

## Gravity Resistance in Plants

**Kouichi Soga**

Department of Biology and Geosciences, Graduate School of Science, Osaka City University, Sumiyoshi-ku, Osaka 558-8585, Japan

### Abstract

**Gravity resistance is a response that enables the plants to develop against the gravitational force. We have analyzed the nature and mechanisms of gravity resistance using both hypergravity conditions produced by centrifugation and microgravity conditions in space. As the final step of gravity resistance, plants develop a short and thick body and increase the cell wall rigidity in response to the magnitude of the gravitational force. Prompt reorientation of cortical microtubules is involved in the modification of body shape. The regulation of the cell wall rigidity is brought about by modification of the metabolisms of anti-gravitational cell wall polysaccharides and changes in the pH of cell wall fluid. Plants may perceive the gravitational force independently of the direction of stimuli by mechanoreceptors on the plasma membrane in gravity resistance. The development of gravity resistance may serve an important function in the transition of plant ancestors from an aquatic environment to a terrestrial environment.** ©2010 Jpn. Soc. Biol. Sci. Space; Article ID: 102403010

### Introduction

Plants have been exposed to various environmental stimuli during their evolution. Of these environmental stimuli, gravity is always present on the earth's surface in a constant direction and magnitude. Although gravity is the stable environmental stimulus, mechanical load of the gravitational force on organisms is extremely different between aquatic and terrestrial environment. Namely, plants living on land have been exposed to mechanical stress of the gravitational force after they first went ashore more than 500 million years ago. Thereby, the development of a tough body may be a critical response for terrestrial plants to survive under 1 *G* conditions. We have termed this reaction gravity resistance and examined its nature and mechanisms (Hoson and Soga, 2003).

Microgravity provides an efficient condition for analysis of gravity resistance. However, it is difficult to produce microgravity conditions on the earth. While

true microgravity conditions are produced by a free fall or a parabolic flight even on the earth, the duration of microgravity obtained by these methods is generally too short for analysis of gravity resistance. The 3-D clinostat is a useful tool for analyzing plant morphogenesis in an averaged gravity environment (Hoson and Soga, 2003; Saiki *et al.*, 2005). However, the mechanical load of the gravitational force is not removed by the clinostat. Water immersion has been used as a simulator of microgravity in animal physiology. Under water, the magnitude of the load actually applied to a plant body is largely reduced by buoyancy. Generally, terrestrial plants are not able to survive under water for a long period. Thus, in terrestrial plants, water immersion is utilized for the analysis of gravity resistance for a short period, whereas, in aquatic or semiaquatic plants such as rice, gravity resistance can be analyzed by water immersion even for a long period. On the other hand, hypergravity conditions, a gravitational acceleration of more than 1 *G*, are easily produced on the earth by centrifugation. Also, the magnitude of acceleration is easily changed by regulating the speed of rotation. Thus, we have examined nature and mechanisms of gravity resistance in hypergravity experiments with the aid of water submergence studies. As a result, we have shown that plants develop a short and thick body and increase the cell wall rigidity to resist the gravitational force (Fig. 1). The data obtained by space experiments have supported the results of hypergravity experiments. In the present article, we describe the mechanisms of development of a tough body to resist the gravitational force in plants.

### Changes under hypergravity conditions

#### *Growth anisotropy*

The responses of various plant materials to centrifugal acceleration have been analyzed. As a result, basipetal hypergravity treatment has been shown to inhibit elongational growth and promote lateral expansion in shoot organs, such as hypocotyls, epicotyls, inflorescence stems, coleoptiles and mesocotyls (Hoson *et al.*, 1996; Soga *et al.*, 1999a, 1999b, 2001; Wakabayashi *et al.*, 2005a; Nakabayashi *et al.*, 2006; Nakano *et al.*, 2007). Namely, plant body becomes shorter and thicker under hypergravity conditions. In general, hypergravity at 30 *G* and above was required to clearly change the growth anisotropy (Hoson *et al.*, 1996; Soga *et al.*, 1999a, 1999b, 2006). Also, hypergravity-induced changes in growth anisotropy were intensified in proportion to the logarithm of the magnitude of gravity. On the other hand, the shape of rice seedlings became longer and thinner under water (Masuda *et al.*, 1998; Kimpura *et al.*, 2008). It has been shown that a part of the changes in growth anisotropy under water are caused by reduction of body weight due to buoyancy. Thus, development of a short and thick body may be regarded as a part of the response that enables plants to grow against the gravitational force.

