



Plant responses to hypergravity: a comprehensive review

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Abstract

Main conclusion Hypergravity is an effective novel stimulus to elucidate plant gravitational and mechanobiological behaviour. Here, we review the current understanding of phenotypic, physio-biochemical, and molecular plant responses to simulated hypergravity.

Abstract Plants readily respond to altered gravity conditions, such as microgravity or hypergravity. Hypergravity—a gravitational force higher than that on the Earth's surface ($> 1g$)—can be simulated using centrifuges. Exposing seeds, seedlings, or plant cell cultures to hypergravity elicits characteristic morphological, physio-biochemical, and molecular changes. While several studies have provided insights into plant responses and underlying mechanisms, much is still elusive, including the interplay of hypergravity with gravitropism. Moreover, hypergravity is of great significance for mechano- and space/gravitational biologists to elucidate fundamental plant behaviour. In this review, we provide an overview of the phenotypic, physiological, biochemical, and molecular responses of plants to hypergravity. We then discuss the involvement of hypergravity in plant gravitropism—the directional growth along the gravity vector. Finally, we highlight future research directions to expand our understanding of hypergravity in plant biology.

Keywords Abiotic stress · Cell wall composition · Germination · Gravistimulation · Mechano-biology · Photosynthesis

Abbreviations

ATPA2	<i>Arabidopsis thaliana</i> Class II peroxidases
CDC	Cell division control protein
CDK	Cyclin-dependent kinase
g	Gravitational acceleration on Earth's surface (9.81 ms^{-2})
HMGR	3-Hydroxy-3-methylglutaryl-coenzyme A reductase
HSP	Heat shock proteins

MAPs	Microtubule-associated proteins
MCA	Mid1-complementing activity channels
MSIC	Mechanosensitive ion channels
RPA	Replication protein A
ROS	Reactive oxygen species
TDH	Total dehydrogenase
XTH	Xyloglucan endotransglucosylase/hydrolase

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Introduction

Throughout evolution, organisms on Earth have been exposed to drastic environmental changes that significantly shaped the species' characteristics in many ways. Eventually, organisms developed adaptive mechanisms that enabled them to thrive and proliferate under changing environmental conditions. Although the gravitational force is constant on the Earth's surface, early plants had to endure a change in the apparent gravitational pull when they first ventured onto land from a primarily aquatic habitat (Hoson et al. 2005). During this transition, plants developed more rigid tissues and other physiological and structural changes to withstand the increased gravitational pull experienced on the land—a

response termed *gravity resistance* (Soga 2010). Ever since this transition, land plants have evolved under constant gravity, and mechanisms developed during the transition are etched in their genomes. As a result, plants exposed to modified gravity conditions such as micro or hypergravity exhibit distinct morphological and physiological responses (Halstead and Dutcher 1987; Hoson and Soga 2003; Zheng et al. 2015; Sathasivam et al. 2021).

Particularly, studying the plant responses under hypergravity—a simulated gravitational acceleration greater than on Earth’s surface ($> 1g$)—has revealed fundamental plant behaviours in terms of gravitropism (Fitzelle and Kiss 2001) and plant mechanoperception (Hattori et al. 2020). More recently, researchers have also focussed on assessing the influence of hypergravity on phenotypic changes for crop improvement (Swamy et al. 2021). Moreover, owing to greater accessibility relative to microgravity, plant and gravitational biologists have used hypergravity to study fundamental plant behaviour. Despite the utility in understanding plant physiology, much about plant responses to

hypergravity and the underlying mechanisms are still poorly understood—including the crosstalk between hypergravity perception and gravitropism. Here, we review the phenotypical, physiological, biochemical, and molecular responses in plants under hypergravity to synthesise the current understanding of the topic. First, we map the field of hypergravity research with plants to gain a broad view of research progress to date. Then, we comprehensively discuss the effects of hypergravity on seeds, seedlings, whole plants, and cell cultures. We also explore the interplay between hypergravity perception and gravitropism. Finally, we highlight focussed research areas for expanding our understanding and utility of hypergravity in plant biology.

Mapping the reviewed research

Bibliometric analysis was conducted to gain a deeper understanding of the state of plant hypergravity research. The keyword co-occurrence network in Fig. 1 shows the

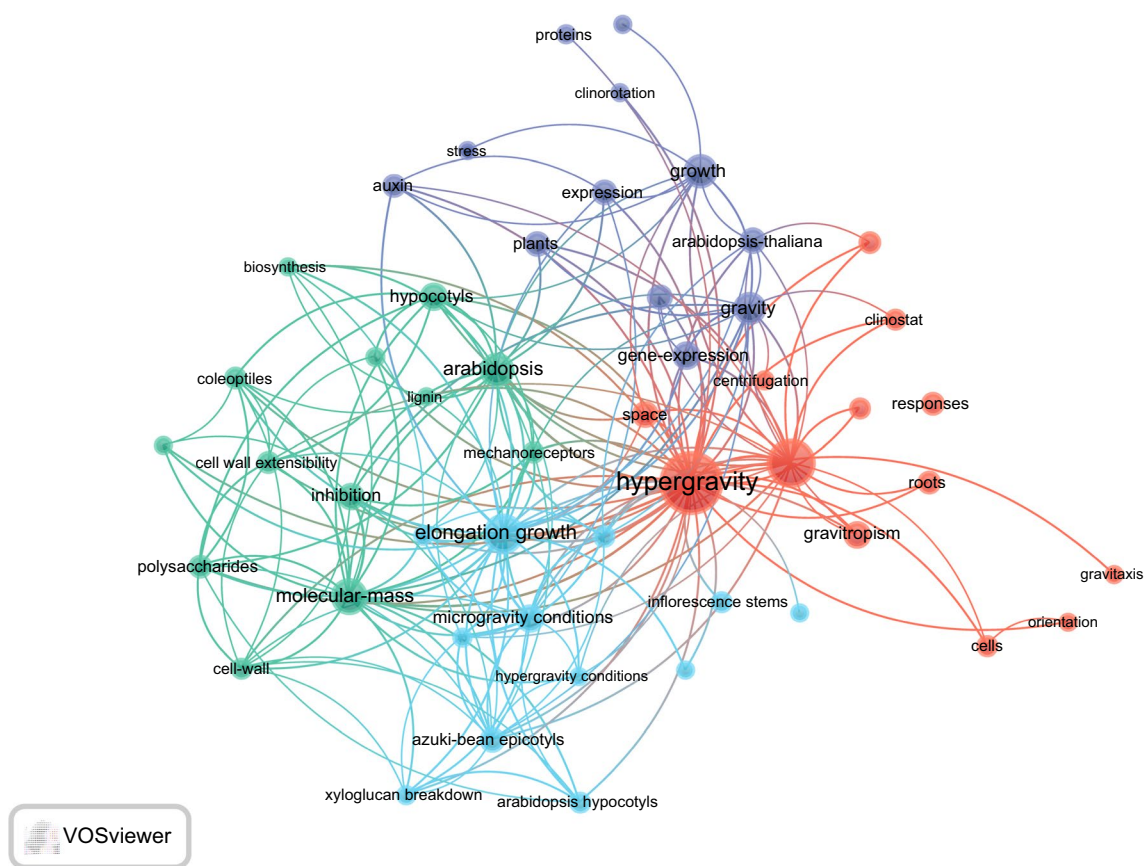


Fig. 1 Bibliometric keyword co-occurrence network for hypergravity research with plants. The size of the labels and nodes is proportional to the prominence of the keyword. The colour of the nodes represents distinct clusters of keywords. Bibliometric analysis was conducted by retrieving literature data from the Web of Science Core Collection with the search query: (ALL=(“hypergravity” OR “hyper-gravity”

