ISSN 0006-2979, Biochemistry (Moscow), 2021, Vol. 86, No. 11, pp. 1388-1394. © Pleiades Publishing, Ltd., 2021.
Published in Russian in Biokhimiya, 2021, Vol. 86, No. 11, pp. 1668-1676.

REVIEW

Role of the Earth's Motions in Plant Orientation – Planetary Mechanism

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Received October 6, 2021
Revised October 6, 2021
Accepted October 7, 2021

Abstract—According to the proposed theory, the starch-rich particles (statoliths) help the plant to convert the signals from Earth's motions into the signals necessary for the plant to perceive its orientation relative to the gravity vector while moving freely because of inertia in the sensory cells (statocytes) of roots and stems. Motions of the Earth are never constant, which, in particular, refers to the so-called polar motions and oscillations of the planet's rotation axis. Statoliths at any given moment move in the cytoplasmic liquid of statocytes due to inertial motion initiated by the action of the Earth's movements, maintaining the trajectory set by the previous movement of the oscillating planet. Unlike statoliths, the walls of a statocyte move in space along with the entire plant and with the Earth, in strict accordance with the current direction of motion of the planet's axis. This leads to the inevitable collision of statoliths with the statocytic wall/membrane. Cytoplasmic liquid, as a substance that is not able to maintain its shape, does not interfere with the inertial motions of the statoliths and collision with the wall of the statocyte. By striking the membrane, statoliths cause the release of ions and other factors at the impact site, which further participate in the gravitropic process. Pressure of the sediment of statoliths at the bottom of the statocyte, as well as position of this sediment, are not the defining factors of gravitropism.

DOI: 10.1134/S0006297921110031

Keywords: plant gravitropism, perception of orientation, reorientation, sine law, statocytes, statoliths, gravisensing, the Earth's movements

INTRODUCTION

Plant geotropism is a plant response that orients the plant's growth parallel to the gravity vector. Clear manifestation of the gravitropic growth is universal ability of the plants to restore orientation of their organs after forced reorientation of the plant. Of particular interest in gravitropism is its earliest stage, "perception of orientation", that is, the mechanism of recognition by a plant of its position relative to the gravity vector. It is commonly believed that the effect is caused by the gravitational attraction to the Earth of the special starch-filled amyloplasts also known as statoliths. Although gravity is one of the most important environmental stimuli that a plant encounters, the plant's ability to orient itself with respect to the gravity vector does not appear to be controlled by attraction of statoliths to the Earth since the action is too weak. In contrast to the accepted paradigm of plant gravitropism, an idea is being put forward according to which plants employ special mechanism for perception of orientation that uses peculiarities of the Earth's movements in space.

Gravitropism of plants has been extensively studied since 19th century [1], and its most popular explanation then became the starch-statolith theory [2-5], according to which statoliths, settle to the bottom of sensitive cells, statocytes, being heavier than the cytoplasm, and then trigger asymmetric bending growth that restores correct orientation of the plant.

Despite the progress in the field, the earliest phase of plant gravitropism, that is the plant's perception of its orientation remains unclear to this day [6]; subsequent stages of gravitropism are successfully deciphered, but the very first stage remains elusive. Meanwhile, there is evidence that plants detect a change in their orientation in a fraction of a second, and therefore it can be assumed that the plant must first perform the perception of orientation, and only then it proceeds to asymmetric distribution of the growth factors that allow it to perform growth bends of organs for a positive (root growth down) and negative gravitropism (upward shoots growth). It is argued here that it would be beneficial for plants to use a special mechanism at the first stage of gravitropism that is based on wobbling motions of the Earth and continual shifts of the Earth's rotational axis. Gravitational attraction of the plant components to the center of the Earth plays a role only in the subsequent stages of gravitropism.

STATE OF THE PROBLEM AND THE PLANETARY MECHANISM

Current explanations of plant graviperception. It has been established in the course of a long history of studying plant gravitropism [4, 7] that the early phases of this process are associated with the role of amyloplastic statoliths that precipitate to the bottom of the endodermal cells of shoots and columella cells of roots, although the mechanism of their functioning remained unknown, despite the abundance of experiments [8].