The shape of plant body depends generally on the shape of its individual cells, which primarily controlled by

Received: January 12, 2011; Accepted: January 28, 2011

Correspondence:

Tel./Fax: +81-(0)6-6605-2577;

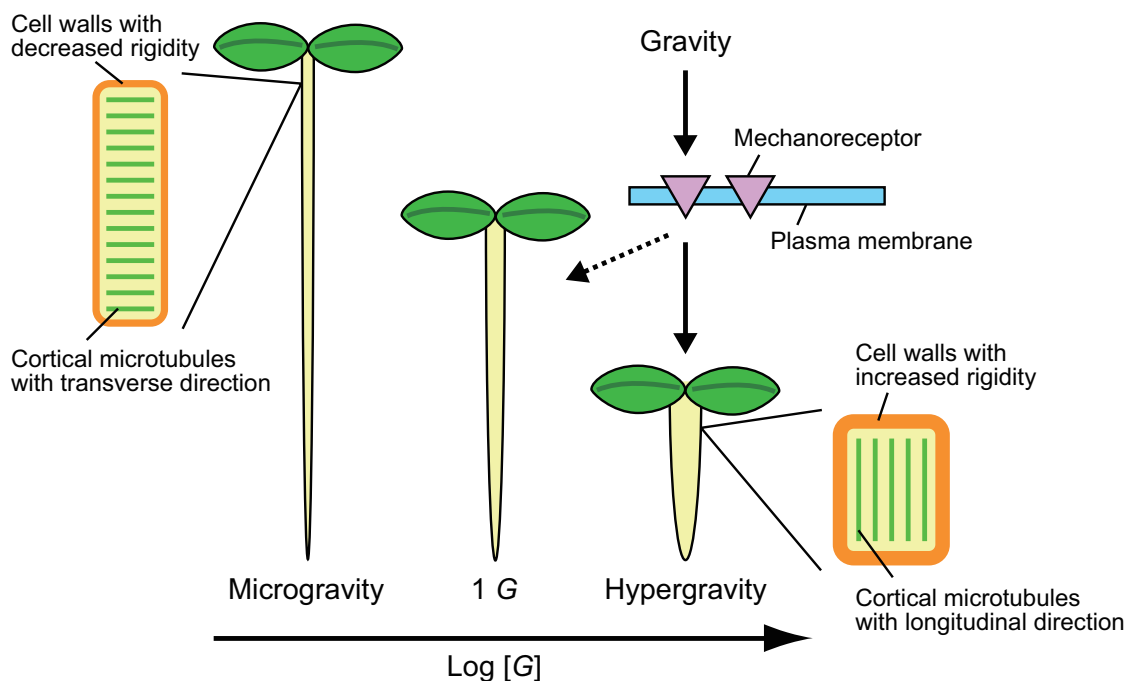
E-mail: soga@sci.osaka-cu.ac.jp

the orientation of cellulose microfibrils. The orientation of cortical microtubules has been considered to determine the orientation of cellulose microfibrils (Shibaoka, 1994). In the epidermis of azuki bean epicotyls and *Arabidopsis* hypocotyls grown at 1 G, cells with transverse cortical microtubules were predominant. The percentage of cells with transverse microtubules was decreased, whereas that with longitudinal microtubules was increased in proportion to the logarithm of the magnitude of gravity (Fig. 1; Soga *et al.*, 2006; Matsumoto *et al.*, 2010).  $\gamma$ -Tubulin complex and katanin are required for the nucleation of microtubules as branches and the severing of microtubules, respectively (Hamada, 2007; Murata and Hasebe, 2007). The transcript level of  $\gamma$ -tubulin complex and katanin in azuki bean epicotyls was increased transiently under hypergravity conditions (Soga *et al.*, 2008, 2009, 2010a). During reorientation of cortical microtubules by ethylene, which also modifies growth anisotropy of shoots, the expression levels of both  $\gamma$ -tubulin complex and katanin genes were increased transiently (Soga *et al.*, 2010a, 2010b). Thus, the increase in the number of the nucleated microtubule branch as well as the microtubule-severing activity via up-regulation of  $\gamma$ -tubulin complex and katanin genes may be involved in the reorientation of cortical microtubule. Taken together, regulation of cortical microtubule orientation may be involved in the development of a short and thick body in response to gravity.

