon (Lu and Neumann 1999). Enzymatic processes also appear to be part of the loosening phenomenon at the growing tip region where

xyloglucan endotransglycosylase has been shown to increase in activity at the sites of loosening (Fig. 2A). This activity appears to be partly regulated by ABA, thus causing polysaccharide backbone scission and concomitant xyloglucan polymer rearrangement (Wu et al. 1994). That apical walls increase in extensibility has also been shown to be related to expansin activity, as well as an increased wall susceptibility to expansins, which increased under drought stress (Wu et al. 1996; Fig. 2A). Expansins appear to mediate wall loosening by disrupting hydrogen bonding in the wall without breaking polysaccharide backbones and are therefore key players in wall modification (Brett and Waldron 1996). The inextensibility of the elongation zone appears to be mediated by different mechanisms. The elongation zone of drought-stressed maize roots accumulates phenolics and lignin (Fan and Neumann 2004; Fig. 2B). It is highly likely that these phenolics and lignin monomers are covalently cross-linked to wall polysaccharides through peroxidases and oxidase enzymes (Brett and Waldron 1996; Fig. 2B). These phenolic cross-links tighten the wall structure, while lignin formation is accompanied by removal of water from the wall (Brett and Waldron 1996). Concomitant with the production of phenolics, it has been shown that transcripts for lignin biosynthetic enzymes increase with water stress in the elongation zone in preparation for lignification (Fan and Neumann 2004). These actions cause the wall to become increasingly inflexible and rigid, which result in a cessation of growth in these areas. The research performed on maize in response to drought has highlighted the spatial and temporal changes that occur to roots when stressed; however, the difficulty with studying an intact organ is that multiple tissue types and cell wall types complicate the analyses.

Work performed on tobacco suspension-cultured cells in response to osmotic (PEG) and saline treatment have



**Fig. 2.** Models summarizing the cell wall responses observed in plants exposed to drought (A and B) and desiccation (i.e. resurrection plants) (C and D). (A) Wall-loosening responses to drought and (B) wall-tightening mechanisms. (C) The inducible responses observed in resurrection plants such as *Craterostigma wilmsii* to desiccation. (D) Constitutive factors (wall pectic plasticizers) observed in the resurrection plant *Myrothamnus flabellifolia* in response to desiccation. Solid arrows represent the movement of substances from the interior of the cell to the wall (i.e. ions, water, phenolic monomers and sucrose).

provided useful information on the response of a relatively uniform cell wall population to a drought-mimicking stress (Iraki et al. 1989a, 1989b, 1989c). Tobacco cells were grown in the presence of sodium chloride or PEG and then the cell suspension cultures were analyzed for various cell wall components (Iraki et al. 1989a, 1989b, 1989c). A common feature of both saline and osmotic stress was a reduction in cellulose and extensin production (Iraki et al. 1989a). Concomitant with this, there appeared to be an increase in the amount of EDTA extractable uronic acid material that showed a higher degree of rhamnose residues present as well as a greater amount of substitution with arabinose- and galactose-containing polymers (Iraki et al. 1989b). It was proposed that a loose shell of rhamnogalacturonan 1 and poly-

galacturonic acid forms around the walls of adapted cells (Iraki et al. 1989b). Furthermore, the adapted cells appear to have blocked the secretion of arabinogalactan and uronic acid polymers as well as proteins into the extracellular medium (Iraki et al. 1989c). Adapted cells were, in general, smaller and possessed weaker cell walls (Iraki et al. 1989a). It was proposed that the load-bearing cellulose and extensin composite are sacrificed in adapted cells so that carbon is redirected to osmotic adjustment while utilizing a hemicellulose–pectin matrix in its stead (Iraki et al. 1989a).

Thus, it is evident that a number of responses involving the cell wall appear to be important in adapting cells, tissues and organs in plants to osmotic and water-deficit stress. Although wall tightening and solute accumulation