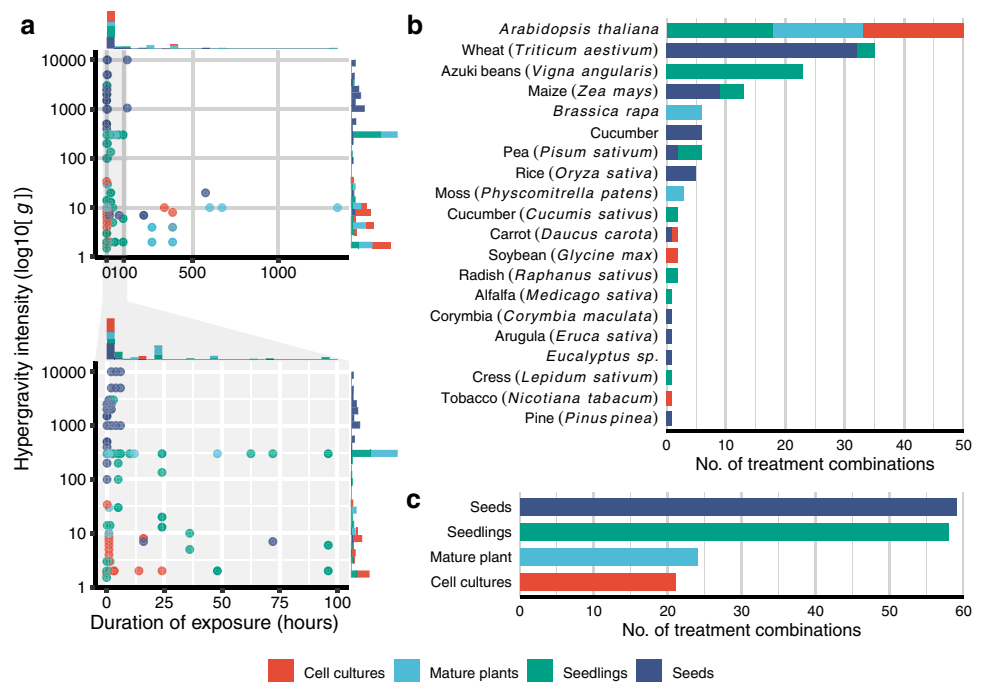
OR “hypergravity*”) AND ALL=(“plant*”). The search yielded 138 studies. Keyword co-occurrence network analysis was performed with VOSviewer (van Eck and Waltman 2010). The minimum number of occurrences of a keyword was set as 6. Fifty of 775 total keywords met the threshold

prominence and relationships between keywords in the literature on plant hypergravity research. Bibliometric analysis was conducted by retrieving literature data from the Web of Science Core Collection with the search query: (ALL = (“hypergravity” OR “hyper-gravity” OR “hypergravity*”) AND ALL = (“plant*”). The search yielded 138 studies. Keyword co-occurrence network analysis was performed with VOSviewer (van Eck and Waltman 2010). The minimum number of occurrences of a keyword was set as 6. Fifty of 775 total keywords met the threshold. Figure 1 also provides an overview of the structure of topics and research focus in the literature. Based on the clustering, hypergravity research has broadly focussed on understanding (a) the cell wall biochemistry and morphology (green and blue clusters) (Hoson et al. 1996, 2009; Wakabayashi et al. 2009a, b), (b) gene expression and transcriptional responses (purple cluster) (Martzivanou and Hampp 2003; Matsumoto et al. 2007; Hausmann et al. 2014), and (c) plant gravitropism (red cluster) (Sievers and Heyder-Caspers 1983; Fitzelle and Kiss 2001; Mugnai et al. 2014). These facets are closely related and act complementary to elucidate plant responses to hypergravity.

The plant responses to hypergravity can be a function of hypergravity intensity and the duration of exposure (Nunes et al. 2018). Moreover, since the plants or seeds perceive hypergravity as a mechanical force—through mechanosensors rather than gravity vector through statoliths (Soga et al. 2005a; Hattori et al. 2020)—it is reported that the mass of the cell/protoplast in totality could also play a role in the hypergravity response (Soga et al. 2005a). Therefore, understanding how these factors play a role in plant

response is crucial. Hence, we present the hypergravity treatment distributions (intensity and duration) used to model plant behaviour in the reviewed literature (Fig. 2). Studies so far have tried various hypergravity intensities and exposure durations (Fig. 2a). However, most studies have low exposure durations (< 5 h) and are limited to *g* levels < 3000*g*. The responses to hypergravity can also be species-specific (Nunes et al. 2018). The effects of hypergravity have been studied in various models and crop species (Fig. 2b). Understandably, *Arabidopsis* is the most commonly investigated species due to its prevalence as a model system in plant biology. Besides *Arabidopsis*, the majority of the species studied are crop species, studying of which could help derive benefits for crop improvement. Developing a deeper understanding and developing response models requires investigating broader combinations of *g* levels and durations. The distribution of model types used (Fig. 2c) shows that majority of the studies focus on plant seeds and seedlings. Very few studies exist on whole plants and cell cultures. Therefore, a broader range of experimental sample types can help us better understand the responses from a sub-cellular to organism level. Regardless, the following sections describe the plant responses in various domains to hypergravity.

Fig. 2 Hypergravity treatment distributions used to model plant behaviour in the reviewed literature. **a** Distribution of hypergravity treatment combinations (*g* × time). The bottom panel zooms in on a subset of exposure duration between 0 and 100 h. Marginal bars show the distribution of variables along the corresponding axes. **b** Plant species and the number of treatment combinations (*g* × time) investigated for each species. **c** Number of treatment combinations (*g* × time) used for various plant model types. Data are derived from all experimental studies referred to in this paper



Influence of hypergravity on plant behaviour

Hypergravity-induced changes in seed germination and seedling growth

The responses of seeds to hypergravity can be species-dependent or hypergravity-dose and duration-dependent. Seeds exposed to hypergravity show enhanced germination and seedling vigour in several vegetables and field crops, such as carrot, wheat, corymbia, and eucalyptus (Santos et al. 2012; Swamy et al. 2021; Nunes et al. 2018) (Table 1). In contrast, imbibed wheat seeds exposed to hypergravity intensities > 1000 g for durations varying between 10 and 180 min, either reduced or failed to germinate/develop radicles (Jagtap and Vidyasagar 2020; Rupiasih and Vidyasagar 2016) (Table 1). Pea seeds, however, exposed to hypergravity at 10,050 g for 2 days showed germination of seeds greater than 50%, although the seeds were flattened due to the extreme 'g' force (Waldron and Brett 1990) (Table 1). Furthermore, the force acting on the seeds under hypergravity is a function of the mass of the seeds in addition to acceleration. Hence, seed size could also play a role in the responses under hypergravity. These varied effects call for species-specific wide-range screening of hypergravity intensity and duration for desired seed germination and seedling growth phenotype.