The Cholodny–Went theory of asymmetric distribution of the phytohormone auxin as a necessary prerequisite to the tropic bending of plant organs remains to be the unifying concept after 100 years of studies [9, 10], but the discovery of asymmetric distribution of the growth hormones, ions and other factors in response to plant reorientation has not clarified the essence of the initiating event – how does the plant "learn" about its position in space?

Current theories of plant gravitropism are based on the paradigm that the process begins with the gravitational attraction of sensory particles, such as statoliths, to the Earth. For some time, the two models for graviperception, known as the starch-statolith pressure and the protoplast-pressure models, competed. However, the assumption that the cell protoplast works instead of statoliths [4, 11] cannot explain the fact that the reoriented plants follow the sine rule [12] according to which the gravitropic response of the plant organ is proportional to the sine of the angle between the organ axis and the vertical, and is mainly of historical interest. It should also be emphasized that the problem of recognizing weak signals is common for both "non-statolith" and statolith theories [13].

According to the classic starch-statolith theory, the mechanosensitive system of a statocyte recognizes that the plant has been reoriented only due to the gravity of the starch-rich amyloplasts that settle to the bottom of the cell [13-15]. The amyloplast sediment further redirects transport of the hormone auxin to the lower flank of the plant organ, resulting in the differential growth of upper and lower flanks, with the root bending down and the stem up [5].

The shoot gravitropic response in the angiosperm species is dependent on the angle of inclination from the direction of gravity. According to the "position sensor hypothesis", a machinery, which detects the position of amyloplasts in statocytes, detects also inclination of the shoots owing to the amyloplasts sediment inclination, whereas mechanosensitive channels are not involved in the sensing the gravitational force exerted on the amyloplasts [16-19]. This proposition suggests that amyloplasts sediment, due to its position and interaction with growth factors, distributes them asymmetrically. The "position sensor hypothesis" cannot answer the key question concerning perception of orientation documented by many observations [8, 20] – why statocytes are able to respond with the intake of calcium ions in a fraction of a second after reorientation.

It has been also assumed that statoliths are equipped with ligands that chemically interact with the membrane receptors [21]. This option eliminates the problem of identifying a useful signal against the background of mechanical interference, but the data on the reduction of the effect of gravitropism in the starch-deficient mutants remain not fully explained.

It is pertinent to emphasize that the different chemical composition of the statoliths, such as starch in higher plants, heavy crystals of barium sulfate in the green alga Chara, and protein crystals in some fungi [22, 23], apparently contradicts the role of statoliths sediment as a universal component regulating the distribution of growth substances. The available data rather suggest that statoliths are used as a universal percussion instrument.

Some effects do not agree with the models of gravitropism. A number of effects are known that do not agree with both the classic starch-rich statoliths model and its modifications. In particular, it is known [24, 25] that: (i) the shortest stimulus needed for the response can be no more than 7 s, while taking into account width of the statocyte cell, it should take an amyloplast several minutes to sediment to the bottom of a cell; (ii) the starchless statoliths are lighter, do not sediment, but these mutants are still able to sense reorientation, although with greater variance of the shoots responses; (iii) amyloplasts, together with actin filaments, perform saltatory movements that do not contribute to the formation of sediment. The presence of starch and sedimentation of the plastids was not required for the gravitropic response of roots in the starchless mutant of Arabidopsis [26]. Meanwhile, almost all theories of gravitropism are based precisely on the deposition of statoliths in the form of a single sediment, with the presumed ability of the sediment to stretch the membrane or regulate growth factors [18, 17].

The plant's perception of its position in space is a prerequisite for gravitropic growth. How a plant can perceive correctness of its position, how does it detect a change in its orientation, if, for example, a plant is placed horizontally? This also applies to any germinating seed that has yet to send stems up and roots down. The initial and most puzzling stage of plant gravitropism is here denoted by the term "perception of orientation", instead of the less precise terms – graviperception or gravisensing, as these impose an unproven and possibly erroneous explanation.