### Cell wall rigidity

Plant cells have well-developed cell walls, which is the major source of mechanical strength for plant body. Thus, it has been assumed that the cell wall plays a principal role in gravity resistance in plants, as do the bones and muscles in animal body. To confirm this possibility, we have analyzed the cell wall rigidity of shoots under hypergravity conditions. As a result, we have shown that hypergravity increases the cell wall rigidity in shoots of various plants, such as cress, azuki bean, maize and *Arabidopsis* (Fig. 1; Hoson *et al.*, 1996; Soga *et al.*, 1999a, 1999b, 2001; Nakabayashi *et al.*, 2006). On the other hand, submergence decreased the cell wall rigidity in rice coleoptiles and azuki bean epicotyls (Masuda *et al.*, 1998; Ooume *et al.*, 2009). Thus, the increase in the cell wall rigidity may be regarded as a part of the response that enables plants to grow against the gravitational force.

Plant cell walls are composed of cellulose, a variety of matrix polysaccharides, proteins, and phenolic substances. The cell wall rigidity is determined by the chemical nature of cell wall constituents, such as the level and molecular size. Hypergravity caused an increase in the levels of cell wall polysaccharides, such as cellulose, per unit length of shoot in various plant materials (Hoson *et al.*, 1996; Soga *et al.*, 1999a, 1999b, 2001; Wakabayashi *et al.*, 2005a; Nakano *et al.*, 2007). Namely, cell wall thickness is increased under hypergravity conditions, resulting in an increase in the cell wall rigidity.



**Fig. 1.** The summary of the results obtained by hypergravity and space experiments. The body shape and the cell wall rigidity varied in proportion to the logarithm of magnitude of gravity. Changes in orientation of cortical microtubules and metabolisms of anti-gravitational cell wall polysaccharides were required for the modification of body shape and regulation of the cell wall rigidity, respectively. Hypergravity-induced changes in the body shape and the cell wall rigidity seem to be mediated by mechanoreceptors on the plasma membrane.

Hypergravity also caused a polymerization of certain matrix polysaccharides, types of which were different between dicotyledonous plants and monocotyledonous Gramineae plants. In dicotyledons, such as azuki bean and *Arabidopsis*, hypergravity increased the molecular size of xyloglucans (Soga *et al.*, 1999a, 2001), whereas submergence decreased their molecular size (Ooume *et al.*, 2009). On the other hand, in monocotyledonous Gramineae plants, such as maize, hypergravity increased the molecular size of  $\beta$ -1,3;1,4-glucans (Soga *et al.*, 1999b). Thus, xyloglucans and  $\beta$ -1,3;1,4-glucans appear to act as anti-gravitational cell wall polysaccharides (Hoson and Soga, 2003).

The molecular size of cell wall polysaccharides is determined by a balance between the synthesis and the depolymerization. Thus, we examined the effects of hypergravity on both processes of anti-gravitational cell wall polysaccharides. Xyloglucans were deposited into the cell wall as large molecules but they were then depolymerized in the cell wall in azuki bean epicotyls (Soga *et al.*, 2007b; Arai *et al.*, 2010). Under hypergravity conditions, the depolymerization of xyloglucans was inhibited by decreasing xyloglucan-degrading activity via down-regulation of a xyloglucan endotransglucosylase/hydrolase (XTH) gene, which is responsible for xyloglucan breakdown (Soga *et al.*, 1999a, 2001, 2007a, 2007b). In maize coleoptiles and mesocotyls, hypergravity decreased  $\beta$ -1,3;1,4-glucanase activity, thereby increasing the molecular size of  $\beta$ -1,3;1,4-glucans (Soga *et al.*, 1999b). Besides the regulation of levels of enzymes by gene expression, the activity of cell wall enzymes *in situ* is regulated by cell wall environment, especially pH. Hypergravity significantly increased the pH of the apoplastic fluid (cell wall fluid), and the increased apoplastic pH caused a decrease in the activities of xyloglucan-degrading enzymes and  $\beta$ -1,3;1,4-glucanases (Soga *et al.*, 2000a, 2000b). These results indicate that hypergravity inhibited the depolymerization of anti-gravitational cell wall polysaccharides by changing both enzyme levels and apoplastic pH, leading to the increase in the molecular size of anti-gravitational cell wall polysaccharides. In addition to polysaccharides, other cell wall constituents, such as lignin, phenolic substances and proteoglycans may play a role in gravity resistance (Wakabayashi *et al.*, 2005a, 2005b, 2009a, 2009b; Kotake *et al.*, 2009). Taken together, plants increase the cell wall rigidity via modifications of the metabolisms of the cell wall constituents to resist the gravitational force.

