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ORIGINAL ARTICLE

Flowering in space

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Abstract
The reproductive success of plants is often dependent on their flowering time being adapted to the terrestrial environment, in which gravity remain constant. Whether plants can follow the same rule to determine their flowering time under microgravity in space is unknown. Although numerous attempts have been made to grow a plant through a complete life cycle in space, apparently no published information exists concerning the flowering control of plants under microgravity in space. Here, we focused on two aspects. Firstly the environmental and intrinsic factors under microgravity related to flowering control. Secondly, the plant-derived regulators are involved in flowering control under microgravity condition. The potential environmental and intrinsic factors affect plant flowering under microgravity may include light, biological circadian clock as well as long-distance signaling, while the plant-derived flowering regulators in response to microgravity could include gibberellic acid, ethylene, microRNA and sugar. The results we have obtained from the space experiments on board the Chinese recoverable satellites (the SJ-8 and the SJ-10) and the experiment on the Chinese space lab TG-2 are also introduced. We conclude by suggesting that long-term space experiments from successive generations and a systematic analysis of regulatory networks at the molecular level is needed to understand the mechanism of plant flowering control under microgravity conditions in space.

Keywords Microgravity · Photoperiod · Flowering · Chinese recoverable satellite · Long-term

Introduction

Plants have evolved in and are highly adapted to 1-g condition of Earth. Removal of gravitational acceleration by spaceflight caused a wide range of morphogenesis and cellular and molecular changes in plants (Cogoli and Gmuňder 1991; Hampp et al. 1997; Paul et al. 2013; Hoson 2014; Zhang and Zheng 2015a). Under microgravity conditions, plants exhibit spontaneous curvatures or changes in growth direction (Driss-Ecole et al. 2008). Much progress on plant growth and development at the molecular levels in response and adaptation to microgravity has recently been made due to advances in plant genomics and proteomics (Zheng et al. 2015; Zhang et al. 2015b). However, the opportunities of space missions were scarce and they needed detailed and well-characteristic ground studies. For this reason, most of previous space experiments focused on response of plant to short-term microgravity (Kiss et al. 1998; Driss-Ecole et al. 2008; Kordyum 2014). The research is currently experiencing a renewed interest in the context of future long-term space missions, where higher plants in a life support system are required to supply food and fiber, purify ambient air, and recycle human waste and water (Massa et al. 2017).

Several early attempts to grow plants through a complete life cycle in space were unsuccessful because of delayed development (Mashinsky et al. 1994). Plants frequently died in the transition from the vegetative to the reproductive stage (Halstead and Dutcher 1987; Nechitailo and Maskinsky 1993). Even when *Arabidopsis thaliana* plants were pre-grown to the flowering stage on Earth and allowed to for seeds on orbit only 55% of seeds were fertile (27% aborted and 18% had non-viable embryos). The first successful complete plant life cycle in microgravity occurred in 1983 with Arabidopsis on board Salyut 7 (Table 1). Although development was delayed, the plants flowered and produced

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Table 1 Highlights of space experiments on plant reproduction

Time	Plants	Platform	Duration (day)	Results	References
1983	*Arabidopsis thaliana*	"Salyut-7"	69	Plants with mature siliques and a few of seeds.	Merkys and Laurinavicius (1983)
1994	*Triticum aestivum*	"Mir"	167	Development delay, failed to flowering and seedingbut developed seeds after return.	Mashinsky et al. (1994)
1997	*Brassica rapa L.*	"Mir"	144	Successfully produced seeds, but the contents were changed	Kuang et al. (2000)
1997	*Triticum aestivum*	"Mir"	163	Flowering and borne a few of seeds	Strickland et al. (1997)
2001	*Arabidopsis thaliana*	ISS	95	70% plant developed inflorescent shoots and borne seeds.	Link et al. (2003)
2002	*Arabidopsis thaliana*	ISS	134	Produced 91 seeds20% plant couldn't flower	Link et al. (2014)
2003	Dwarf pea	ISS	368	Four successive pea crops (from seeds to seeds)	Sychev et al. (2007)
2006	Chinese cabbage	SJ-8	21	Seed germination; inflorescence development; flowering opening	Zheng et al. (2008)
2009	*Arabidopsis thaliana*	ISS	62	From seeds to seeds	Yano et al. (2013)
2016	*Arabidopsis thaliana*, Rice	SJ-10	12	Transition from vegetative to reproductive stage, expression of *HSP17.4* gene promoter controlled the *GFP* and*FT* gene, photoperiod on flowering time controlling	Wang et al. (2016)
2016	*Arabidopsis thaliana* Rice	TG-2	850	From seeds to seeds; Expression of FT promoter controlled the GFP and the FT genes; photoperiod on flowering time controlling	Zheng et al. (2017)