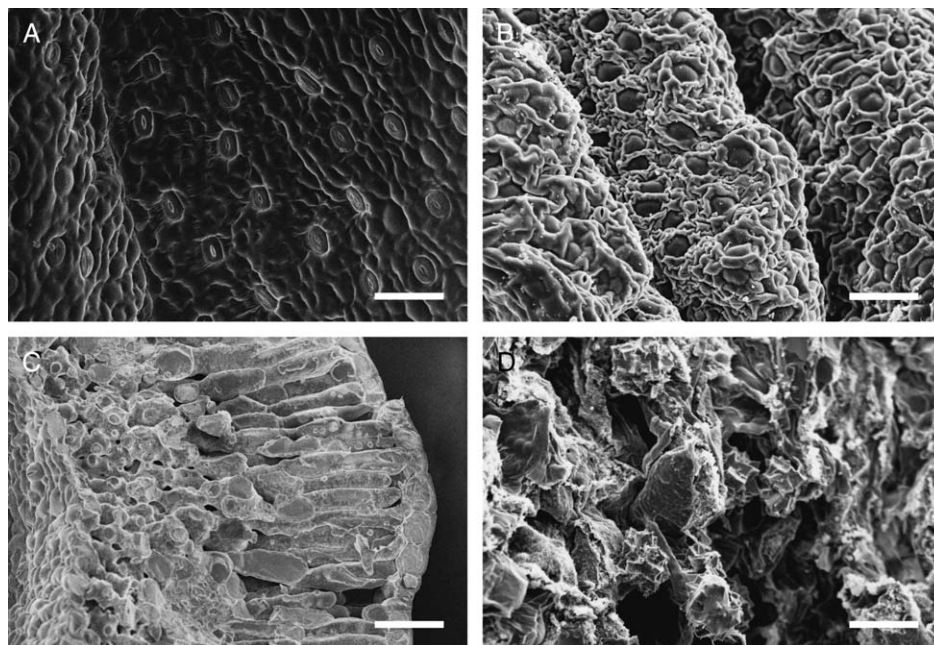
appear to be a general phenomenon in response to drought and other stresses in plants (Clifford et al. 1998, Degenhardt and Gimmler 2000, Kim and Lee-Stadelmann 1984, Wakabayashi et al. 1997), there also appears to be species-specific responses as well. For example, a comparison of wheat, barley and rice grown under drought stress has shown that rice leaves do not undergo changes in wall extensibility, whereas the other species do (Lu and Neumann 1998). Clearly, wall adjustment is a critical factor in the adaptation of plants to drought stress, but the specific and general mechanisms responsible require further investigation. Although drought stress poses problems to plant cells by modifying the balance between wall extensibility and turgor pressure, the effects of desiccation are even more severe by directly affecting the non-covalent intra- and interpolymeric bonds within the wall through the almost complete removal of water.

### **Desiccation stress and the cell walls of resurrection plants**

Desiccation stress causes considerable loss of cellular water and thus significant cellular disorganization. Early studies on desiccation tolerance in resurrection plants focused on ultrastructural studies with microscopy revealing folded cell walls in *Borya nitida*, *Talbotia elegans* and *Xerophyta villosa* (Gaff et al. 1976, Hallam and Luff 1980a, 1980b). A non-aqueous immersion method (Hallam 1976) proved useful for resurrection plant tissues by preventing rehydration and swelling of carbohydrate-rich cell walls from occurring, thus confirming that folded cell walls occur in many angiosperm resurrection plants when desiccated. Similar studies have shown collapsed cell walls in lower plants such as bryophytes when desiccated (Proctor 2001, Proctor et al. 2007). Studies of cell wall folding in the endosperm of dry seeds suggested the importance of cell wall folding as a mechanism to maintain structural organization as well as cell viability in the desiccated state (Webb and Arnott 1982). In addition, it was suggested that cell wall folding occurred in a species-specific manner and was related to the biochemical composition of the cell wall (Webb and Arnott 1982). Models summarizing the known responses of desiccation-tolerant resurrection plant cell walls to water loss are provided (Fig. 2). The first in-depth study of the cell wall of a resurrection plant was performed on the small herbaceous *Craterostigma wilmsii* and focused on the leaves (Vicré et al. 1999, 2004b). Immunocytochemical analysis revealed that xyloglucan epitopes were found to be present in greater abundance in desiccated tissue, whereas no change in pectin epitopes such as those associated with rhamnogalacturonan 1 or homo-

galacturonan polymers were observed (Vicré et al. 1999). This suggested that either more xyloglucan was synthesized during dehydration promoting cross-linking and tightening the wall or that hydrolysis of xyloglucan polymers occurred exposing more epitopes to the antibody (Vicré et al. 1999; Fig. 2C). Support for wall strengthening was suggested by the observation that calcium ions were found in higher concentration in desiccated tissues possibly forming egg-box type linkages in the wall pectin (Vicré et al. 2004a; Fig. 2C). Further analysis using biochemical techniques revealed no change in xyloglucan composition between states suggesting that either xyloglucan epitopes were more exposed in desiccated tissue or hydrolysis of xyloglucan polymers had occurred releasing more potential epitopes (Vicré et al. 2004b; Fig. 2C). In addition, desiccated tissue showed altered wall extractability compared with hydrated tissue, suggesting a reorganization of the cell wall had occurred during dehydration (Vicré et al. 2004b). Thus, in the case of *C. wilmsii*, wall modification seems to involve a number of induced factors such as calcium-pectin associations and xyloglucan modification (Fig. 2C). A role for expansins has also been suggested in the related species, *Craterostigma plantagineum*, where transcripts encoding an alpha expansin have been shown to be upregulated upon desiccation concomitant with increased wall extensibility (Jones and McQueen-Mason 2004; Fig. 2C). Sucrose is a common osmoticum produced upon desiccation in resurrection plants (Moore et al. 2007a) and thus it is tempting to speculate that such substances may also occur in the wall and act to buffer the lost water and stabilize polymers to desiccation (Fig. 2C). In contrast, a study on the leaf cell wall changes in the large woody resurrection plant *Myrothamnus flabellifolia* showed a different response (Moore et al. 2006, 2007a) (Fig. 2D and Fig. 3). This resurrection plant possesses fan-like leaves composed of sclerenchyma-rich ribs that remain unfolded, whereas the inter-rib vegetative tissue shrinks during dehydration (Moore et al. 2007b) (Fig. 3). Immunocytochemical analysis revealed no change between desiccated and hydrated states with respect to epitopes associated with pectin, xyloglucan and arabinogalactan proteins (Moore et al. 2006). The biochemical analysis revealed some minor changes with respect to the pectic fractions, but the predominant results confirmed no change between states (Moore et al. 2006). The most significant factor appeared to be a high concentration of arabinose, likely in the form of arabinans and arabinogalactan polymers, associated with the pectin matrix in this species (Moore et al. 2006; Fig. 2D). These arabinose polymers have been suggested to act as 'pectic plasticizers', and a model suggesting how they might function to maintain flexible cell walls during dehydration and