### Reversibility

We have analyzed gravity resistance using hypergravity of fairly high magnitude, such as 300 G. Here, there is one possibility that the effects of hypergravity observed are caused by physiological damage to cells. However, hypergravity-induced changes in growth anisotropy in azuki bean and maize seedlings were nullified immediately after transfer of seedlings kept for several hours at 300 G conditions to 1 G conditions (Soga *et al.*, 2003, 2006). The orientation of cortical microtubules was restored to the original direction by transiently increasing

expression of  $\gamma$ -tubulin complex and katanin genes after removal of hypergravity stimulus (Soga *et al.*, 2006, 2008, 2009). Also, hypergravity-induced modifications of cell wall properties, such as cell wall rigidity, metabolisms of cell wall polysaccharides and apoplastic pH, were cancelled immediately after transfer to 1 G conditions (Soga *et al.*, 2003, 2007a). In addition, the synthesis of cell wall polysaccharides was similar between the 1 and 300 G conditions (Soga *et al.*, 2007b). These lines of evidence strongly indicate that hypergravity at 300 G is not an extraordinary stimulus for plants and that plant response to this magnitude of gravity can be recognized as normal physiological responses.

### Changes in space

From the results of experiments using conditions of centrifugal hypergravity and water submergence, it was expected that plants would develop a long and thin body and decrease the cell wall rigidity under true microgravity conditions in space. In the STS-95 RICE experiment, we analyzed gravity resistance in space-grown *Arabidopsis* and rice seedlings. *Arabidopsis* hypocotyls elongated in a variety directions (Hoson *et al.*, 1999). On the other hand, rice coleoptiles grown in space showed automorphic curvature toward the caryopsis in the elongating region (Hoson *et al.*, 1999, 2004). Microgravity stimulated elongation growth and inhibited lateral expansion in both *Arabidopsis* hypocotyls and rice coleoptiles (Soga *et al.*, 2001, 2002; Hoson *et al.*, 2002). In roots of rice, elongation growth was also promoted by microgravity (Hoson *et al.*, 2003). Namely, plant body becomes longer and thinner under microgravity conditions in space. The body shape of *Arabidopsis* varied in proportion to the logarithm of the magnitude of gravity in the range from microgravity to hypergravity (Fig. 1; Soga *et al.*, 2001). As described above, the hypergravity-induced development of a short and thick body may be mediated by reorientation of cortical microtubules. Therefore, the increase in the percentage of cells with transverse microtubules may contribute to formation of a long and thin body under microgravity conditions in space.

Microgravity decreased the cell wall rigidity of both *Arabidopsis* hypocotyls and rice coleoptiles (Soga *et al.*, 2001, 2002; Hoson *et al.*, 2002). The cell wall rigidity of *Arabidopsis* hypocotyls varied in proportion to the logarithm of the magnitude of gravity in the range from microgravity to hypergravity (Fig. 1; Soga *et al.*, 2001). As to the chemical nature of cell wall constituents, the space-grown seedlings had lower levels of cell wall polysaccharides per unit length than the controls, indicating that microgravity decreases cell wall thickness (Soga *et al.*, 2001, 2002; Hoson *et al.*, 2002). The molecular size of anti-gravitational cell wall polysaccharides, xyloglucans and  $\beta$ -1,3;1,4-glucans, was decreased under microgravity conditions. The activity of xyloglucan-degrading activity in space-grown *Arabidopsis* hypocotyls was increased, suggesting that microgravity reduces the molecular size of xyloglucans by stimulating xyloglucan breakdown (Soga *et al.*, 2001, 2002). Thus, the regulation of the cell wall rigidity via modification of



metabolisms of anti-gravitational cell wall polysaccharides may be regarded as a part of the response that enables plants to grow against the gravitational force. As mentioned above, hypergravity-induced increase in the apoplastic pH caused an inhibition of breakdown of anti-gravitational cell wall polysaccharides, leading to the increase in the cell wall rigidity. On the other hand, auxin decreased the apoplastic pH, when it decreased the cell wall rigidity in inflorescence stems of *Arabidopsis* (Soga *et al.*, 2000c). Thus, microgravity may decrease the pH of the apoplastic fluid, which may lead to the decrease in the cell wall rigidity by stimulating breakdown of anti-gravitational cell wall polysaccharides.

