Growth and cortical microtubule dynamics in shoot organs under microgravity and hypergravity conditions

Kouichi Soga, Kazuyuki Wakabayashi & Takayuki Hoson

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Resistance to the gravitational force is a critical response for terrestrial plants to survive under 1 g conditions. We have termed this response ‘gravity resistance’ and have analyzed the nature and mechanisms of gravity resistance using hypergravity conditions produced by centrifugation and microgravity conditions in space. Hypergravity inhibited elongation growth and promoted lateral expansion in shoot organs, such as pea epicotyls, radish and cucumber hypocotyls, garden cress hypocotyls, azuki bean epicotyls, maize coleoptiles and mesocotyls, Arabidopsis hypocotyls and inflorescence stems, and wheat coleoptiles. Namely, plants developed a short and thick body under hypergravity conditions. On the other hand, microgravity promoted elongation growth and inhibited lateral expansion in shoot organs, such as rice coleoptyls, Arabidopsis hypocotyls, and inflorescence stems, and azuki bean epicotyls, i.e., the plant body became longer and thinner under microgravity conditions in space. The body shape of Arabidopsis hypocotyls varied in proportion to the logarithm of the magnitude of gravity in the range from microgravity to hypergravity (Fig. 1). Taken together, these results indicated that the development of a short and thick body is the main mechanism that enables plants to grow against the gravitational force.

Cortical microtubules are essential for modification of the body shape because they regulate the direction of cell expansion. Hypergravity induced reorientation of cortical microtubules from transverse to longitudinal directions in azuki bean epicotyls and Arabidopsis hypocotyls. We carried out a space experiment, denoted as Aniso Tubule, to examine the effects of microgravity on the cortical microtubule dynamics in Arabidopsis hypocotyls, using lines in which microtubules are visualized by labelling tubulin or microtubule-associated proteins (MAPs) with green fluorescent protein (GFP). The dynamics of cortical microtubules in hypocotyls were analyzed using a fluorescence microscope, which was controlled from ground by commanding, in the Kibo Module in the International Space Station. Under microgravity conditions, cells having transverse microtubules were predominant, as observed in 1 g samples. However, the percentage of cells having transverse microtubules in seedlings grown under microgravity conditions was higher than that at 1 g. We analyzed the average angle of the cortical microtubules, and showed that the angle decreased by microgravity. These results indicate that cortical microtubules orient more in transverse directions in microgravity conditions in space. Thus, these findings suggest that the reorientation of cortical microtubules is involved in the regulation of growth anisotropy by gravity in plant cells (Fig. 1).

How is the orientation of cortical microtubules regulated by gravity? MAPs bind to microtubules and regulate their dynamics, stability, and organization. The 65 kDa MAP (MAP65) family proteins form cross-bridges between adjacent microtubules and are required for the bundling of microtubules and the maintenance of transverse microtubule orientation. The
transcript levels of MAP65-1 in azuki bean epicotyls was down-regulated by hypergravity. We also determined the protein levels of MAP65-1, expressed by the native promoter, by analyzing GFP fluorescence in Arabidopsis hypocotyls of GFP-MAP65-1 line. The protein levels of MAP65-1 in Arabidopsis hypocotyls were decreased by hypergravity. On the other hand, microgravity increased the protein levels of MAP65-1 in Arabidopsis hypocotyls. These results suggest that changes in the protein levels of MAP65-1 via modification of the expression of its gene may be one of the mechanisms for the regulation of orientation of cortical microtubules by gravity (Fig. 1). The levels of other MAPs, such as γ-tubulin complex and katanin, which are required for the nucleation and the severing of microtubules, respectively, also changed during reorientation of cortical microtubules by hypergravity. These findings suggest that changes in the levels of particular types of MAPs are involved in the modification of the dynamics of the cortical microtubules by gravity.

Conclusions

Figure 1 summarizes the results obtained by space and hypergravity experiments. The body shape varied in proportion to the logarithm of magnitude of gravity in the range from microgravity to hypergravity. The regulation of orientation of cortical microtubules via changes in the levels of MAP65-1 may contribute to the modification of the body shape of plants by gravity. Thus, the regulation of the body shape by modification of cortical microtubule dynamics may be required for terrestrial plants to survive at 1 g gravity on the earth.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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