new viable seeds (Merkys and Laurinavicius 1983). The second successful experiment was performed with *Brassica rapa* on board the Mir space station (Musgrave et al. 2000; Kuang et al. 2000). The seeds obtained in this experiment were healthy and viable, but less protein, fewer cotyledon cell, and aberrant deposition of starch grains. Wheat crop under the same environment on board Mir was failed to develop seeds (Strickland et al. 1997). Both of these experiments indicated that ethylene concentration in the growth chambers was considered responsible for influence of plant reproduction. As international space station (ISS) established, more long-term experiments goal on growing plant for a full life cycle could be carried out in space. The first seed-to-seed experiment on board ISS was performed in the advanced astroclulture (ADVASC) plant growth unit, which is capable of providing nutrients to the plant and controlling soil moisture, light, air temperature, humidity, ethylene, and CO_2 level (Link et al. 2003). Since then, advances in plant culture technology have led to more frequent successful seed set in space (Sychev et al. 2007; Link et al. 2014; Yano et al. 2013). However, seeds developed in space are still often of lower quality in compared with control seeds formed in normal gravity conditions (De Micco et al. 2014; Link et al. 2014). Seeds produced in space exhibited delayed embryo development, alteration of storage reserves, delay in starch use in cotyledons and decreased cotyledon cell number (Kuang et al. 2000; Musgrave et al. 2000; Link et al. 2014).

The quality of reproduction often depends on the development of the vegetative stage and the transition to flowering is controlled to coincide with conditions that enhance the production of seeds. To understand the main constraints in space on plant flowering control, we currently focus on the environmental factors related to the phase transition in which the plant life cycle in space can be interrupted more easily than in others also on Earth and discuss reasons for flowering disturb that often occurs under microgravity conditions.

Environmental and intrinsic factors related to flowering control in space

Light

According to the response of plants to light during the induction of flowering, they can be classified as long day (LD) plants that induce flowering when day length exceeds a certain threshold, short day (SD) plants that flower when days are short and nights are long, and day neutral plants whose flowering is not dependent on the length of the day (Fig. 1). *Arabidopsis thaliana* is a long-day plant, which floral transition is promoted by the long day condition (i.e.16h light/8h dark). The phenomenon that plant flowering in response to day length is dubbed photoperiod response, which has been observed to be perceived in the leaves from which the long-distance signal called the florigen is transmitted to the shoot apex to induce flowering. The studies on florigen have been recently made tremendous progress due to identification of numerous genes involved in flowering regulation. In Arabidopsis, a protein called FLOWERING LOCUS T (FT) was proven to be established as florigen, which is contributing to the floral induction by acting as a long-distance signal between leaves and the shoot meristem (Fig. 1). Transcription of florigen genes is tightly regulated by environmental conditions. For example, light is the major signal, which is perceived by photoreceptors and synchronized the circadian clock in day length. Analysis of FT expression in Arabidopsis revealed not only that its expression is much higher in long day, but also that it follows a circadian pattern. Apart from day length, the quality of light also plays a significant role in the transition to flowering (Srikanth and Schmid 2011). A shift the red to far-red ratio could induce early flowering. The phytochromes, which are red and far-red light photoreceptors, are involved in regulated expression of *FT*. In addition, blue light is also known to regulate the transition to flowering. Evidences from different experiments clearly showed that various aspects of light (in particular day length, light quantity and quality) control the floral transition in many plant species (Putterill et al. 2004).

Gravity and light are two of most important environmental factors to regulate plant growth and development on earth. As mention above, effects of light on the regulation of plant flowering have been extensively studied. However, because gravity is a permanent and always present in a constant direction and magnitude on the terrestrial envirnonment, there is no way to eliminate the influence of gravity on plants on the surface of the earth. Plant have utilized gravity as the most stable and reliable signal to direct their developmental processes. The other environmental factors, including light, humidity, touch, nutrients, and phytohormones, interact with gravity to determine complex growth patterns that optimize plant's survival under the terrestrial conditions (Blancaflor and Masson 2003). With the increased interest of plants in space, altered gravity cannot be ignored in studies of plant developmental processes, including plant flowering control.

The velocity and pattern of movement of the florigen was found to match those of photosynthetic assimilates (King et al. 1968; King and Zeevaart 1973), indicating that the florigen might move with phloem exudates. Although how phloem transport is driven is not known, fluxes of carbohydrates to all components of a tree decline with increasing tree height (Ryan and Asao 2014; Drake et al. 2011) might imply that gravity is involved in this process. Thus, we predict that long distance signal transport of florigen in phloem will be greatly modified under microgravity in space conditions. To test this hypothesis, the effects of microgravity on the flowering induction of long-day Arabidopsis and short-day rice were examined by living image on board the Chinese satellite SJ-8 and SJ-10, and the Chinese spacelab TG-2, which will describe later.