#### *Signal perception and transduction*

Gravitropism is a response that enables plants to orient their photosynthetic organs to sunlight and to develop a root system for anchoring and absorbing water and minerals. In gravitropism, the gravity signal is supposed to be perceived by sedimentation of amyloplasts in statocytes. The *pgm1* (*phosphoglucomutase 1*) and *sgr1* (*shoot gravitropism 1*) mutants of *Arabidopsis* show reduced or no gravitropic responses in inflorescence stems and hypocotyls, because of reduction or lack of sedimentable amyloplasts (Tasaka *et al.*, 2001). If graviperception in gravity resistance is mediated by sedimentable amyloplasts, both *sgr1* and *pgm1* mutants are expected not to respond, or to respond only weakly, to hypergravity stimuli. However, we revealed that hypocotyls of both mutants showed gravity resistance responses similar to those of wild type hypocotyls (Soga *et al.*, 2004). In addition, the removal of statocytes did not influence gravity resistance response in azuki bean roots, although the gravitropic bending was completely inhibited (Soga *et al.*, 2005a). These results suggest that the gravity perception mechanism in gravity resistance is independent of that in gravitropism, which involves amyloplasts as statoliths.

Mechanoreceptors (mechanosensitive ion channels) on the plasma membrane are supposed to sense physical deformation of the plasma membrane. If mechanoreceptors are involved in the graviperception in gravity resistance, the shoots are expected not to respond to hypergravity stimuli under conditions in which mechanoreceptors do not act. To ascertain this possibility, we examined the effects of lanthanum and gadolinium ions, blockers of mechanoreceptors, on the hypergravity response of azuki bean and *Arabidopsis* seedlings. Hypergravity at 300 G had no effects on growth and orientation of cortical microtubules in the presence of lanthanum and gadolinium ions (Soga *et al.*, 2004, 2005a, 2006). Also, the cell wall rigidity or the cell wall metabolism was not affected by hypergravity in the presence of lanthanum and gadolinium ions (Soga *et al.*, 2004, 2007a). These results suggest that mechanoreceptors are involved in the perception of the gravity signal in gravity resistance (Fig. 1). Also, these results indicate again that 300 G are not excessive for plants but within the physiological response spectrum. Horizontal and acropetal hypergravity modified growth

anisotropy and the cell wall rigidity, as did basipetal hypergravity, all of which were nullified by lanthanum and gadolinium ions (Soga *et al.*, 2005b, 2006). Thus, mechanoreceptors may perceive the gravity signal independently of its direction in gravity resistance.

To understand the signal transformation and transduction processes, we have identified genes whose expression was changed by hypergravity in *Arabidopsis* hypocotyls. One of isolated genes encoded 3-hydroxy-3-methylglutaryl-coenzyme A reductase (HMGR), which catalyzes a reaction producing mevalonic acid, a key precursor of terpenoids such as membrane sterols (Yoshioka *et al.*, 2003). Lovastatin, an inhibitor of HMGR, made azuki bean epicotyls hypersensitive to the gravitational force (Koizumi *et al.*, 2007). Also, the expression of most  $\alpha$ - and  $\beta$ -tubulin genes was up-regulated by hypergravity (Yoshioka *et al.*, 2003; Matsumoto *et al.*, 2007). Tubulin mutants showed hypersensitivity to the gravitational force (Hoson *et al.*, 2010; Matsumoto *et al.*, 2010). To examine the roles of membrane sterols and cortical microtubules in the signal transformation and transduction processes, we carried out the Resist Wall space experiment (Hoson *et al.*, 2007). We obtained a result that the phenotype of tubulin mutants was partially rescued in space, suggesting that cortical microtubules are involved in the signal transformation and transduction processes (Hoson *et al.*, 2009b). For details on the signal transformation and transduction processes, see Hoson *et al.* (2005, 2009a).

#### **Conclusions**

We have clarified the nature and mechanisms of gravity resistance using both hypergravity conditions and in space experiments. Figure 1 summarizes the results obtained by both hypergravity and space experiments. The body shape and the cell wall rigidity varied in proportion to the logarithm of magnitude of gravity in the range from microgravity to hypergravity. The regulation of the body shape and the cell wall rigidity may be required to survive at 1 G gravity on the earth for terrestrial plants. Hypergravity-induced changes in the body shape and the cell wall rigidity seem to be mediated by mechanoreceptors on the plasma membrane. Therefore, gravity at 1 G on the earth may be also perceived by mechanoreceptors. We need to clarify the details of gravity resistance by further space experiments.

#### **Acknowledgements**

The author is grateful to numerous colleagues and collaborators. Thanks also due to Professor T. Hoson and Dr. K. Wakabayashi of Osaka City University for critical reading the manuscript and valuable suggestions.