The mechanism/s of how hypergravity influences seed germination especially on the dry state of seed is completely unclear. However, one of the putative mechanisms speculated in increased germination in response to hypergravity in imbibed seed is through increased activities of metabolic enzymes that catalyses and provides increased access to energy source for germinating embryo. In favour of this argument, hypergravity (20 g) delayed germination and seedling growth in oilseed *Pinus pinea* was attributed to a reduction in key enzymes such as isocitrate lyase and malate synthase involved in the seed glyoxylate cycle (Faraoni et al. 2019). Reduced activity of these enzymes leads to less conversion of storage lipids to sugars and fail to provide enough readily available energy source to germinating embryo and early seedling (Eastmond and Graham 2001; Faraoni et al. 2019). Another enzyme possibly involved in hypergravity-mediated germination is α -amylase. The reduction of α -amylase could delay the germination process (Damaris et al. 2019), by decreasing the breakdown of complex endosperm starch to simpler forms to provide energy to the germinating embryo (Muralikrishna and Nirmala 2005). In line with this argument, acute hypergravity exposure (> 500g) has been shown to reduce α -amylase activity in wheat caryopses with a reduced germination phenotype (Dixit et al. 2017) (Table 1).

Effect of hypergravity is a function of intensity, duration of exposure, and apparent force experienced by the seeds. Growth enhancements effects of hypergravity are not only restricted to the seedling stage but carry forward to the vegetative growth. Corymbia and eucalyptus seeds exposed to hypergravity showed increased stem diameter, height, and plant survival at 120 days after germination (Nunes et al. 2018). Wheat seeds exposed to 10g for 12 h and immediately sown in normal (1g) condition greenhouse significantly enhanced root growth parameters such as length, volume, and dry weight on the 45th day in a greenhouse study (Swamy et al. 2021). In contrast, rice seeds exposed to acute hypergravity (500, 1000, 2000, and 3000g for 10 min) and then germinated under normal gravity showed a reduction in root length, biomass and chlorophyll content (Vidyasagar et al. 2008). In yet another study, hypergravity exposure between 100 and 500g for 10 min and sown in normal (1g) condition significantly reduced the length and weight of both roots and shoots in wheat seedlings (Jagtap and Vidyasagar 2010). Reduction in shoot growth rate was also observed in pea grown under hypergravity, cucumber and radish post-hypergravity grown at normal (1g), cress, and *Arabidopsis* grown under hypergravity condition (Waldron and Brett 1990; Kasahara et al. 1995; Hoson et al. 1996; Soga et al. 2001). Decoupling of cell growth and cell proliferation mechanisms (Manzano et al. 2013, 2016; Kamal et al. 2018) may play a critical role in teasing out altered plant growth under hypergravity.

Another interesting phenotype observed in response to hypergravity is reduced elongation and increased lateral expansion in shoots. As a result, plants look more short and stout. This phenotype was observed consistently in epicotyls of a pea, azuki bean (Waldron and Brett 1990; Soga et al. 1999b), hypocotyls of cucumber, radish, cress, *Arabidopsis* (Kasahara et al. 1995; Hoson et al. 1996; Soga et al. 2001), and wheat coleoptiles (Wakabayashi et al. 2005b). This change in phenotype was attributed to the reorientation of cortical microtubules, which in turn control the pattern of cellulose microfibril deposition (Fig. 3). The cellulose microfibrils in the cell walls control the shape, rate, and direction of cellular expansion in plants (Thomas et al. 2013). Under hypergravity, cells reorient their cortical microtubules from the transverse to the longitudinal direction (Soga et al. 2006; Matsumoto et al. 2010) (Fig. 3c). This reorientation results in increased lateral growth and reduced longitudinal growth of cells (Soga 2010). Further, the reorientation of cortical microtubules to longitudinal was more predominant in the upper elongation zone of the stem resulting in a thicker stem in seedlings (Fig. 3d, e) (Soga et al. 2012).

Interestingly, reversibility of certain phenotypes was also observed in response to hypergravity. For instance, wheat hypergravity-treated seeds sown after 6 days of storage

Table 1 Hypergravity-induced changes in germination, seedling/plant growth and development

Hypergravity exposure	Crop/plants	Seed status during exposure	Salient findings	References
<i>Seed germination and seedling/plant growth and morphogenesis</i>				
5 and 7g for 8 and 12 h	Corymbia and Eucalyptus	Seeds on moist germination paper	Increased germination and seedling vigour at the nursery stage	Nunes et al. (2018)
7g for 8 h followed by rest of 16 h at 1g up to 18 days	Carrot and rocket plant seeds	Seeds on humidified germination paper	Faster germination and increased growth in rocket plant seeds, and higher germination rate in carrot seeds were observed in intermittent hypergravity exposure	Santos et al. (2012)
10g for 12 h (22 °C at 94% RH)	Bread wheat	Seeds on germination paper	Enhanced vigour, root growth parameters—length, volume and dry weight at seedling and vegetative growth stages	Swamy et al. (2021)
500, 1000, 2000 and 3000g for 10 min	Rice	Imbibed seeds	Reduced root length, biomass and chlorophyll content at seedling stage	Vidyasagar et al. (2008)
100 to 500g for 10 min	Wheat	Imbibed seeds	Decreased length and weight of both roots and shoots at seedling stage	Jagtap and Vidyasagar (2010)
140 and 368g for 5 days and 10,050g 2 days	Pea (<i>Pisum sativum</i>)	Imbibed seeds	Reduced elongation and increased lateral expansion of shoot	Waldron and Brett (1990)
1000, 2000 and 2500g for 10 min	Wheat	Imbibed seeds	Decreased germination and seeds were flattened under hypergravity	Jagtap and Vidyasagar (2020)
500–2500g for 10 min in acceleration steps of 500 g	Wheat caryopses	Imbibed seeds	Reduced germination at 1000g and seeds exposed to 2000 and 2500g for 10 min failed to germinate/develop radicle	Dixit et al. (2017)
300g for 5 h (Azuki), and 3 h (maize)	Azuki bean and Maize	Seedlings	Reduced germination when sown immediately after the exposure Recovery of germination rate to normal when sown after 6 days of storage	Soga et al. (2003)
300g for 62.5 h; and 300g for 2 to 4 days	<i>Arabidopsis</i> hypocotyls; and wheat coleoptiles	Seedlings	The reversal in seedling growth (from reduced to normal) when seedlings from hypergravity were brought back to 1g Reduced elongation and increased lateral expansion, short and stout plants under hypergravity	Soga et al. (2001); Wakabayashi et al. (2005b)
13 and 20g for 24 h (acropetal and basipetal)	Radish and Cucumber hypocotyls	Seedlings	Elongation of radish hypocotyls was reduced under basipetal hypergravity (20g) but not under acropetal hypergravity (13g) Elongation of cucumber hypocotyls growth was inhibited in both acropetal and basipetal	Kasahara et al. (1995)

Table 1 (continued)

Hypergravity exposure	Crop/plants	Seed status during exposure	Salient findings	References
<i>Seed enzyme activity (effect on seed germination)</i> 20g for 24 days	Oil seed (<i>Pinus pinea</i>)	Seeds placed in cotton wool imbibed with distilled water	Delayed germination and seedling growth by reducing isocitrate lyase (ICL) and malate synthase (MS) activities involved in the seed glyoxylate cycle under hypergravity	Faraoni et al. (2019)
10g for 12 h (22 °C at 94% RH)	Bread wheat	Seeds with germination paper	Enhanced activities of α -amylase and total dehydrogenase (TDH) enzymes in hypergravity-treated seeds	Swamy et al. (2021)

showed normal germination rate and seedling growth recovery from reduced germination rate compared to seeds sown immediately after hypergravity exposure (Dixit et al. 2017). A similar reversal in growth was also observed in azuki beans and maize when seedlings from hypergravity (300g) were brought back to 1g (Soga et al. 2003). The reversibility of hypergravity-induced phenotype may be attributed to the re-adaptation strategy of plants to normal gravity.