Biological circadian clock

Circadian rhythms are an internal biochemical oscillator, which control processes ranging from human sleep-wake cycles to cyanobacterial cell division. Like most organisms, plants have endogenous biological clocks that coordinate physiological processes with daily changes in the environment on the earth, such as the onset of dawn and dusk. The rhythm of daily on the earth is formed by the combined actions between the earth, the sun and the moon. Physiological processes regulated by the clock in higher plants include photoperiodic induction of flowering and rhythmic hypocotyl elongation, cotyledon movement,

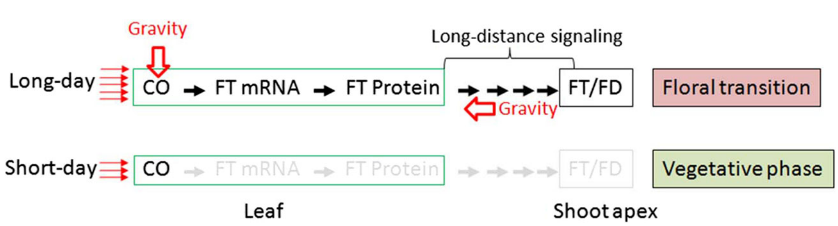

Fig. 1 Working model for the long-day and the short-day pathways in Arabidopsis and how it is possible regulated by altered gravity. The upper panel shows simplified outline of the long-day pathway, in which two steps could be affected by gravity (opening arrows indicate), including expression of FT protein and FT protein transport from the leaf to shoot apex, where flowers will be induced. The lower panel shows simplified outline of the short-day pathway, in which CO couldn't promote FT gene expression and this results in delay flowering

and stomatal opening (Harmer et al. 2000). For example, plants grown on the earth have the behavior of solar tracking movements that are driven by antiphasic patterns of elongation on the east and west sides of the stem. A recent study showed that circadian regulation of directional growth pathways accounts for leads to increased vegetative biomass (Atamian et al. 2016).

A number of flowering-time genes have been previously reported to be under clock control (Samach and Coupland 2000). For example, FT is genetically down-stream of CONSTANS (CO), which expression is under the control of the circadian clock with a phase of 24h. The CO-FT module is conserved in both LD and SD plants (Srikanth and Schmid 2011). The circadian clock of plant on the earth is relative stable under a certain photoperiod condition. When plants grow in space, new biological clocks could form instead of the intrinsic rhythm formed on the earth and the biological processes related to this rhythm would be coordinately changed. Ultradian rhythms in leaves and circumnutation in stems of Arabidopsis apparently changed in microgravity (Solheim et al. 2009; Johnsson et al. 2009). Whether photoperiodic induction of flowering is influenced by microgravity due to the alteration of circadian clock in space is unknown, because this biological process needs a long-term space experiment. As more long-term space mission set-up, the detail research should be carried out on the influence of circadian clock in space, specially its effects on the key developmental process of plants including the flowering induction.

Long-distance signaling

Long-distance signaling in plants is known to be important for the regulation of several processes including leaf development and flowering (Jaeger and Wigge 2007). Flowering time is a key developmental switch that is affected by environmental conditions. Environmental cues, such as light and temperature, are sensed by the leaves while the responses occur at the shoot apex, requiring long-range communication within the plant (Jaeger and Wigge 2007). The FT protein act as a systemic inducer of flowering that is expressed in the companion cells of the phloem and exported to the phloem sieve elements in leaves from where it is transported to the shoot apex (Fig. 1). This process includes at least three critical steps in florigen signalling. Firstly, FT protein exports from companion cells to the sieve element. Secondly, FT transport from leaves to the shoot apex through phloem. Thirdly, activation of its effector genes at the shoot apex that trigger subsequent flower development. This is a typical long-distance signaling process by the phloem translocation stream of higher plants, where a multitude of small molecules and macromolecules, including proteins, mRNA and small RNAs, have been transport from leaves to the shoot apexes (Lough and Lucas 2006; Ruiz-Medrano et al. 2001). The turgor pressure is thought to drive the mass flow in phloem, called turgor-driven phloem transport (Münch 1930). Gravity is an obstacle in xylem transport and it may aid phloem transport in tall trees by reducing the viscosity and osmotic pressure required to push phloem fluid down to the roots (Hölttä et al. 2009). Although effects of gravitational potential on phloem transportation in tall trees has attracted attention, little is known whether gravity is involved in long distance signaling in most of crop plants, because of the difficulties in measuring effect of gravity on phloem transport. Some space experiments indicated that long-distance mobile of micro- and macro-molecules in both phloem and xylems could be affected by gravity. For example, auxin polar transport in xylem of epicotyls of etiolated pea seedlings was strongly reduced under both clinorotational condition and microgravity in space (Miyamoto et al. 2005; Ueda et al. 1999). Transport of sugar in phloem were also observed to affect by microgravity. Thus, we predict that altered gravitational conditions in space could also affected the transport of FT protein from leaves to shoot apexes and cause a delay flowering which have observed in many previously space experiments (Halstead and Dutcher 1987; Nechitailo and Maskinsky 1993; Zheng et al. 2008; Link et al. 2014).