#### **References**

- Arai, K., Wakabayashi, K., Soga, K. and Hoson, T. (2010) Fucosylated high molecular mass but not non-fucosylated low molecular mass xyloglucans undergo

- an extensive depolymerization in cell walls of azuki bean epicotyls. *J. Plant Physiol.*, **167**, 800-804.
- Hamada, T. (2007) Microtubule-associated proteins in higher plants. *J. Plant Res.*, **120**, 79-98.
- Hoson, T., Nishitani, K., Miyamoto, K., Ueda, J., Kamisaka, S., Yamamoto, R. and Masuda, Y. (1996) Effects of hypergravity on growth and cell wall properties of cress hypocotyls. *J. Exp. Bot.*, **47**, 513-517.
- Hoson, T., Soga, K., Mori, R., Saiki, M., Wakabayashi, K., Kamisaka, S., Kamigaichi, S., Aizawa, S., Yoshizaki, I., Mukai, C., Shimazu, T., Fukui, K. and Yamashita, M. (1999) Morphogenesis of rice and *Arabidopsis* seedlings in space. *J. Plant Res.*, **112**, 477-486.
- Hoson, T., Soga, K., Mori, R., Saiki, M., Nakamura, Y., Wakabayashi, K. and Kamisaka, S. (2002) Stimulation of elongation growth and cell wall loosening in rice coleoptiles under microgravity conditions in space. *Plant Cell Physiol.*, **43**, 1067-1071.
- Hoson, T. and Soga, K. (2003) New aspects of gravity responses in plant cells. *Int. Rev. Cytol.*, **229**, 209-244.
- Hoson, T., Soga, K., Wakabayashi, K., Kamisaka, S. and Tanimoto, E. (2003) Growth and cell wall changes in rice roots during spaceflight. *Plant Soil*, **255**, 19-26.
- Hoson, T., Soga, K., Mori, R., Saiki, M., Nakamura, Y., Wakabayashi, K. and Kamisaka, S. (2004) Cell wall changes involved in the automorphic curvature of rice coleoptiles under microgravity conditions in space. *J. Plant Res.*, **117**, 449-455.
- Hoson, T., Saito, Y., Soga, K. and Wakabayashi, K. (2005) Signal perception, transduction, and response in gravity resistance. Another graviresponse in plants. *Adv. Space Res.*, **36**, 1196-1202.
- Hoson, T., Matsumoto, S., Soga, K., Wakabayashi, K., Hashimoto, T., Sonobe, S., Muranaka, T., Kamisaka, S., Kamada, M., Omori, K., Ishioka, N. and Shimazu, T. (2007) The Outline and Significance of the Resist Wall Experiment: Role of Microtubule-Membrane-Cell Wall Continuum in Gravity Resistance in Plants. *Biol. Sci. Space*, **21**, 56-61.
- Hoson, T., Soga, K. and Wakabayashi, K. (2009a) Role of the cell wall-sustaining system in gravity resistance in plants. *Biol. Sci. Space*, **23**, 131-136.
- Hoson, T., Matsumoto, S., Soga, K., Wakabayashi, K., Hashimoto, T., Sonobe, S., Muranaka, T., Kamisaka, S., Kamada, M., Omori, K., Ishioka, N. and Shimazu, T. (2009b) Growth and cell wall properties in hypocotyls of *Arabidopsis tua6* mutant under microgravity conditions in space. *Biol. Sci. Space*, **23**, 71-76.
- Hoson, T., Matsumoto, S., Soga, K. and Wakabayashi, K. (2010) Cortical microtubules are responsible for gravity resistance in plants. *Plant Signal. Behav.*, **5**, 752-754.
- Kimpara, T., Aohara, T., Soga, K., Wakabayashi, K., Hoson, T., Tsumuraya, Y. and Kotake, T. (2008)  $\beta$ -1,3:1,4-Glucan synthase activity in rice seedlings under water. *Ann. Bot.*, **102**, 221-226.