Hypergravity alters cell wall composition

The cell wall is responsible for the mechanical structure of the cell, which enables plants to withstand and grow against the gravitational force. To cope with the additional mechanical load on the plant body under hypergravity, the plant cell undergoes structural changes such as reduced elongation and increased lateral growth through altered cell wall composition, and cytoskeletal changes (Hoson and Soga 2003; Hoson et al. 2009; Hoson and Wakabayashi 2015). The aforementioned changes in the cell wall impart additional rigidity to the plant body under the added load of hypergravity. These changes in cell wall composition under hypergravity are relatively well investigated and reviewed in greater detail by Hoson and Wakabayashi (2015). The detailed cell wall composition changes in response to hypergravity have been described in Table 2.

The structural components of the cell wall include polysaccharides such as cellulose, hemicellulose, pectin, lignin, phenolic substances, and structural proteins. The quantity and molecular mass of these components ultimately determine the cell wall rigidity (Hoson et al. 2009). Exposure to hypergravity increased the cell wall polysaccharide content in the early seedling stages of cress (Hoson et al. 1996), azuki beans (Soga et al. 1999b), wheat (Wakabayashi et al. 2005a), and maize (Soga et al. 1999a). Specifically, increased molecular size of hemicelluloses, namely xyloglucans (Soga et al. 1999b) and hemicellulosic polymers (Soga et al. 1999a, 2000a), and increased amount of arabinoxylans (Wakabayashi et al. 2005a), imparted increased structural rigidity to the plants. The increase in rigidity and polysaccharide contents are not limited to primary and secondary cell walls. Hypergravity also promotes the development of metaxylem components of xylem vessels, as observed in *Arabidopsis* inflorescence (Tamaoki et al. 2006; Nakabayashi et al. 2006). However, the pathways leading to change in the xylem under hypergravity are unknown.

The change in cell apoplast pH also influences the molecular size of hemicellulose (Hoson 1998; Hoson et al. 2009). When activated, mechanosensors generate signals, hypothesised to travel through a sterol raft to the H⁺-ATPase (proton pump). The H⁺-ATPase (proton pump) activity in the plasma membrane is reduced, leading to an increase in the apoplast pH beyond the optimum level for the activity of enzymes

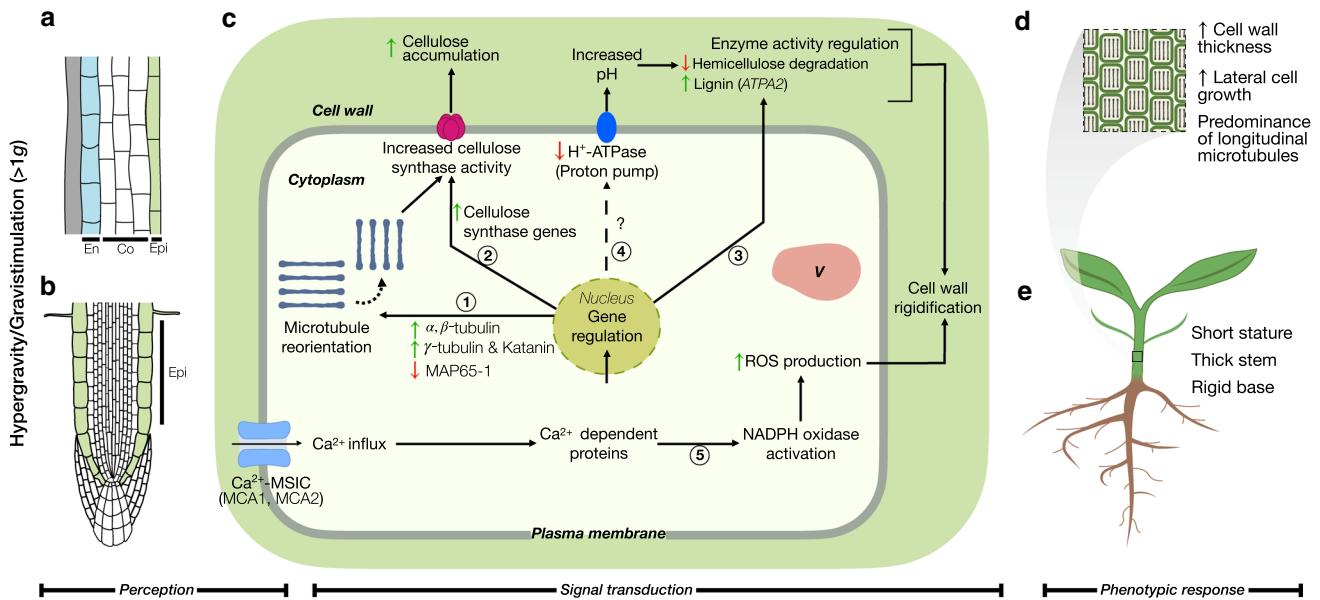


Fig. 3 Hypergravity-induced signal perception, transduction, and response in a plant cell. **a** Schematics of a longitudinal section of stem cells, and **b** primary root cells showing the Epidermis (Epi), Cortex (Co), and Endodermis (En). The perception, transduction, and response to hypergravity mainly occur in the epidermal cells of roots and shoots. **(c)** Pathways of hypergravity signal perception, transduction, and cell wall modifications in epidermal cells. The Ca²⁺-permeable mechanosensitive ion channels (Ca²⁺-MSIC) (e.g. MCA1 and MCA2), located on the plasma membrane, act as mechanoreceptors to perceive the mechanical stimulation due to hypergravity and induce a Ca²⁺ influx into the cytosol. The Ca²⁺ ions act as a signalling molecule and regulate gene functions triggering various downstream transduction pathways resulting in altered cell wall metabolism. *Pathway 1* Up-regulation of α-, β-, γ-tubulin and katanin genes and reduction in microtubule-associated proteins (MAPs) leads to the reorientation of cortical microtubules from transverse to longitudinal. The reoriented cortical microtubules direct the deposition of cellulose microfibrils by cellulose synthase enzyme, thereby affecting the direction of cell growth from longitudinal to lateral.