Plant-derived regulators controlling flowering in space

Microgravity is known to modify dynamics of fluids and small particles thus altering the diffusion of gases and the alteration of convective air movement, which caused an increase in ethylene concentrations in the growth chambers. Ethylene has been considered as one of the most important plant hormone affected flowering in space. In the early space experiments, severe hardware constraints prevented even vegetative growth and the transition between vegetative and reproductive phase (Halstead and Dutcher 1997). This problem was resolved by the improvement of plant cultivation hardware, such as flow-through of cabin air, supply CO_2 and remove ethylene from culture chamber and the completion of the seed-to-seed cycle in space were then achieved in space (Kuang et al. 2000; Link et al. 2003, 2014. In addition, higher concentration of microenvironments within plant structures have also been the reason for interruption of the reproductive process, delay in completion of single reproductive phases, the lowering of reproductive success in space. Ethylene delayed flowering of plants grown on the earth has been found by repressing LEAFY (LFY) and SOC1 in a DELLA-dependent signaling pathway (Achard et al. 2007). DELLA proteins have been shown to be important integrators of GA signaling and play a significant role in many aspects of plant development, in particular photomorphogenesis (Achard et al. 2007). However, how ethylene affects plant reproduction under microgravity in space still remains to known and whether this signaling pathway under microgravity condition still work as it is on the earth need to be further studied.

The other factor affect plant flowering in space could be sugars, which are the major products of photosynthesis and are essential for regulation of several metabolic and developmental processes such as germination, flowering, senescence, and stress responses, particularly in promoting flowering in various plant species. Previous studies have shown that the sugar concentration and the metabolic fluxes of plant cells were affected by various altered gravity conditions, including microgravity and hypergravity (Martzivanou and Hampp 2003; Hampp et al. 1997; Obenland and Brown 1994; Wang et al. 2006; Tan et al. 2011). However, how sugar regulate flowering under microgravity condition still remain unknown. In addition, microRNA involved in integration of carbohydrate status into flowering time was reported recently (Wang et al. 2009). microR156 decreased with increasing age of the plant by which defines a novel flowering time pathway that acts independently of the photoperiod, vernalization, and GA pathway. Many plants grown under microgravity condition in space exhibited delay in development, but how changes of microRNA in plant in space are still unknown.

Space experiments on board the Chinese recoverable satellites (SJ-8 and SJ-10) and the Chinese space lab TG-2

Using live imaging technique, we have studied the growth and development of Chinese cabbage in space on board in the Chinese SJ-8 recoverable satellite on September 2006. Our results indicated that plant flowering was apparently delayed under microgravity (Zheng et al. 2008). Beside the course of flower expansion and opening were inhibited by exposure to spaceflight, anthers of the SJ-8 plants did not

Fig. 2 Reproductive development in Chinese cabbage on the Chinese SJ-8 recoverable satellite. **a** the appearance of the plant cultivation box. **b** The cultivation chamber included two root modules and one seed module, two cameras, one camera used for monitoring plant flowering (left panel) and the other used for photographed seedling growth and seed germination (right panel). **c** a diagram of the plant cultivation box and its control system. **d**–**g** Example images of plants grown 4h, 58h, 5days and 11days, respectively on board the SJ-8. **h**–**k** examples of images showing flower developing in flight after plant grown 20h, 44h, 46h and 52.2h, respectively on board the SJ-8. CC, cultivation chamber

