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Review

Role of the plant cell wall in gravity resistance

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ABSTRACT

Gravity resistance, mechanical resistance to the gravitational force, is a principal graviresponse in plants, comparable to gravitropism. The cell wall is responsible for the final step of gravity resistance. The gravity signal increases the rigidity of the cell wall via the accumulation of its constituents, polymerization of certain matrix polysaccharides due to the suppression of breakdown, stimulation of cross-link formation, and modifications to the wall environment, in a wide range of situations from microgravity in space to hypergravity. Plants thus develop a tough body to resist the gravitational force via an increase in cell wall rigidity and the modification of growth anisotropy. The development of gravity resistance mechanisms has played an important role in the acquisition of responses to various mechanical stresses and the evolution of land plants.

Contents

1. Introduction

Plants are surrounded by a great variety of environmental signals to which they have developed efficient response systems during their evolution. Gravity is unique among the environmental signals important for plant life in that it is always present in a constant direction and magnitude on earth. Plants have utilized gravity as the most stable and reliable signal for their survival. Gravitropism is a typical graviresponse that enables plants to orient their leaves to sunlight and to develop a root system for anchoring and absorbing water and minerals.

To study gravitropism, mutants with impaired graviperception and signal transduction pathways have been isolated and

Abbreviations: DFA, diferulic acid; FA, ferulic acid; XTH, xyloglucan endo-transglucosylase/hydrolase.

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effectively used for the characterization and understanding of these mechanisms (Tasaka et al., 2001; Morita, 2010; Baldwin et al., 2013; Blancaflor, 2013). Weeping, which is characterized by hanging branches and is most common in trees, is also caused by a genetic mutation. Branches of most weeping trees show normal gravitropism, but they are too soft to support their own weight (Nakamura et al., 1994). Weeping is not a mutant of gravitropism, but one where the plant loses the capacity to maintain enough mechanical rigidity to resist the gravitational force.

Plant stem organs, when turned on their sides, begin to bend upward and then continue to grow in the direction opposite to the pull of gravity. In the dark, the whole process has been ascribed to gravitropism. However, the initial curvature, true gravitropism, and the following straight growth against gravity are quite different in origin and mechanisms. Thus, mechanical resistance to the gravitational force may be a principal graviresponse in plants, independent of gravitropism. Nevertheless, the presence of this gravity response has not been properly recognized for long.

We have termed this response 'gravity resistance' and examined its nature and mechanism mainly by ground-based experiments using hypergravity conditions, produced by centrifugation, and by space experiments (Hoson and Soga, 2003; Hoson et al., 2005, 2009). As a result, we have clarified the outline of the sequence of events in gravity resistance, and shown that gravity resistance is surely the major graviresponse in plants, distinct from gravitropism. In gravitropism, the gravity signal is perceived by the sedimentation of amyloplasts in statocytes. The perceived signal is then transformed by the relocalization of auxin efflux carriers and transmitted intercellularly to growing cells via the polar transport of auxin, and the resultant asymmetric distribution of auxin induces differential growth, leading to gravitropic curvatures (Tasaka et al., 2001; Morita, 2010; Blancaflor, 2013; Baldwin et al., 2013). On the other hand, in gravity resistance, the gravity signal may be perceived by mechanoreceptors (mechanosensitive ion channels) on the plasma membrane of not only statocytes but also other types of cells, and amyloplast sedimentation in statocytes is not directly involved (Soga et al., 2004, 2005). The perceived signal may be then transformed and transduced intracellularly within each cell, which may involve modulations of the expression of diverse genes, leading to modifications to the formation and functions of various cellular components.

Plant cells are surrounded by well-developed cell walls, which are the major source of mechanical strength for plant bodies. The cell wall is also the site where the plant cell first meets a variety of environmental signals, and as such is the major location of plant responses to these signals (Hoson, 1998, 2002). Thus, the plant cell wall may be responsible for gravity resistance, like the bones and muscles in an animal body. We have obtained evidence supporting this hypothesis by extensive analyses of the changes in the mechanical and chemical properties of the cell wall in plant materials grown under different gravity conditions. In the preset article, we discuss, based on data obtained, the role of the cell wall in gravity resistance in plants.