**Fig. 3.** A surface (A and B) and cross-sectional (C and D) view using a scanning EM of hydrated (A and C) and desiccated (B and D) leaves of the resurrection plant *Myrothamnus flabellifolia*. The degree of cell wall folding in desiccated leaves is clearly evident in micrographs B and D. Scale bars: A, 40  $\mu\text{m}$ ; B, 60  $\mu\text{m}$ ; C, 50  $\mu\text{m}$ ; D, 10  $\mu\text{m}$ .

rehydration in an analogous manner to that observed in stomatal guard cells has been proposed (Jones et al. 2003, Moore et al. 2008, ; Fig 2D). Hence, *M. flabellifolia* appears to use a predominantly constitutive strategy, having evolved cell walls permanently prepared for relatively rapid and extreme water loss. The only other research on wall-associated effects and desiccation in resurrection plants has been performed on the grass genus *Eragrostis* that consists of both desiccation tolerant *Eragrostis nindensis* and sensitive *Eragrostis curvula* species (Vander Willigen et al. 2003). Research on this genus has been useful in ascertaining the specific responses to desiccation associated with tolerance using the sensitive species as a useful background control. The resurrection grass *E. nindensis* in addition displays both tolerant and sensitive tissue (Vander Willigen et al. 2003). An ultrastructural study revealed folded intact cell walls present in tolerant tissue, whereas tissues that had lost tolerance were composed of significantly more brittle cell walls that fractured during preparation for microscopy (Vander Willigen et al. 2003). A study of the tensile properties of these *Eragrostis* species has revealed a greater degree of elasticity in tolerant species compared with sensitive species, strongly supporting a role for the cell wall in relation to the desiccation tolerance of these resurrection grasses (Balsamo et al. 2005, 2006). Unfortunately, no biochemical or immunocytochemical ana-

lysis has been undertaken on these grass species, which could provide more information on possible cell wall changes and complement the ultrastructural and biophysical studies. Wall flexibility appears to be the common theme in the adaptation of resurrection plant cell walls to desiccation either by using constitutive or induced or a combination of both in counteracting the extreme loss of water experienced by these plants (Fig. 2C, D). This is in contrast to drought tolerance responses where the response includes both wall tightening and loosening (Fig. 2A, B) with the aim of limiting growth and conserving water usage. Further research on resurrection plants and their cell walls should hopefully provide more insight into how these remarkable plants are capable of surviving such harsh environmental conditions.

### Conclusions and future prospects

Changes in wall extensibility appear to be a common response to both drought as well as more severe desiccation. Drought appears to result in both wall tightening and loosening. The tightening appears to be caused by number of mechanisms including phenolic cross-linking and lignification of wall polymers. The wall loosening process that occurs in tissues that need to be maintained in a growing state appears to be the result of

a number of complex mechanisms including physiological (e.g. pH) and biochemical (e.g. specific enzymes) processes acting on the wall structure. Desiccation appears to cause a controlled collapse of the cell walls present in resurrection plants, which appears to be achieved through a similarly complex mechanism including constitutive (specific polymer composition) and induced (calcium cross-links and xyloglucan cleavage) processes. Resurrection plant cell walls are extremely flexible probably as a result of the plasticizing effect of various constituents present within their wall structure. Clearly, cell wall adjustment under water stress is an important phenomenon in plant adaptation. The mechanisms, however, appear to be quite complex and variable among species. Much research to date has focused on the biophysical relationships between wall extension and water potential (Neumann 1995), while less research has been undertaken on compositional changes because of water stress. Ascertaining the biochemical components of the cell wall that change upon water stress in plants is of crucial importance in developing a rational genetic engineering approach to develop drought-tolerant crop plants. A few possible biochemical targets highlighted in this review include pectin-associated arabinan polymers as well as genes encoding expansin proteins and xyloglucan-modifying enzymes. Only by assessing which biochemical, and therefore genetically encoded, components need to be modified or introduced into crop species can a clear strategy be developed. Understanding the changes that occur in drought-tolerant species and 'resurrection plants' that facilitate the survival of these organisms under adverse conditions of water availability is therefore of great importance. The cell wall is composed of over 60% water (Brett and Hillman 1985), and this fundamental, although often forgotten, constituent is a vital and integral component of wall structure and functioning. Understanding how the wall adjusts to water loss should provide not only new strategies in plant improvement but also accrue fundamental scientific knowledge in plant biology.

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