It can be assumed that, the plants turned to the oscillations of the Earth's spin axis for the perception of orientation, and not to the attraction of plants to the center of the Earth, which is expected in terms of graviperception and gravisensing. The role of attraction of the plant components to the center of the Earth is important, but only at the stages following the perception of orientation. Plants could use oscillations of the planet's axis as a factor presumably influencing the dynamics of statoliths. The statoliths of algae and fungi, despite their different composition, could apparently function according to the same universal principle as in higher plants. It is important for all of them to execute perception of orientation, and common mechanism could be realized in all of them.

The role of changes in the orientation of the Earth's rotation axis for the orientation of plants in space. It is known from geophysical and astronomical studies that the Earth's rotational axis experiences changes in its orientation. Rotation and orientation of the Earth is subject to irregularities. Among these changes are polar motions, i.e., a wobble of the spin axis of the Earth about its figure axis, and oscillating movements of the Earth's spin axis (nutations). The origin of nutations is associated with many factors, including, in particular, external gravitational torques exerted by the Moon, Sun, and, to a lesser extent, also by the planets. These effects cause the angular momentum exchanges between the reservoirs of orbital and rotational motions [27, 28].

The Earth's shape is approximately an ellipsoid flattened at its poles; the Earth's oblateness, in turn, controls, in addition to the astronomical precession–nutation, the nutations and wobbling motions manifested as intrinsic rotational normal modes belonging to the Earth system [29-31].

The changes of the Earth's axis orientation in space are associated also with the existence of a wobbling solid inner core inside the Earth. Various processes have their impacts on the axis orientation, involving mass circulation of the atmosphere and ocean, mantle convection, coupling mechanisms at the interfaces of a liquid outer core and solid inner core, resonance effects of the free core nutation patterns, etc. [32]. Because of all this, the combined forces acting upon the Earth produce continual small changes both in orientation of the Earth's rotational axis and in the speed of its rotation.

Study of the movements of the Earth has brought a lot to geophysics and astronomy, but plants probably also "know" how to benefit from them. And they could do this using the proposed planetary mechanism.

Planetary mechanism as an initiator of the plant's perception of its orientation. It is proposed that, in the case of plant reorientation, that is, in the case of a change in its position relative to the gravity vector, statoliths hit the membrane/wall of the statocyte. Statoliths-wall collision is generated due to the planetary mechanism, functioning of which depends on the Earth as a planet moving in accordance with its gravitational interactions, as well as on the inertial motion of statoliths in the cytoplasmic liquid. Regular and irregular movements of the planet are the main cause of the inertial motions of statoliths, bombarding the membrane/wall of the statocyte, as soon as the plant changes its position, that is, its orientation in space. The walls of the statocyte move along with the planet Earth, while the statoliths, being in the cytoplasmic liquid, have the ability to move by inertia and to maintain the direction of motion that the planet had in the previous moment. Unlike statoliths, cell walls, like the entire plant, move in space with the planet, in strict accordance with the current movement of the Earth. Thus, statoliths must move in the cytoplasmic liquid due to inertia for some time, regardless of the movement of the statocyte as a whole. This relative independence of the movements of the cellular wall and the statolith inside the cell inevitably leads to a collision of statoliths with some sector of the cell wall. The exact sector of the cell wall, which will be bombarded by statoliths, is determined by the angle of inclination of the statocyte, as a part of the plant organ, relative to the gravity vector.

Thus, the proposed planetary mechanism (PM) functions due to the inertial motions of the particles that are generated by the motions of the Earth in outer space. This mechanism would be impossible if the Earth's motions were strictly uniform. The biophysical stimulus in the form of PM-dependent bombardment of the statocytic wall by any statoliths, regardless of their chemical nature, serves as the primary cause of the "perception of orientation". Collisions cause activation of mechanosensitive membrane ion channels, and this leads to the local entry of calcium ions into the statocytes, as well as to the local release of auxin transporters and other factors "exfoliated" from the membrane and participating in the subsequent gravitropic growth. The success of the perception process is facilitated by the higher mass of the statoliths, so they are filled with starch in higher plants, and barium sulfate in algae.