Pathway 2 Up-regulation of cellulose synthase genes increases the activity of the cellulose synthase enzyme complex on the plasma membrane leading to increased cellulose accumulation in the cell wall. *Pathway 3* Up-regulation of *ATPA2* increases lignin deposition and down-regulation of *VaXTHS4* reduces hemicellulose degradation in the cell wall. *Pathway 4* Hypergravity signals also down-regulate the activity of H⁺-ATPase (proton pumps) on the plasma membrane, which decreases the proton extrusion into the cell wall leading to an increased apoplast pH. The increased pH also reduces the activity of hemicellulose (e.g. xyloglucan) degrading enzymes. However, the mechanisms leading to a reduction in H⁺-ATPase activity are unclear. *Pathway 5* Ca²⁺ influx could also activate NADPH-oxidase leading to increased reactive oxygen species (ROS) production. This ROS could act as a further signalling molecule and can rigidify the cell wall. **d** These pathways in concert rigidify the cell wall matrix, and increase cell wall thickness and lateral cell growth. **e** These cellular changes result in distinct morphological responses such as short plant stature, thickened stem, and rigid stem base

responsible for hemicellulose depolymerisation (Table 2) (Soga et al. 2000a, b). Thus, hemicellulose breakdown significantly reduces, leading to increased molecular size. However, the mechanism by which hypergravity decreases the activity of H⁺-ATPase is not yet clear.

The change in polysaccharide content and the resultant increase in mechanical rigidity show distinct spatial variations in the hypergravity-treated seedlings. Hemicellulose levels increased acropetally, whereas cellulose levels increased basipetally in hypergravity-exposed azuki bean (Nakano et al. 2007) and cress seedlings, respectively (Hoson et al. 1996). Lignin is another cell wall component that is reported to increase in response to hypergravity (Hoson et al. 1996; Tamaoki et al. 2006). An increase in lignin is directly linked to the enhanced activity of *Arabidopsis thaliana* class II peroxidase (*ATPA2*) that polymerises lignin (Tamaoki et al. 2009), possibly mediated

by endogenous auxin (Tamaoki et al. 2011). Further, cell wall-bound ferulic acid and diferulic acid increased in wheat seedlings under hypergravity (Wakabayashi et al. 2005a). Phenolic compounds further undergo coupling reactions to form cross-links with arabinoxylans and impart rigidity to the tissues in azuki bean seedlings (Wakabayashi et al. 2009b).

Understandably, the mechano-cellular changes are dependent on the magnitude of gravity. However, changes in the cell wall are typically observed at higher gravity levels (> 30g) with no effect on the direction of the force vector applied (Hoson and Wakabayashi 2015). Azuki bean seedling cell wall exhibited the same changes irrespective of the direction of the hypergravity vector (Soga et al. 2005b). Similar to germination and seedling vigour phenotype, mechanical extensibility was also found to be reversible in maize and azuki beans (Soga et al. 2003).

Table 2 Hypergravity-induced changes in cell wall composition

Hypergravity exposure	Crop/plant	Salient findings	References
<i>Changes in hemicellulose, cellulose and lignin</i>			
300g for 6 h; and 300g for 3 days	Maize seedlings and wheat caryopses	Increased molecular size of hemicellulose, namely xyloglucans and hemicellulosic polymers, and increased amount of arabinoxylans under hypergravity	Soga et al. (1999a, b), Wakabayashi et al. (2005a)
300g for 6 h; and 135g with 12 h interval	Azuki bean epicotyls and Cress seedlings	Acropetally increased hemicellulose level and basipetally increased cellulose level under hypergravity	Nakano et al. (2007); Hoson et al. (1996)
300g for 24 h; and 300g for 6 h	<i>Arabidopsis</i> and Azuki bean epicotyls	Increased lignin content with enhanced activity of cell wall-bound peroxidase under hypergravity	Tamaoki et al. (2009); Wakabayashi et al. (2009a)
<i>Phenolic acids</i>			
300g for 3 days	Wheat seedlings	Enhanced cell wall-bound phenolic acids—ferulic acid and diferulic acid under hypergravity	Wakabayashi et al. (2005a)
<i>Reversibility of phenotypes</i>			
300g for 5 h (Azuki) and 3 h maize	Azuki bean and Maize seedlings	Decrease in molecular mass of cell wall polysaccharides and drop in apoplastic pH, and increase in polysaccharide degrading enzyme activity when hypergravity-exposed plants were brought back to normal g condition	Soga et al. (2003)

Bringing hypergravity-exposed plants back to 1g decreased the molecular mass of cell wall polysaccharides, lowered the apoplastic pH, and increased polysaccharide degrading enzyme activity (Table 2) (Soga et al. 2003).

Hypergravity influences chlorophyll, photosynthesis, phytohormones and secondary metabolites

All the observable phenotypic responses under hypergravity stem from biochemical changes in the plants or cells. Being a mechanical stimulus, hypergravity induces physiological and biochemical changes at a cellular level. The main physio-biochemical changes under hypergravity are summarised in Table 3. First, photosynthesis and chlorophyll changes in plants can be one of the most consequential effects due to their direct implications on growth, development, and yield. In response to acute hypergravity (100 to 500g for 10 min and 500 to 3000g for 10 min), wheat and rice seedlings showed significantly reduced chlorophyll content (Jagtap and Vidyasagar 2010; Vidyasagar et al. 2008). In addition, acute hypergravity also lowered photosynthesis, transpiration rate, and CO₂ conductance in wheat seedlings (Vidyasagar et al. 2014). Similarly, imbibed wheat caryopses

first exposed to hypergravity (unlike germinated seedlings) and then germinated also showed a decline in photosynthesis rate and chlorophyll content (Dixit et al. 2017). On the contrary, a recent study reported a significant increase in total chlorophyll content coupled with increased RUBISCO quantity when wheat seeds were exposed to hypergravity (10g for 12 h) (Swamy et al. 2021).

The photosynthetic responses to hypergravity have also been investigated with non-plant model organisms. In photosynthetic unicellular alga *Euglena gracilis*, Ortiz et al (2000) showed that hypergravity (3, 6, and 10g) significantly reduced photosynthetic CO₂ fixation. Further, it is reported to reduce the Chl_a/Chl_b ratio without affecting the total chlorophyll content in *Euglena gracilis* (Ortiz et al. 2000). Unlike unicellular alga, moss responds differently under hypergravity. Exposing moss (*Physcomitrella patens*) to hypergravity (10g for 8 weeks) increased chloroplast size leading to enhanced photosynthetic rate and biomass production (Takemura et al. 2017a, b).