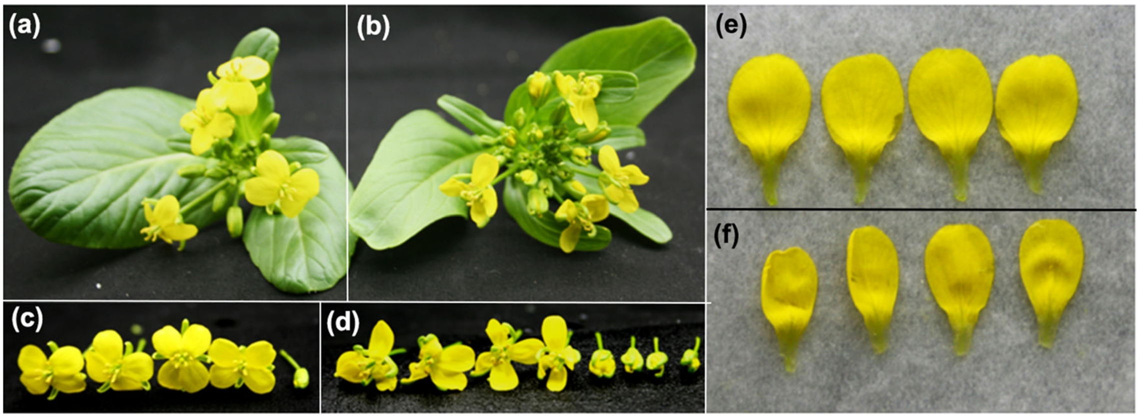

Fig. 3 Morphology of Chinese cabbage flowers was grown under the 1g gravitational condition on ground and the 3-D clinorotation, respectively. Flowers grown under the 1g control condition were normal in appearance (**a** and **c**) with petals fully opened and expanded (**e**), while the petals of the flowers grown on the clinostat exhibited curved and couldn't fully expand (**b**, **d** and **f**)

open before the flower withered (Fig. 2). In addition, the flowers of plants grown in space or on the 3-D clinostat exhibited smaller petals and shorter stamens in comparison with those grown on the1g ground condition (Fig. 3). Although microgravity has been found to significantly influence plant reproductive development, the molecular basis in plant flowering control still remain to be known.

To further address the possibility that microgravity affect photoperiod induced flowering and to assess whether the movement of FT from leaf to shoot apex under microgravity was different from the control on ground condition, we have designed an experiment to study the regulation of photoperiod controlling flowering in a long-day plant Arabidopsis and short-day plant rice onboard SJ-10 recoverable satellite. In the SJ-10 experiment, we used the advantages of heat shock (HS)-inducible gene switch and developed transgenic Arabidopsis containing the *HSP17.4* gene promoter linked to the green fluorescent protein (GFP) reporter gene (HSPpro:: GFP) and the FT gene (*HSPpro*::*FT*), respectively. The expression of *HSPpro*:: *GFP* and *HSPpro*::*FT* in Arabidopsis leaves were induced by half hour 37° heating under the short-day condition and then expression of*GFP* in these leaves were monitored by a plant GFP imager. In the same time, time-lapse images also documented the effect of microgravity on the flowering induction of Arabidopsis and rice plants under a long-day (16h light::8h dark) and a short-day (8h light::16h dark) conditions, respectively (Fig. 4). Our results showed that 37° heating induced strong expression of GFP in the leaves of the SJ-10 plants in microgravity while the appearance of the flowering in the SJ-10 plants was apparently delayed in comparison with those on ground (Wang et al. 2016; Zheng et al. 2017). This is the first time that the influence of gravity in expression of FT gene and its induction flowering in microgravity was unequivocally demonstrated. On board the Chinese spacelab TG-2, we performed an experiment with the objective to grow Arabidopsis and rice plants from seed-to-seed under different photoperiod conditions. Dry Arabidopsis and rice seeds were planted in the culture container of the Plant Growth Box (PGB). The seeds of Arabidopsis were successfully germinated, grew and completed a full life cycle in microgravity under the long-day condition and the short-day

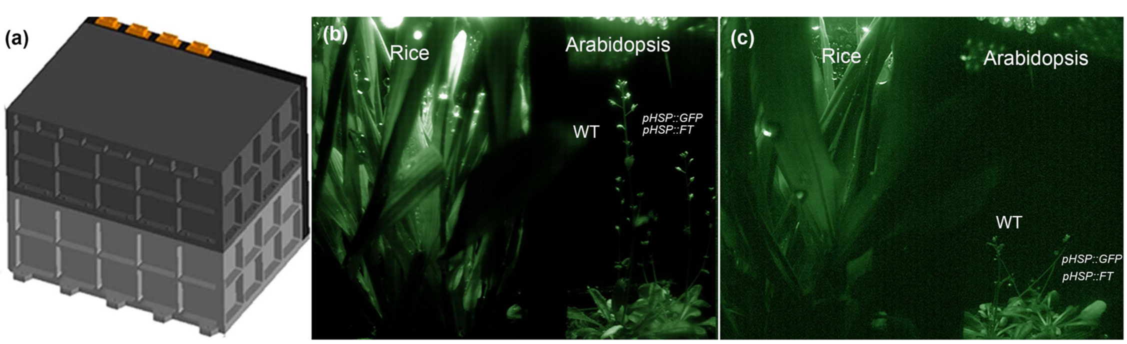

Fig. 4 Reproductive development in rice and Arabidopsis under long-day (**b**) and short-day (**c**) photoperiod conditions in a plant cultivation box (**a**) on board the Chinese SJ-10 recoverable satellite. Representative images of rice, Arabidopsis wild-type (WT) and transgenic plants (*pHSP*::*GFP*; *pHSP*::*FT*) day 10 on board the SJ-10

condition transferred to the long-day condition before flowering. This experiment demonstrated that the flowering of both Arabidopsis and rice plants was significantly delayed in microgravity condition. To delineate the transcriptional response mechanisms, we also carried out whole-genome microarray analysis of Arabidopsis leaves of plants which grown on board the TG-2 and its control condition on ground, respectively. We identified a novel set of microgravity response genes, recognized mainly by quantitative differences. These included a transcriptome signature of more pronounced proline transport in developing leaves. This study provides developmental stage specific molecular resolution of different age leaves and demonstrates that a new molecular plasticity in Arabidopsis to adaptation to microgravity by adjusted genome status during development in space. The network of transcriptional regulation of flowering gene expression is going to be analyzed and will be the topic of a future paper.