In experiments, it would be possible to replace amyloplasts in a statocyte with inert particles and get presumably the same result in the test for the accumulation of calcium ions after reorientation. Forced dissolution of artificial statoliths, immediately after the act of perception of orientation, should not interfere with subsequent gravitropic growth. This would show that statoliths play a key role in the first phase, and not in the subsequent stages of gravitropism. The observed sedimentation of statoliths is a simple side effect of their presence in a cell. As for Brownian motion and other conventional interferences, they are unable to withstand the effect initiated by the planet's movements.

As for the sector of a statocyte, which is hit by statoliths, it further serves as a source of positional information, that is, its topography plays the role of a set-point. It is in this sector that an instantaneous response is initiated in the form of local influx of calcium ions transported through the activated mechanosensitive channels of the membrane. Next, that is after the perception of orientation, a cascade of signaling events unfolds, in which the asymmetric auxin distribution plays a central role, as was envisaged in the Cholodny–Went theory a century ago [9, 33, 34].

The saltatory movements of statoliths initiated by the cytoskeleton are apparently important for their involvement in the planetary mechanism. Evolutionary acquisition of the heavy amyloplasts by plants may have simply improved the ability for the hit-dependent sensing that they might have had even before the emergence of specialized statoliths. It must be mentioned that in the gravity-sensitive cells saltations are observed not only in the behavior of amyloplasts, but also in other organelles [35, 36]. When coming out on land, the ancestors of higher flowering plants, apparently, already used statoliths in the functioning of the planetary mechanism, but the subsequent cascade of gravitropic processes was not yet effective. This assumption is consistent with the observations according to which amyloplasts in the roots of ferns and lycophytes showed random localization in the root cells, and these organisms demonstrate slow, rudimentary gravitropic reaction of the roots [37].

Instant plant response to reorientation using calcium ions. It has been shown that presentation time (the shortest time needed for the stimulus to generate a response to reorientation) can be 1s or less, whereas it should take an amyloplast several minutes to sediment to the bottom of a cell [24]. This directly indicates that the influx of Ca^{2+} from the cell environment into cytoplasm of statocytes is triggered not by the formation of sediment, but by some other mechanism that acts instantly, that is, in the same way as the planetary mechanism works. When the effects of Ca^{2+} concentration increase in the certain structures of Arabidopsis seedlings were analyzed under a variety of gravity intensities combined with rapid switching of seedlings between hypergravity and microgravity (in ground studies and in parabolic flights), it turned out that seedlings possess a very rapid sensing mechanism that linearly transduces a wide range of gravitational changes (0.5-2 g) into Ca^{2+} signals within the subsecond time scale [38, 39]. Under such conditions, the ability of statoliths to move in the cytoplasmic liquid relative to the wall/membrane of the statocyte because of inertia could well manifest itself in full. The proposed mechanism could work both on the ground and in space, but the artificial change in weight should affect the subsequent stages of plant gravitropism.

Top and bottom detection is carried out in plants only after perception of orientation. The plant's perception of its orientation creates a key prerequisite for the subsequent events of gravitropism. At this stage, mechanosensitive ion channels are activated through the PM-dependent collisions of membrane with statoliths. The activated ion channels are able to regulate osmotic pressure by supplying ions [40]. Increase in the osmotic pressure in statocytes and surrounding tissue, which occurs after the perception of orientation, leads to local accumulation of the fluid enriched with growth factors (PIN transporters, auxin, etc.). This liquid then flows down, and only now the Earth's gravity turns out to be important for the plant gravitropism. Only at this stage does the root "learn" where the "bottom" is, and the stem receives information about the "top".