Most of the developmental and adaptive processes in plants are underpinned by hormone regulation. Several hormonal changes were observed under hypergravity possibly involved in the response mechanisms. A significant increase in endogenous auxins (IBA and IAA) and stress/defence

Table 3 Hypergravity-induced changes in chlorophyll, photosynthesis, phytohormone and secondary metabolite levels

Hypergravity exposure	Crop/plant	Salient findings	References
<i>Photosynthesis and chlorophyll</i>			
10g for 8 weeks	Moss (<i>Physcomitrella patens</i>)	Increased chloroplast size, photosynthetic rate and biomass under hypergravity	Takemura et al. (2017a, b)
10g for 12 h	Bread wheat	Enhanced chlorophyll content coupled with increased Rubisco protein at seedling and vegetative stages	Swamy et al. (2021)
100 to 500 g for 10 min; and 500, 1000, 2000 and 3000g for 10 min	Wheat and Rice	Reduced chlorophyll content, photosynthesis rate, transpiration rate at seedling stage	Jagtap and Vidyasagar (2010); Vidyasagar et al. (2008)
<i>Hormone level changes</i>			
10g for 12 and 24 h	Bread wheat	Increased auxins (IAA and IBA) Decreased ABA Increased stress/defence hormones such as cis-JA, met-JA, and SA at seedling and vegetative stages	Swamy et al. (2021)
<i>Secondary metabolites</i>			
4 and 8g for 16 days	Soybean callus culture	Reduced isoflavonoid and glucosinolates under hypergravity	Downey et al. (2013)

hormones (i.e. cis-jasmonate, methyl-jasmonate, and salicylic acid), and a decrease in abscisic acid in response to hypergravity exposure (10g for 12 and 24 h) were observed (Swamy et al. 2021). Enhanced IBA, IAA and reduced abscisic acid might have further played a role in enhancing root growth (root length and volume) (Sathasivam et al. 2022). The concentration of secondary metabolites also varies with the changing environmental conditions. Under hypergravity, a reduction in isoflavonoid concentration in soybean callus culture (Downey et al. 2013) and glucosinolates in *Brassica rapa* seedlings was observed (Allen et al. 2009). Allen et al (2009) postulated that the decrease in glucosinolates under hypergravity is either due to increased breakdown under the mechanical stress or a decrease in synthesis as carbon is diverted to cell wall maintenance. The reduction in secondary metabolites under hypergravity was attributed to mechanical stress. In addition, since secondary metabolites are an essential part of plant defence mechanism against biotic stress, mechanical stress can have agricultural implications.

Hypergravity elicits oxidative stress and salt tolerance response in seedlings

An increased gravitational acceleration imparts mechanical stress on plants and plant cells. Naturally, plants trigger tolerance mechanisms in response to hypergravity through changes at transcriptional, translational, and biochemical levels (Detailed in Table 4). *Arabidopsis* callus cultures treated with hypergravity increased the production of proteins associated with the detoxification of reactive oxygen species (ROS) (Barjaktarovic et al. 2007, 2009). However,

up to 2g on parabolic flight experiments with maize root apex showed negligible ROS production (Mugnai et al. 2014). Germination and ROS production appears to be linked closely, and success of seed germination may partially depend on ROS level and balance of ROS-scavenging systems (Gomes and Garcia 2013). Although ROS were long considered hazardous molecules, in seeds, particularly during germination process, it plays a critical role in weakening endosperm and in mobilising seed reserves (Gomes and Garcia 2013). ROS may also act as messengers or transmitters of environmental cues during seed germination process (Gomes and Garcia 2013). The increase in stress/defence hormones and bio-chemicals implies sustained physiological stress caused by hypergravity on plants, which could further lead to a priming reaction.

Hypergravity exposure also up-regulated genes associated with particular heat shock proteins (HSPs)—proteins typically produced in response to high-temperature stress. Kozeko and Kordyum (2009) reported a time-dependent increase in *Hsp70* and *Hsp90* in pea seedlings exposed to hypergravity conditions (3–14g). In contrast, brief hypergravity (2g for ~20 s) during parabolic spaceflight failed to induce *Hsp17.6A* or *Hsp101* proteins in *Arabidopsis* cell cultures (Zupanska et al. 2013). The difference in HSP expression suggests that very specific HSP proteins are involved in the stress responses to hypergravity. Alternatively, hypergravity exposure to cell cultures in parabolic spaceflight was insufficient to generate stress-related signatures such as HSPs or ROS comparable to higher hypergravity intensities for longer durations.

Salt stress is one of the major abiotic stressors and hypergravity has been reported to induce salt tolerance. Chen and

Table 4 Hypergravity elicits oxidative stress and salt tolerance response in seedlings

Hypergravity exposure	Crop/Plant	Salient findings	References
8g for 2 and 16 h	<i>Arabidopsis</i> callus culture	Increased production of proteins associated with detoxification of reactive oxygen species (ROS) under hypergravity	Barjaktarovic et al. (2009; 2007)
1000, 2000, and 3000 g for 1 and 2 h	Cucumber (imbibed seeds)	Enhanced salt tolerance as evident from increased germination rate, germination index, and seedling vigour at seedling stage	Chen and Shen (2011)
600g for 4 h; and 3000g for 3 h	Wheat seedlings and Alfalfa seedlings	Salt tolerance is attributed to enhanced dehydrogenase activity, and increased proline, superoxide dismutase, and malondialdehyde level	Xiaojian and Chun-Rong (2008); Meihong et al. (2005)
3-14 g for 15 min and 1 h	Pea seedlings	Increased hsp70 and hsp90 protein expression in 5-day-old seedlings exposed to hypergravity	Kozeko and Kordyum (2009)

Shen (2011) reported that treating cucumber seeds with acute hypergravity (1000, 2000, and 3000g for 1 and 2 h) significantly induced salt (NaCl) tolerance, as evident from increased germination rate, germination index, and seedling vigour when compared to untreated seeds. Similar salt tolerance phenotype was observed in alfalfa (3000g for 3 h), wheat (600g for 4 h), and carrot callus cultures (10 g) in response to varied hypergravity intensities (Yang et al. 2005; Guo and Guo 2008; Scherer 2006). Specifically, in wheat, salt tolerance was attributed to enhanced dehydrogenase and superoxide dismutase activities (Guo and Guo 2008; Slama et al. 2015), and proline and malondialdehyde levels (Yang et al. 2005).

Hypergravity-induced differential gene expression associated with cell wall structure and root growth phenotype

Studies on changes at molecular levels in response to hypergravity are relatively sparse, largely inconsistent, and mostly

focussed on the model plant *Arabidopsis* (Table 5). However, few existing studies provide a preliminary understanding of molecular underpinnings of altered phenotype under hypergravity (Table 5). The role of microtubule reorientation in increased lateral growth and decreased longitudinal growth is well defined (Soga 2010). The reorientation of cortical microtubules is brought about by a decrease of Microtubule Associated Proteins (MAPs)—responsible for maintaining a transverse orientation (Soga et al. 2012; 2018). In line with this argument, a reduction in *MAP65-1* transcript level/s was observed under hypergravity (Soga et al. 2012, 2018). Genes coding for α -tubulin and β -tubulins, proteins required for the reorientation of cortical microtubules, were up-regulated under hypergravity (Yoshioka et al. 2003; Matsumoto et al. 2007). In addition, transcripts associated with MAPs— γ -tubulin complex (Soga et al. 2008), katanins (Soga et al. 2009) and actin filaments (Tanabe et al. 2018) linked to microtubule reorientation were also altered in response to hypergravity. In response to 300g, an increased expression of HMGR (3-hydroxy-3-methylglutaryl-Coenzyme A

Table 5 Hypergravity-induced differential gene expression associated with cell wall structure, and root growth phenotype