Conclusion

Many space experiments using different space vehicles have been a fascinating tool for microgravity research in plant development (Baster et al. 2013). Specially, after space missions become longer and permanently manned stations, many works focused on how to grow plants for long-term in space in order to finally set up a plant-basis self-sustained bioregenerative life support system for human long-duration missions. One of the key developmental processes for plant produce seeds is the differentiation of the shoot apical meristem into a floral meristem. This process has been proven to be regulated by both endogenous and environmental factors. Endogenous factors, such as, GA, ethylene, sugar and microRNA, have been found to play important roles in flowering induction and their interaction with biological circadian clock. Light is considered as one of the most important environmental factors that control plant flowering development, but how it is involved in plant flowering regulation still remains to study. On board the Chinese recoverable satellites (SJ-8 and SJ-10) and the Chinese space lab TG-2, we have applied a systematic approach to reveal the molecular mechanisms that control the transition from vegetative growth to reproductive development under microgravity in space. The data we have obtained showed that the transition of Arabidopsis flowering regulated by photoperiod under microgravity was apparently delayed and this result could be caused by the alteration of long distance signaling of FT protein in space.

In the future, long-term space experiments from successive generations and a systematic analysis of regulatory networks at the molecular level is needed to understand the mechanism of plant flowering control under microgravity condition in space. The genes involved microgravity response identified in the previous space experiments represent only a very small part of the plant genome and many other microgravity-responsive genes, including those in regulating plant flowering will likely be identified in the future. For example, genes that control the activities of the pathways in the regulation of flowering timing in plants under microgravity will be very interesting, because they will enable the manipulation of flowering time in crop species, which could have a major impact on the production of plants in bioregenerative life support system (BLSS). The energy using in plant cultivation on board spacecrafts such as space shuttle and space station, and even the future space farm must rely on solar battery or fuel cell, which will be severely restricted on board long-term missions. How to increase of production efficiency of plant will be the most important task in setting up BLSS. An acceleration of flowering time in seed crops, such as rice and wheat, while prevention of bolting in vegetable plants, such as sugarbeet, many *Brassica* species, potato, spinach, and lettuce would significantly improve yield. Thus, control of flowering time by manipulation will be clearly an important biotechnological method to increase the production of BLSS.

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References

Achard, P., Baghour, M., Chapple, A., Hedden, P., Van Der Straeten, D., Genschik, P., Moritz, T., Harberd, N.: The plant stress hormone ethylene controls floral transition via DELLA-dependent regulation of floral meristem-identity genes. Proc. Natl. Acad. Sci. USA **104**, 6484–6489 (2007)

Atamian, H.S., Creux, N.M., Brown, E.A., Garner, A.G., Blackman, B.K., Harmer, S.L.: Circadian regulation of sunflower heliotropism, floral orientation, and pollinator vists. Science **353**, 587–590 (2016)

Baster, P., Robert, S., Kleine-Vehn, J., Vanneste, S., Kania, U., Grunewald, W., De Rybel, B., Beeck, T., Friml, J.: SCF Tir1/AFB-auxin signaling regulates PIN vacuolar trafficking and auxin fluxes during root gravitropism. EMBO J. **32**, 260–274 (2013)

Blancaflor, E.B., Masson, P.H.: Plant gravitropism. Unraveling the ups and downs of a complex process. Plant Physiol. **133**, 1677–1690 (2003)

Cogoli, A., Gmuńder, F.K.: Gravity effects on single cells: techniques, findings and theory. Adv. Space Biol. Med. **1**, 183–248 (1991)

De Micco, V., De Pascale, S., Paradiso, R., Aronne, G.: Microgravity effects on different stages of higher plant life cycle and completion of the seed-to-seed cycle. Plant Biol. **16**(suppl. 1), 31–38 (2014)

Driss-Ecole, D., Legue, V., Carnero-Diaza, E., Perbal, G.: Gravisensitivity and automorphogenesis of lentil seedling roots grown on board the international space station. Physiol. Plant. **134**, 191–201 (2008)

Drake, J.E., Davis, S.C., Raetz, L.M., Delucia, E.H.: Mechanisms of age-related changes in forest production: the influence of physiological and successional changes. Glob. Change Biol. **17**, 1522–1535 (2011)

