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Review

# The plant cell wall integrity maintenance mechanism – A case study of a cell wall plasma membrane signaling network

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ABSTRACT

Some of the most important functions of plant cell walls are protection against biotic/abiotic stress and structural support during growth and development. A prerequisite for plant cell walls to perform these functions is the ability to perceive different types of stimuli in both qualitative and quantitative manners and initiate appropriate responses. The responses in turn involve adaptive changes in cellular and cell wall metabolism leading to modifications in the structures originally required for perception.

While our knowledge about the underlying plant mechanisms is limited, results from *Saccharomyces cerevisiae* suggest the cell wall integrity maintenance mechanism represents an excellent example to illustrate how the molecular mechanisms responsible for stimulus perception, signal transduction and integration can function. Here I will review the available knowledge about the yeast cell wall integrity maintenance system for illustration purposes, summarize the limited knowledge available about the corresponding plant mechanism and discuss the relevance of the plant cell wall integrity maintenance mechanism in biotic stress responses.



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## 1. Introduction

The cuticula, plant cell wall and plasma membrane encompass a space that forms the interface between the plant cell and its environment. The limited data available show that within this space different types of sensors exist that can perceive stimuli originating in the environment or deriving from the plant itself (Humphrey et al., 2007). The stimuli can either have a chemical (ligands, fragments) or a physical character (exemplified by plasma membrane distortion or displacement of membrane vs. wall).

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Examples for plant-derived chemical stimuli are cell wall fragments (oligogalacturonides (OG)), metabolites or peptides while invading pathogens represent sources of non-plant-derived stimuli (like FLG22, ELF; Fig. 1) (Ferrari et al., 2013). These two types of chemical stimuli can initiate specific responses like differentiation between *self* and *non-self*, thus allowing detection of invading pathogens and initiation of specific defense responses (Dangl, 2013). Physical stimuli on the other hand can be indicative of abiotic stress (reductions in turgor pressure due to drought stress) or changes in the mechanical characteristics of cell walls (primordium formation in the shoot meristem) (Sampathkumar et al., 2014). During the last years novel insights into the mechanisms translating combinations of different stimuli or stresses into distinct response patterns have illustrated how a plant can perceive different stimuli simultaneously, and integrate the resulting signals to generate quantitative, adaptive responses (Meldau et al., 2012).

While the available data sometimes provide very detailed insights into the sophisticated signaling cascades and networks responsible for signal generation and integration in plants, our knowledge of the "molecular infrastructure" responsible for the initial stimulus detection and its mode of action at the wall is still limited. By contrast in *Saccharomyces cerevisiae* (bakeŕs yeast) the cell wall integrity (CWI) maintenance mechanism, which monitors the functional integrity of the cell wall and initiates adaptive changes in cell wall and cellular metabolism to maintain wall integrity in response to environmental (like hypo-osmotic shock) or developmental (like cell division) stresses is well characterized (Levin, 2011). The mechanism involves mechano-perception, turgor pressure monitoring and dedicated cell wall stress/damage detection components. The evidence that in plants like *Arabidopsis thaliana* a similar mechanism exists has been reviewed recently (Hamann, 2012; Wolf et al., 2012a,b). The available information suggests that its importance has been underestimated because in the past it was difficult to separate its activities from developmental processes and general stress responses arising during interactions between plants and their environment.

This review consists of three components. It will review the knowledge available regarding the mode of action of the yeast CWI maintenance mechanism to illustrate how molecular mechanisms for stimulus perception, signal generation and integration in a plasma membrane-cell wall space can work. It will assess the available knowledge regarding the plant CWI maintenance mechanism with a focus on studies using cellulose biosynthesis inhibition as tool to cause cell wall damage. It will finish by briefly discussing how CWI maintenance processes could be part of biotic stress responses and their regulation during development.

## 2. The cell wall integrity maintenance mechanism in *S. cerevisiae*

During recent years evidence supporting the existence of dedicated CWI maintenance mechanisms has emerged in a large number of different fungal organisms (*Aspergillus fumigatus*, *Botrytis cinerea*, *Coniothyrium minitans*, *Cryptococcus neoformans*, *Magnaporthe oryzae*, *Ustilago maydis*) (Gerik et al., 2005; Jain et al., 2011; Jeon et al., 2008; Liu et al., 2011; Zeng et al., 2012; Carbó and Pérez-Martín, 2010). Here the focus will be on CWI maintenance in *S. cerevisiae*, since this is currently the best-understood mechanism and the underlying design principles seem similar in the different organisms. The available data show that the CWI maintenance mechanism in yeast is activated during exposure to Endoplasmatic reticulum (ER)/heat stress, hypo-osmotic shock, pheromone-induced morphogenesis, actin cytoskeleton de-polymerization, exposure to artificial cell wall stress agents (zymolase) and in cell wall biogenesis mutants (Levin, 2011). This long list serves as a reminder of the key position the cell wall and its functional integrity occupy during yeast development and interaction with the environment. The obvious implication being that a plant CWI maintenance mechanism may be involved in a similarly diverse number of biological processes in plants, making a functional analysis somewhat challenging.

The organization of fungal cell walls is significantly simpler than that of plant cell walls, has been discussed in a recent comprehensive review and will therefore not be covered here again (Free, 2013). The available evidence suggests that plasma membrane stretch or displacement of the membrane versus the wall is the principal underlying physical stress in fungal cells, which activates three different signaling mechanisms that are located in the cell wall plasma membrane space (Levin, 2011). Chlorpromazine, an amphipathic molecule causing membrane stretch by asymmetric insertion into the membrane activates the MAPKinase MPK1-mediated CWI maintenance mechanism (Kamada et al., 1995). Membrane stretch/displacement represents a highly sensitive indicator of external stress and cellular processes (polarized cell expansion or cell wall remodeling) because it can be caused by different stresses while also providing quantitative information about absolute stress levels. Mutants experiencing increased turgor pressure levels illustrate this point since they exhibit constitutive activation of the CWI signaling cascade (Merchan et al., 2004; Beese et al., 2009). Importantly manipulation of extracellular osmolarity, preventing membrane stretch by neutralizing intracellular turgor levels, blocks activation of the CWI maintenance mechanism (Harrison et al., 2001; Kamada et al., 1995; Mensonides et al., 2005; De Nobel et al., 2000; Torres et al., 2002).

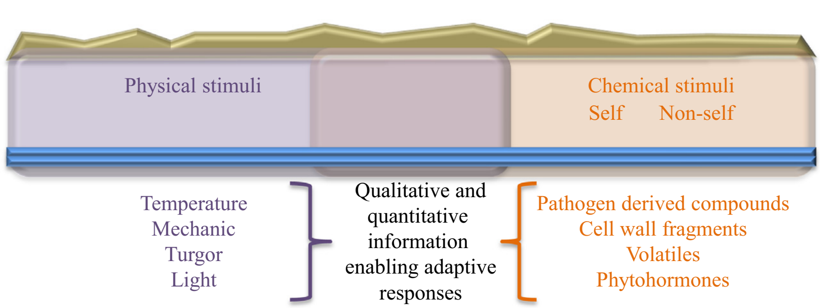


**Fig. 1.** Schematic overview of the plant cell wall – plasma membrane space highlighting the different types of stimuli perceived. Two blue lines indicate the plasma membrane while beige represents the plant cell wall. Semi-transparent areas overlapping with cell wall and plasma membrane indicate space containing early signaling components and sensors required for stimulus perception.

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