Hypergravity exposure	Crop/Plant	Salient findings	References
300g in the shoot to root direction for 24 h	<i>Arabidopsis</i>	Up-regulation of β -1,3 glucanase and decreased expression of β -galactosidase in flower bud of 26-day-old seedlings exposed to hypergravity	Tamaoki et al. (2014)
300g for 1 h	Azuki bean epicotyls	Down-regulation of genes responsible for hemicellulose-degrading enzymes, i.e. xyloglucan endotransglucosylase/hydrolase (<i>VaXTHS4</i>) under hypergravity	Soga et al. (2007)
10g for 12 h	Bread wheat	Decreased expression of CDK inhibitor, and cell number regulator-associated genes Increased expression of CDK, RPA, and CDC-associated genes in 45-day-old wheat roots	Sathasivam et al. (2022)

reductase) genes was probably involved in increasing the molecular mass of polysaccharides through modulating the production of membrane sterols and hormones (Yoshioka et al. 2003). Particularly, the up-regulation of *HMGR* genes triggered terpenoids synthesis in the hypocotyl region of *Arabidopsis* (Yoshioka et al. 2003). Increased molecular mass of hemicellulose reported to impart enhanced structural rigidity to the plants. This increase in hemicellulose mass is attributed to the down-regulation of genes responsible for producing the respective hemicellulose-degrading enzymes, i.e. xyloglucan endotransglucosylase/hydrolase (*VaXTHS4*) (Soga et al. 2007) and reduced activity of β -glucanases (Soga et al. 1999a). In an independent study, transcriptome analysis in *Arabidopsis* root apex under mechano-gravitational stimulation significantly activated transcripts associated with stress responses to drought, cold, and light (Kimbrough et al. 2004). Microarray analysis of global gene expression of *Arabidopsis* flower bud (20–26 days old) revealed up-regulation of β -1,3 glucanase and decreased expression of β -galactosidase responsible for modifying pectin and inhibiting pollen germination, respectively, under hypergravity (300g for 24 h) (Tamaoki et al. 2014). Furthermore, a gene associated with aspartate aminotransferase was up-regulated, while genes related to cell wall invertase and sugar transport were down-regulated, indicating inhibition of starch accumulation under hypergravity (Tamaoki et al. 2014). Substantial changes in the expression of genes associated with biosynthesis of abscisic acid and auxin were also observed in response to 300g for 24 h (Tamaoki et al. 2014).

In addition, a recent study from our lab investigating the molecular basis of hypergravity-induced enhanced root growth in bread wheat showed up-regulation of genes associated with cell division, regulation of auxin biosynthesis, and cell wall biosynthesis/organisation (Sathasivam et al. 2022). Further, significant change in carbohydrate metabolism, photosynthesis, cellular respiration, and lignin biosynthesis indicating the formation of sugars, ATP, and cell wall composition in support of increased cell proliferation has also been reported in response to hypergravity (Table 5). On the other hand, significant down-regulation of abscisic acid synthesis-associated transcripts confirms a reported inverse

relationship between abscisic acid level and increased root growth. More specifically, positive regulators such as Abscisic acid 8'-hydroxylase 1 (abscisic acid degradation), Indole-3-glycerol phosphate synthase (Auxin biosynthesis), Replication protein A, cell division control protein 25-like CDC42 Homolog (cell division), and cellulose synthase that directly promote root growth were significantly up-regulated (Sathasivam et al. 2022).

Hypergravity influence on plant reproductive phase

While most studies focussed on the seedling stage, few have investigated hypergravity effects on the reproductive growth of plants (Described in detail in Table 6). Understanding plant responses to altered gravity is important to elucidate how plants reproduced and evolved during the transition from aquatic to land plants. Growing *Brassica rapa* plant under 2 and 4 g for 16 days within chambers mounted on large-diameter centrifuges revealed no adverse effects on flowering, fertilisation, and seed formation (Musgrave et al. 2009a). Moreover, hypergravity improved seed development by increasing seed and embryo weights (Musgrave et al. 2009a). *Arabidopsis* exposed to similar hypergravity intensities (2g/4g for 11 days) showed increased flower production at 4g, however, with no seed set. The difference in seed formation between *Arabidopsis* and *Brassica rapa* was attributed to the duration of hypergravity exposure that may have further curtailed pollen tube growth after pollination compared to 1g controls (Musgrave et al. 2009b). The growing tip of pollen tube is rich in pectin molecule, and optimum cross-linking of pectic polysaccharides is critical for pollen tube growth. Changes in transcripts associated with cell wall pectin modification are reported to influence significant pollen tube development in *Arabidopsis* (Tamaoki et al. 2014).

In vitro plant cell culture response to hypergravity

Cell culture studies provide invaluable insights into the fundamental responses at the sub-cellular level to complement studies on whole-plant models. *In vitro* callus culture

Table 6 Impact of hypergravity on plant reproductive phase

Hypergravity exposure	Crop/plant	Salient findings	References
2 and 4g for 16 days	<i>Brassica rapa</i>	No adverse effects on flowering, fertilisation and seed formation Improved seed development and embryo weights in plants grown under hypergravity	Musgrave et al. (2009a)
2 and 4g for 11 days	<i>Arabidopsis thaliana</i>	Increased flower production at 4 g with no seed set and decreased pollen growth in plants grown under hypergravity	Musgrave et al. (2009b)
300g for 24 h	<i>Arabidopsis</i>	Change in gene expressions associated with cell wall polysaccharides and amino acid transport in the pollen tube in flower bud of 26-day-old seedlings exposed to hypergravity	Tamaoki et al. (2014)

experiments have revealed responses comparable to whole plants/seedlings under hypergravity treatments. Cell culture studies show that hypergravity triggers responses at a cellular level (Table 7). *Arabidopsis* callus cultures exposed to hypergravity triggers significant changes in transcripts associated with cell wall formation/reorganisation, hormone synthesis, defence, stress-response, and gravity-sensing mechanism/s (Martzivanou and Hampp 2003; Herranz et al. 2013). On a basic level, hypergravity acts as stress, triggering the production of ROS in the cell cultures. As a response to the stress, phosphorylation of enzymes detoxifying the reactive oxygen species increases under hypergravity (Hausmann et al. 2014).

Cellular changes form the basis for responses observed at a tissue, organ, or organism level. Cells divide, develop, grow and form new cells in an organism. Any changes in cell growth and proliferation can be consequential to plant growth and development. Hypergravity, as low as 2g, uncoupled cell growth and cell proliferation in *Arabidopsis* cell cultures, slowing down the rate of cell proliferation (Manzano et al. 2016; Kamal et al. 2018). Epigenetic modifications such as DNA hypermethylation and histone acetylation were also triggered in cell cultures under 2g for 24 h (Kamal et al. 2018).