- Koizumi, T., Sakaki, T., Usui, S., Soga, K., Wakabayashi, K. and Hoson, T. (2007) Changes in membrane lipid composition in azuki bean epicotyls under hypergravity conditions: Possible role of membrane sterols in gravity resistance. *Adv. Space Res.*, **39**, 1198-1203.
- Kotake, T., Hirata, N., Kitazawa, K., Soga, K. and Tsumuraya, Y. (2009) Arabinogalactan-proteins in the evolution of gravity resistance in land plants. *Biol. Sci. Space*, **23**, 143-149.
- Masuda, Y., Kamisaka, S. and Hoson, T. (1998) Growth behavior of rice coleoptiles. *J. Plant Physiol.*, **152**, 180-188.
- Matsumoto, S., Saito, Y., Kumasaki, S., Soga, K., Wakabayashi, K. and Hoson, T. (2007) Up-regulation of expression of tubulin genes and roles of microtubules in hypergravity-induced growth modification in *Arabidopsis* hypocotyls. *Adv. Space Res.*, **39**, 1176-1181.
- Matsumoto, S., Kumasaki, S., Soga, K., Wakabayashi, K., Hashimoto, T. and Hoson, T. (2010) Gravity-induced modifications to development in hypocotyls of *Arabidopsis* tubulin mutants. *Plant Physiol.*, **152**, 918-926.
- Murata, T. and Hasebe, M. (2007) Microtubule-dependent microtubule nucleation in plant cells. *J. Plant Res.*, **120**, 73-78.
- Nakabayashi, I., Karahara, I., Tamaoki, D., Masuda, K., Wakasugi, T., Yamada, K., Soga, K., Hoson, T. and Kamisaka, S. (2006) Hypergravity stimulus enhances primary xylem development and decreases mechanical properties of secondary cell walls in inflorescence stems of *Arabidopsis thaliana*. *Ann. Bot.*, **97**, 1083-1090.
- Nakano, S., Soga, K., Wakabayashi, K. and Hoson, T. (2007) Different cell wall polysaccharides are responsible for gravity resistance in the upper and the basal regions of azuki bean epicotyls. *Biol. Sci. Space*, **21**, 113-116.
- Ooume, K., Inoue, Y., Soga, K., Wakabayashi, K., Fujii, S., Yamamoto, R. and Hoson, T. (2009) Cellular basis of growth suppression by submergence in azuki bean epicotyls. *Ann. Bot.*, **103**, 325-332.
- Saiki, M., Fujita, H., Soga, K., Wakabayashi, K., Kamisaka, S., Yamashita, M. and Hoson, T. (2005) Cellular basis for the automorphic curvature of rice coleoptiles on a three-dimensional clinostat: Possible involvement of reorientation of cortical microtubules. *J. Plant Res.*, **118**, 199-205.
- Shibaoka, H. (1994) Plant hormone-induced changes in the orientation of cortical microtubules: Alterations in the cross-linking between microtubules and the plasma membrane. *Ann. Rev. Plant Physiol. Plant Mol. Biol.*, **45**, 527-544.
- Soga, K., Wakabayashi, K., Hoson, T. and Kamisaka, S. (1999a) Hypergravity increases the molecular size of xyloglucans by decreasing xyloglucan-degrading activity in azuki bean epicotyls. *Plant Cell Physiol.*, **40**, 581-585.
- Soga, K., Harada, K., Wakabayashi, K., Hoson, T. and Kamisaka, S. (1999b) Increased molecular mass of hemicellulosic polysaccharides is involved in growth inhibition of maize coleoptiles and mesocotyls under hypergravity conditions. *J. Plant Res.*, **112**, 273-278.
- Soga, K., Wakabayashi, K., Hoson, T. and Kamisaka, S.