The release of ions in response to plant reorientation is documented as an earliest and fast-transient Ca^{2+} concentration increase followed by other events [39]. The mechanosensitive plasma membrane of statocytes is reinforced with auxin transporters organized into clusters [33]. Probably, in addition to the calcium response of statocytes, PINs and some other factors can be locally released from the membrane in response to its bombardment by statoliths. Thus, the biophysical process of collisions of statoliths with the membrane/wall triggers all subsequent biochemical and cellular events of gravitropism.

Microgravity environment offers the opportunity to nullify any pressure applied by statoliths, however physical contact of statoliths with membrane under microgravity is sufficient to generate calcium ions release [21]. Although the planetary mechanism is able to function against the background of microgravity, the downward flow of growth factors released after the statoliths' impact can be hindered and the final result can therefore be modified. However, statoliths moving in the cytoplasmic liquid due to inertia even under microgravity conditions have the ability to strike the membrane/wall of statocytes; this always happens, when orientation of the plant changes compared to the previous position. The force of inertia is proportional to the body mass, therefore, for example, the starch-rich amyloplasts are more effective than the lighter starch-free amyloplasts in mutants.

Thus, the initiating event in the perception of orientation, not only in the plant kingdom, but also in fungi, is the mechanical strain exerted by the statolith's impact on the cell wall due to the planetary mechanism. Gravitropic growth is a process secondary to the perception of orientation. According to the proposed mechanism of initiation of the plant gravitropism, statoliths do not play the role that has been attributed to them for the last hundred years. Restoration of the disturbed orientation by a plant is achieved only due to the movements of the Earth, forcing statoliths to bombard the walls of statocytes. Significance of the weight of the amyloplast sediment in the membrane activation is negated in this concept, significance of the position of the settled sediment as an initiator of gravitropism is also negated. Without collisions of the statoliths with the cell wall mediated by the planet motions, plant gravitropism would be impossible due to interferences obscuring the weak signal.

Noises in plant gravitropism. Intracellular activities (noise) complicate identification of the primary gravity signal [13, 41]. In search of an answer to the most difficult question of plant gravitropism, how a weak signal could be detected, discriminated, and amplified in the natural noisy environment, assumptions were made that the noise itself may play some role in perception of the weak signals due to the possible participation of electrical processes, stochastic resonance, etc. [13]. It is known that normal fluctuations of the resting tension of the membrane are much greater than the sediment of statoliths could induce [42]. Staves posed a question that applies to most of the theories of plant gravitropism, including the dominant starch-statolith theory: how is it possible that the small, vectoral, gravity-caused pressure is perceived over the much larger turgor pressure (about $1 : 10^5$ signal-to-noise ratio)? [11]. The answer to this question proposed here is that plants, with the help of the Earth and statoliths, can overcome all the usual obstacles, such as Brownian motion and osmotic pressure.

However, this alone is not enough. What else would plants have to do in evolution to get rid of all hindrances associated with the first stage of gravitropism? The simplest and most effective method for eliminating the influence of interferences is to lower the sensitivity threshold to them. In evolution, it was required to make the perceptual mechanism sensitive only to the physical stimulus that is stronger than all the usual noises, and by this to solve the problem.

Sine law and plant gravitropism. As established in the 19th century by Julius Sachs, a plant stem placed, for example, horizontally would show the strongest bending response, which would gradually decline as the axis of the stem approaches the vertical [43, 44]. This observation is known as the so-called "sine law", according to which the gravitropic response varies linearly with the sine of the inclination angle between the plant organ axis and the vertical. For example, the gravitropic response of maize and rice coleoptiles during an early but substantial part of the curvature development is directly related to the initial stimulation angle, i.e., the response of the shoot inclined at an angle from vertical indeed varies linearly with the sine of the inclination angle [45]. It has also been shown that changes in the orientation of Arabidopsis seedlings relative to the gravity vector (inclining the specimens) are able to increase their cytoplasmic calcium concentrations [39, 46]. The existence of this effect known for a century [16, 44] requires a reliable explanation.

Based on the positional information obtained from the impact of statoliths on the membrane, plant organs are developed at particular angles, in accordance with the gravitropic set-point angles [47]. This allows plant organs to respond to small deviations from the vertical, and this is an alternative to the idea that the sediment's position is a tilt angle sensor [18].