The interplay between hypergravity and gravitropism

In addition to counteracting the gravitational load, plants also have to orient themselves along the gravity vector—a phenomenon known as gravitropism. Plants grow along the gravitational vector to enable the availability of light to the shoots while ensuring the supply of nutrients and water to the roots (Chen et al. 1999). The widely accepted mechanism of gravity sensing is through the ‘starch-statolith model’, wherein amyloplasts (starch-filled plastid) in specialised gravity-sensing cells called statocytes act as gravisensors (Morita 2010; Takahashi et al. 2021). Based on the gravitational angle, the amyloplasts settle at the bottom of the cell, providing signals for differential growth of the plant along the gravity vector (Nakamura et al. 2019). As gravitational acceleration imparts a force proportional to mass, it was initially thought that amyloplasts sense the

hypergravitational accelerations under the force acting on the amyloplasts. Studies using mutants and mechanoreceptor blockers showed that (a) amyloplasts are not involved in perceiving hypergravity and (b) hypergravity is indeed perceived by stretch-activated mechanosensitive ion channels (Soga et al. 2004, 2005b). Moreover, recent studies have shown that amyloplasts sense the inclination of the plants and not the force of gravity acting on the plants (Chauvet et al. 2016). Therefore, gravitropism relies on the inclination and not on the acceleration of gravity. These results have led to the ‘position-sensor hypothesis’, which proposes that amyloplasts sense the gravity vector based on the position of the statoliths within the cell (Pouliquen et al. 2017).

Despite the likelihood of amyloplasts not being involved in the perception of hypergravity, at least directly, the converse could be true: hypergravity can affect gravitropism. Exposure to hypergravity in wild-type and starch-less mutants improved gravitropism in *Arabidopsis* (Kiss 2000). This involvement of hypergravity in gravitropism was putatively attributed to increased sedimentation of plastids under the influence of apparent force under > 1g conditions (Fitzelle and Kiss 2001). The enhancement of gravitropism was also observed in *shoot gravitropism 2 (sgr2)* mutant—a mutant that does not exhibit shoot gravitropic response and amyloplast sedimentation at 1g (Toyota et al. 2013b). Hypergravity, therefore, enhances gravitropism by inducing sedimentation of amyloplasts.

Stretch-activated mechanosensitive ion channels detect the mechanical load that plants experience under hypergravity. Studies have identified the Ca²⁺-permeable mechanosensitive ion channels (MSIC), namely MCA1 and MCA2 located on the plasma membrane of epidermal cells of root and shoot, to be involved in sensing hypergravity (Hattori et al. 2020). When exposed to hypergravity, the MS ion channels are activated, increasing the cytoplasmic Ca²⁺ concentration in the cells (Nakano et al. 2021). The Ca²⁺ ions function as signalling molecules. The signals generated are then transduced through various downstream mechanisms leading to changes in cell wall components and increased cell wall rigidity. While the amyloplasts are considered the primary sensors for gravity vectors, the involvement of MS ion channels in gravitropism has long been hypothesised (Toyota and Gilroy 2013). Based on this hypothesis, experiments have also suggested that changing the angle of the

Table 7 In vitro plant cell culture response to hypergravity

Hypergravity exposure	Crop/plant	Salient findings	References
7g for 1 h	<i>Arabidopsis thaliana</i> callus culture	Transcriptomic changes associated with cell wall formation/reorganisation, hormone synthesis, defence, stress-response, and gravity-sensing transcripts in callus exposed to hypergravity	Martzivanou and Hampp (2003)
10g for 14 days	Carrot callus culture	Enhanced callus growth	Scherer (2006)

plant with respect to the gravity vector also increases Ca^{2+} concentration (Toyota et al. 2013a) and triggers mechano-sensitive microtubule reorientation (Ikushima and Shimmen 2005), suggesting the involvement of MS ion channels in graviperception and gravitropism (Bastien et al. 2013).

A recent study presents data supporting the hypothesis that MCA1, an ion channel involved in sensing mechanical force under hypergravity, is also involved to some degree in sensing the change in gravity vector (Nakano et al. 2021). The involvement of MCA1 provides some evidence for the already challenged ‘force-sensor’ model of amyloplasts, where the force of sedimenting amyloplasts stretches the plasma membrane either directly or indirectly (via actin filaments or cytoskeleton), activating the MSIC (Tatsumi et al. 2014; Nakano et al. 2021). However, the MCA channels are activated mainly by membrane tension, without the involvement of the cytoskeleton or extracellular matrix (Yoshimura et al. 2021). There is still the possibility that amyloplasts directly stretch the MSIC channels on the plasma membrane leading to activation (Tatsumi et al. 2014). More studies are required to elucidate the mechanisms of MCA1 activation and the involvement of amyloplasts in MCA1 activation, if at all. There seems to be interplay between mechanisms for hypergravity perception and gravitropism. Interactions between amyloplasts and mechanosensitive ion channels leading to responses of graviperception and perception of hypergravity are unclear and need further study. Hypergravity, therefore, is an invaluable tool to elucidate the mechanisms of both graviperception and hypergravitational mechanoperception.

Perspectives and conclusion

In this review, we described our current understanding of plant responses to hypergravity from the organism to the sub-cellular level. Although plant behaviour under hypergravity, especially cell wall changes, has been well studied, much remains unknown. Synthesising the literature on plant responses to hypergravity has allowed us to highlight some knowledge gaps:

- We have just begun to understand the mechanisms for the perception of hypergravity. As first postulated by Soga et al. (2005a, b), recent evidence supports the hypothesis that MSIC (MCA1 and MCA2) perceive hypergravity as a mechanical load in plants (Hattori et al. 2020). Several other MSICs besides MCAs (for example, MSL family MSICs) could also be involved in perceiving hypergravity. Further studies on various candidate MSICs will contribute to a greater understanding of hypergravity and mechanoperception in plants.

- Studies so far have provided significant insights into the physiological responses of plants to hypergravity. However, much of our current knowledge on plant behaviour under hypergravity, especially with seeds and cell cultures, is limited to the observed phenotypic and biochemical responses. The downstream signal transduction cascades between perception and phenotypic responses remain elusive. Further studies using advanced techniques, mainly the omics approach can elucidate the biochemical pathways and molecular entities involved in processes leading to phenotypic responses.
- Hypergravity is perceived as mechanical stress mostly by MSICs in plants. Research also suggests the involvement of MSICs in gravitropism. Moreover, hypergravity improves gravitropism in starch-less mutants. Based on these results, there seems to be interplay between hypergravity mechanisms and gravitropism. We further propose that mechanoperceptive mechanisms involved in hypergravity are involved in gravitropism by acting as a secondary feedback system to the primary starch-statolith system. In this line, studies using hypergravity can aid our understanding of gravitropism.
- Hypergravity imparts changes in plants, many of which could have implications for agriculture. For instance, subjecting wheat seeds to specific hypergravity regimens increased the root growth parameters in bread wheat (Swamy et al. 2021; Sathasivam et al. 2022). In addition, hypergravity significantly affects cell wall composition and rigidity. The plant cell wall is of considerable significance to agriculture due to its role in plant defence and biomass production (Zhao and Dixon 2014). Understanding the mechanisms, biochemical pathways, and genes responsible for cell wall modification under hypergravity could contribute to cell wall-based crop improvement through biotechnological tools (Hoson and Wakabayashi 2015). Therefore, understanding plant physiology under hypergravity could help in crop improvement.

Author contribution statement RH and BKS conceptualised the topic. BKS, AD and MS drafted the manuscript. AD, BKS and MS prepared the visualisations. RH edited the manuscript. All the authors have read and approved the final version of the manuscript.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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