Harmer, S.L., Hogenesch, J.B., Straume, M., Chang, H.-S., Zhu, T., Wang, X., Kreps, J.A., Kay, S.A.: Orchestrated transcription of key pathways in Arabidopsis by the circadian clock. Science **290**, 2110–2113 (2000)

Halstead, T.W., Dutcher, F.R.: Plants in Space. Annual Review of Plant Physiology **38**, 317–345 (1997)

Halstead, T.W., Dutcher, F.R.: Plants in space. Ann. Rev. Plant Physiol. **38**, 317–345 (1987)

Hampp, R., Hoffmann, E., Schoñherr, K., Johann, P., Filippis, L.D.: Fusion and metabolism of plant cells as affected by microgravity. Planta **203**, S42–53 (1997)

Hölttä, T., Nikinmaa, E., Mencuccini, M.: Linking phloem function to structure: analysis with a coupled xylem-phloem transport model. J. Theor. Biol. **24**, 519–570 (2009)

Hoson, T.: Plant growth and morphogenesis under different gravity conditions: relevance to plant life in space. Life **4**, 205–216 (2014)

Jaeger, K.E., Wigge, P.A.: FT Protein acts as a long-range signal in Arabidopsis. Curr. Biol. **17**, 1050–1054 (2007)

Johnsson, A., Solheim B.G., Iversen T.H.: Gravity amplifies and microgravity decreases circumnutations in Arabidopsis thaliana stems: results from a space experiment. New Phytol. **182**, 621–629 (2009)

King, R.W., Evans, L.T., Wardlaw, I.F.: Translocation of the floral stimulus in Pharbitis nil in relation to that of assimilates. Z. Pflanzenphysiol **59**, 573–594 (1968)

King, R.W., Zeevaart, J.A.: Floral stimulus movement in perilla and flower inhibition caused by noninduced leaves. Plant Physiol. **51**, 727–738 (1973)

Kiss, J.Z., Katembe, W.J., Edelmann, R.E.: Gravitropism and development of wild-type and starch-deficient mutants of Arabidopsis during spaceflight. Physiol. Plant **102**, 493–502 (1998)

Kordyum, E.L.: Plant cell gravisensitivity and adaptation to microgravity. Plant Biol. **16**(S1), 79–90 (2014)

Kuang, A., Xiao, Y., Mcclure, G., Musgrave, M.E.: Influence of Microgravity on ultrastructure and storage reserves in seeds of Brassica rapa. L. Ann. Bot. **85**, 851–859 (2000)

Link, B.M., Durst, S.J., Zhou, W., Stankovic, B.: Seed-to-seed growth of Arabidopsis thaliana on the in ternational space station. Adv. Space Res. **31**, 2237–2243 (2003)

Link, B.M., Busse, J.S., Stankovic, B.: Seed-to-seed-to-seed growth and development of Arabidopsis in microgravity. Astrobiol **14**, 866–875 (2014)

Lough, T.J., Lucas, W.J.: Integrative plant biology: role of phloem long-distance macromolecular trafficking. Annu. Rev. Plant Biol. **57**, 203–232 (2006)

Mashinsky, A., Ivanova, I., Derendyaeva, T., Nechitailo, G., Salisbury, F.: From 'seed-to-seed' experiment with wheat plants under spaceflighlt conditions. Adv. Space Res. **13**, 33–39 (1994)

Massa, G.D., Newsham, G., Hummerick, M.E., Morrow, R.C., Wheeler, R.M.: Plant pillow preparation for the veggie plant growth system on the international space station. Gravait. Space Res. **5**, 24–34 (2017)

Merkys, A.L., Laurinavicius, R.S.: Complete cycle of individual development of Arabidopsis thaliana (L.) Heynh. Plants on board the Salyut-7 orbital station. Dokladi. Akademii. Nauk. SSSR **271**, 509–512 (1983)

Miyamoto, K., Hoshino, T., Yamashita, M., Ueda, J.: Automorphosis of etiolated pea seedlings in space is simulated by a three-dimensional clinostat and the application of inhibitors of auxin polar transport. Physiol. Plant **123**, 467–474 (2005)

Martzivanou, M., Hampp, R.: Hyper-gravity effects on the Arabidopsis transcriptome. Physiol. Plant. **118**, 221–231 (2003)

Musgrave, M.E., Kuang, A., Xia, Y., Staut, S.C., Binham, G.E., Briarty, G., Levinskikh, M.A., Sychev, V.N., Podolski, I.G.: Gravity independence of seed-to-seed cycling in Brassica rapa. Planta **210**, 400–406 (2000)

Münch, E.: Die Stojjbewegungen in der Pflanze, p. 73. Jena: Fischer. pp. 234 (1930)

Nechitailo, G.S., Maskinsky, A.L.: Space biology: studies at orbital station, pp. 293–330. Mir Publishers, Moscow (1993)