- (2000a) Changes in the apoplastic pH are involved in regulation of xyloglucan breakdown of azuki bean epicotyls under hypergravity conditions. *Plant Cell Physiol.*, **41**, 509-514.
- Soga, K., Wakabayashi, K., Hoson, T. and Kamisaka, S. (2000b) Hypergravity-induced increase in the apoplastic pH and its possible involvement in suppression of  $\beta$ -glucan breakdown in maize seedlings. *Aust. J. Plant Physiol.*, **27**, 967-972.
- Soga, K., Wakabayashi, K., Hoson, T. and Kamisaka, S. (2000c) Flower stalk segments of *Arabidopsis thaliana* ecotype Columbia lack the capacity to grow in response to exogenously applied auxin. *Plant Cell Physiol.*, **41**, 1327-1333.
- Soga, K., Wakabayashi, K., Hoson, T. and Kamisaka, S. (2001) Gravitational force regulates elongation growth of *Arabidopsis* hypocotyls by modifying xyloglucan metabolism. *Adv. Space Res.*, **27**, 1011-1016.
- Soga, K., Wakabayashi, K., Kamisaka, S. and Hoson, T. (2002) Stimulation of elongation growth and xyloglucan breakdown in *Arabidopsis* hypocotyls under microgravity conditions in space. *Planta*, **215**, 1040-1046.
- Soga, K., Wakabayashi, K., Kamisaka, S. and Hoson, T. (2003) Growth restoration in azuki bean and maize seedlings by removal of hypergravity stimuli. *Adv. Space Res.*, **31**, 2269-2274.
- Soga, K., Wakabayashi, K., Kamisaka, S. and Hoson, T. (2004) Graviperception in growth inhibition of plant shoots under hypergravity conditions produced by centrifugation is independent of that in gravitropism and may involve mechanoreceptors. *Planta*, **218**, 1054-1061.
- Soga, K., Wakabayashi, K., Kamisaka, S. and Hoson, T. (2005a) Mechanoreceptors rather than sedimentable amyloplasts perceive the gravity signal in hypergravity-induced inhibition of root growth in azuki bean. *Funct. Plant Biol.*, **32**, 175-179.
- Soga, K., Wakabayashi, K., Kamisaka, S. and Hoson, T. (2005b) Hypergravity inhibits elongation growth of azuki bean epicotyls independently of the direction of stimuli. *Adv. Space Res.*, **36**, 1269-1276.
- Soga, K., Wakabayashi, K., Kamisaka, S. and Hoson, T. (2006) Hypergravity induces reorientation of cortical microtubules and modifies growth anisotropy in azuki bean epicotyls. *Planta*, **224**, 1485-1494.
- Soga, K., Wakabayashi, K., Kamisaka, S. and Hoson, T. (2007a) Effects of hypergravity on expression of *XTH* genes in azuki bean epicotyls. *Physiol. Plant.*, **131**, 332-340.
- Soga, K., Arai, K., Wakabayashi, K., Kamisaka, S. and Hoson, T. (2007b) Modifications of xyloglucan metabolism in azuki bean epicotyls under hypergravity conditions. *Adv. Space Res.*, **39**, 1204-1209.
- Soga, K., Kotake, T., Wakabayashi, K., Kamisaka, S. and Hoson, T. (2008) Transient increase in the transcript levels of  $\gamma$ -tubulin complex genes during reorientation of cortical microtubules by gravity in azuki bean (*Vigna angularis*) epicotyls. *J. Plant Res.*, **121**, 493-498.
- Soga, K., Kotake, T., Wakabayashi, K., Kamisaka, S. and Hoson, T. (2009) The transcript level of katanin gene is increased transiently in response to changes in gravitational conditions in azuki bean epicotyls. *Biol. Sci. Space*, **23**, 23-28.
- Soga, K., Yamaguchi, A., Kotake, T., Wakabayashi, K. and Hoson, T. (2010a) Transient increase in the levels of  $\gamma$ -tubulin complex and katanin are responsible for reorientation by ethylene and hypergravity of cortical microtubules. *Plant Signal. Behav.*, **5**, 1480-1482.
- Soga, K., Yamaguchi, A., Kotake, T., Wakabayashi, K. and Hoson, T. (2010b) 1-Aminocyclopropane-1-carboxylic acid (ACC)-induced reorientation of cortical microtubules is accompanied by a transient increase in the transcript levels of  $\gamma$ -tubulin complex and katanin genes in azuki bean epicotyls. *J. Plant Physiol.*, **167**, 1165-1171.
- Tasaka, M., Kato, T. and Fukaki, H. (2001) Genetic regulation of gravitropism in higher plants. *Int. Rev. Cytol.*, **206**, 135-154.
- Wakabayashi, K., Soga, K., Kamisaka, S. and Hoson, T. (2005a) Changes in levels of cell wall constituents in wheat seedlings grown under continuous hypergravity conditions. *Adv. Space Res.*, **36**, 1292-1297.
- Wakabayashi, K., Soga, K., Kamisaka, S. and Hoson, T. (2005b) Increase in the level of arabinoxylan-hydroxycinnamate network in cell walls of wheat coleoptiles grown under continuous hypergravity conditions. *Physiol. Plant.*, **125**, 127-134.
- Wakabayashi, K., Soga, K. and Hoson, T. (2009a) Modification of cell wall architecture in gramineous plants under altered gravity conditions. *Biol. Sci. Space*, **23**, 137-142.
- Wakabayashi, K., Nakano, S., Soga, K. and Hoson, T. (2009b) Cell wall-bound peroxidase activity and lignin formation in azuki bean epicotyls grown under hypergravity conditions. *J. Plant Physiol.*, **166**, 947-954.
- Yoshioka, R., Soga, K., Wakabayashi, K., Takeba, G. and Hoson, T. (2003) Hypergravity-induced changes in gene expression in *Arabidopsis* hypocotyls. *Adv. Space Res.*, **31**, 2187-2193.