2. Cell wall changes under hypergravity conditions

2.1. Mechanical properties

Removing the gravitational force and analyzing the changes induced can be effective for understanding the nature and mechanisms of gravity resistance. However, true microgravity produced by free fall or parabolic flight on earth lasts too briefly to induce obvious changes in plant growth or cell wall properties. Therefore, basipetal hypergravity produced by centrifugation has mainly been used for the analysis of gravity resistance (Hoson and Soga, 2003; Hoson et al., 2005), the same as for gravitropism (Hodick and Sievers, 1998; Fitzelle and Kiss, 2001). Hypergravity generally suppresses elongation growth but promotes the lateral expansion of plant organs (Soga et al., 2006; Allen et al., 2009). The effects of hypergravity on the mechanical properties of the cell wall have been analyzed in the stem organs and roots of various plant materials. The data have shown that hypergravity increases cell wall rigidity (Hoson and Soga, 2003; Hoson et al., 2005).

Plant organs are highly resistant to the gravitational force, and hypergravity at 30 *g* and above is required to induce significant changes in the mechanical properties of the cell wall (Hoson and Soga, 2003). Cell wall rigidity varied in proportion to the logarithm of the magnitude of the gravitational force up to 300 *g*. When plant seedlings grown under hypergravity at 300 *g* for several hours were transferred to 1 *g* conditions, cell wall rigidity recovered fully within a couple of hours, indicating that the effects of the gravitational force on the cell wall mechanical properties are prompt and reversible. In addition, horizontal and acropetal hypergravity increased cell wall rigidity, as did basipetal hypergravity.

2.2. Cellulose

The mechanical properties of the cell wall are determined by the chemical nature of cell wall constituents and the interactions among them. The levels and the molecular size of cell wall constituents are important for the regulation of cell wall rigidity. The effects of hypergravity on the levels of cell wall polysaccharides were examined along azuki bean epicotyls (Nakano et al., 2007; Wakabayashi et al., 2009). Cellulose microfibrils in general play an important role in determining cell wall rigidity. The levels of cellulose gradually increased from the apical to the basal regions. Hypergravity increased the levels in the basal regions, but not in the upper growing regions, suggesting that cellulose acts as an anti-gravitational polysaccharide only in the supporting regions of seedlings. Cellulose accumulation was also induced by hypergravity in pollen tubes (Chebli et al., 2013). Cellulose is synthesized on the plasma membrane by cellulose synthase complexes. It has been reported that the expression of cellulose synthase genes is upregulated by hypergravity (Martzivanou and Hampp, 2003; Tamaoki et al., 2009). The contribution of the up-regulation of cellulose synthase genes to cellulose accumulation in gravity resistance remains to be evaluated by further studies.

Not only the levels but also the orientation of cellulose microfibrils influence the mechanical properties of the cell wall. The co-alignment hypothesis states that the movement of cellulose synthase complexes on the plasma membrane is constrained by interactions with cortical microtubules. It is likely that cellulose microfibrils and cortical microtubules are mutually dependent in their functions in gravity resistance. The expression of most α- and β-tubulin genes was upregulated by hypergravity in Arabidopsis hypocotyls, depending on the magnitude of the gravitational force (Yoshioka et al., 2003; Matsumoto et al., 2007). In the epidermis of azuki bean epicotyls grown at 1 *g*, cells with transverse cortical microtubules were predominant. With increasing gravitational force, the percentage of cells with transverse microtubules decreased, but the percentage with longitudinal microtubules increased (Soga et al., 2006). The reorientation of cortical microtubules occurred promptly after the transfer of seedlings from 1 *g* to hypergravity conditions. Hypergravity also transiently increased the expression of γ-tubulin and katanin genes (Soga et al., 2008, 2009), which are assumed to be responsible for the reorientation of cortical microtubules (Murata et al., 2005). On the other hand, the hypocotyls of Arabidopsis tubulin mutants were shorter and thicker than those of the wild-type, and showed either left-handed or right-handed helical growth at 1 *g*. The degree of the twisting phenotype was intensified under hypergra-

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