Obenland, D.M., Brown, D.S.: The influence of altered gravity on carbohydrate metabolism in excised wheat leaves. J. Plant Physiol. **144**, 696–699 (1994)

Paul, A.-L., Wheeler, R.M., Levine, H.G., Ferl, R.J.: Fundamental plant biology enabled by the space shuttle. Amer. J. Bot. **100**, 226–234 (2013)

Putterill, J., Laurie, R., Macknight, R.: It's time to flower: the genetic control of flowering time. BioEssays **26**, 363–373 (2004)

Ryan, M.G., Asao, S.: Phloem transport in trees. Tree Physiol. **34**, 1–4 (2014)

Ruiz-Medrano, R., Xoconostle-Cazares, T., Lucas, W.J.: The phloem as a conduit for inter-organ communication. Curr. Opin. Plant Biol. **4**, 202-209 (2001)

Samach, A., Coupland, G.: Time measurement and the control of flowering in plants. BioEssays **22**, 38–47 (2000)

Srikanth, A., Schmid, M.: Regulation of flowering time: all roads lead to Rome. Cell. Mol. Life Sci. **68**, 3013–2037 (2011)

Solheim, B.G., Johnsson A., Iversen, T.H.: Ultradian rhythrns in Arabidopsis thaliana leaves in microgravity. New Phytol. **183**, 1043–1052 (2009)

Strickland, D.T., Campbell, W.F., Salisbury, F., Bingham, G.E.: Morphological assessment of reproductive structures of wheat grown on Mir. Grav. Space Biol. Bull. **11**, 14 (1997)

Sychev, V.M., Levinskikh, M.A., Gostimsky, S.A., Bingham, G.E., Podolsky, I.G.: Spacefl ight effects on consecutive generations of peas grown onboard the Russian segment of the International Space Station. Acta Astronaut. **60**, 426,432 (2007)

Tan, C., Wang, H., Zhang, Y., Qi, B., Xu, G., Zheng, H.Q.: A proteomic approach to analyzing responses of Arabidopsis thaliana root cells to different gravitational conditions using an agravitropic mutant, pin2 and its wild type. Proteome Sci. **9**, 72 (2011)

Ueda, J., Miyamoto, K., Yuda, T., Hoshino, T., Fujii, S., Mukai, C., Kamigaichi, S., Aizawa, S., Yoshizaki, I., Shimazu, T., Fukui, K.: Growth and development, and auxin polar transport in higher plants under microgravity conditions in space: BRIC-AUX on STS-95 space experiment. J. Plant Res. **112**, 487–492 (1999)

Wang, H., Zheng, H.Q., Sha, W., Zeng, R., Xia, Q.C.: A proteomic approach to analyzing responses of Arabidopsis thaliana callus cells to clinostat rotation. J. Exp. Bot. **57**, 827–835 (2006)

Wang, J., Czech, B., Weigel, D.: miR156-regulated SPL transcription factors define an endogenous flowering pathway in Arabidopsis thaliana. Cell **138**, 738–749 (2009)

Wang, L., Xie, J., Zhang, Y., Zheng, H.Q.: Method and technology of monitoring the expression of flowering gene marked with green fluorescent protein in space culture chamber. Chin. J. Space Sci. **36**, 562–565 (2016)

Yano, S., Kasahara, H., Masuda, D., Tanigaki, F., Shimazu, T., Suzuki, H., Karahara, I., Soga, K., Hoson, T., Tayama, I., Tsuchiya, Y., Kamisaka, S.: Improvements in and actual performance of the plant experiment unit onboard Kibo, the Japanese experiment module on the international space station. Adv. Space Res. **51**, 780–788 (2013)

Zhang, Y., Zheng, H.Q.: Changes of protein expression in plastid and mitochondria of Arabidopsis thaliana callus on board Chinese spacecraft SZ-8. Microgravity Sci. Tech. **27**, 387–401 (2015a)

Zhang, Y., Wang, L., Xie, J., Zheng, H.Q.: Differential protein expression profiling of Arabidopsis thaliana callus under microgravity on board the Chinese SZ-8 spacecraft. Planta **241**, 475–488 (2015b)

Zheng, HQ., Wang, H., Wei, N., Chen, A.D., Wang, L., Zheng, W.B., Zhang, T.: Live imaging technique for studies of growth and development of Chinese cabbage under microgravity in a recoverable satellite (SJ-8). Microgravity Sci. Tech. **20**, 137–143 (2008)

Zheng, H.Q., Han, F., Le, J.: Higher plants in space: microgravity perception, response, and adaptation. Microgravity Sci. Tech. **27**, 377–386 (2015)

Zheng, H.Q., Xie, J., Wang, L.: Microgravity Effects on Flowering of Plants Grown on the Chinese Space Lab TG-2. In: International Academy of Astronautics 21st Humans in Space Symposium. Shenzhen, pp. P260 (2017)