Protein factors, e.g., PINs, which potentially could be detached and released from the membrane when statoliths hit the wall, should probably be localized in statocytes unevenly. The PINs proteins are known to mediate asymmetric distribution of auxin in tissues [33]. Probably, the localization of PINs in the elongated statocytes is evolutionarily selected to help vertical growth. Let's assume that PINs are localized in a stem mainly at the ends of cylindrical statocytes. With the vertical growth of the stem, the statoliths, moving by inertia in the plane of the Earth rotation, would hit mainly the side walls, which are relatively free of PINs. Increase in the angle of inclination from the gravity vector should, apparently, increase the number of PINs proteins that are "peeled off" from the sector of the membrane bombarded by the statoliths. As a consequence, gravitropic response of the stem could change linearly depending on the sine of the tilt angle, and the strongest bending response would be at the horizontal position of the stem, as observed by Sachs [43].

Plants constantly monitor their orientation. Initiation of gravitropism by the planetary mechanism allows plants to be relatively independent of their reorientation caused by various factors. The root, meeting a stone in the soil and changing the direction of growth, is forced to redetect where the top and bottom are. Plants also overcome the destabilizing effects of elongation growth and flexion under their own weight. For all this, the dynamics of statoliths and direction of their impacts on the wall are important, providing a gravitropic set point angle. Statoliths should not lie in the form of a sediment, and here the cytoskeleton comes to their aid. Most amyloplasts are known to continuously exhibit dynamic, saltatory movements in the statocytes of higher plant stems [6, 35, 48]. Actin filaments are capable of forcibly shaking statoliths so that they do not lie like a useless load. Only when suspended in a liquid, statoliths can be used according to the planetary mechanism for perception of orientation. Apparently, it is for this reason that the saltatory movements of statoliths, otherwise seemingly mysterious, are maintained in the statocytes.

The abnormally thick actin bundles surrounding amyloplasts interfere with gravitropism, while destruction of these bundles restores both the saltatory dynamics of amyloplasts and normal gravitropism [8, 36, 49, 50]. In cells that carry out perception of orientation, such as statocytes of the root cap, the nucleus is attached by actin filaments to the cell periphery, close to the plasma membrane [51]. This adaptation creates free space for unimpeded motion of statoliths in the cytoplasm, which favors operation of the planetary mechanism.

CONCLUSIONS

The Earth's motions are characterized by a wobbling of the spin axis of the planet about its figure axis (polar motions), and also by oscillations of the planet's spin axis (nutations). The continual small changes in orientation of the Earth's rotation axis should affect physiology of its inhabitants. The possible effects associated with this are not limited to plants and fungi. The processes in which the planetary movements and, accordingly, the planetary mechanism could influence the organism, can also be important for animals that could use this mechanism in their specific structures, which differ from those of plants. In animal organisms, the threshold of possible sensitivity to continuous changes in the orientation of the Earth's axis must be evolutionarily adjusted not to interfere with the normal behavior. Planetary mechanism could influence their development, biorhythms, and other activities, and this actually gives rise to a new field of research, but analysis of the corresponding research direction is beyond the scope of the present communication.

Plant gravitropism has been under investigation for more than 200 years, but this old and basic biological problem remained not fully understood [21, 52]. The article formulates the idea according to which statocytes, sensitive cells of plants, use changes in orientation of the Earth's rotational axis to trigger gravitropism. With the help of statoliths and planetary mechanism, the plant gets the opportunity to use the energy of the planet movements to generate a signal that initiates the perception of orientation. The use of planetary mechanism by plants allows them to bypass the problem of detecting a weak signal against the background of such interferences as Brownian motion and turgor. Without the sequence of events mediated by the planetary mechanism, realization of the plant gravitropism would have been impossible. Can the proposed concept lead to practical benefits in plant cultivation, or will it serve only to expand basic biological knowledge? The future will answer this question.

Ethics declarations. The author declares no conflicts of interest in financial or any other sphere. This article does not contain any studies with human participants or animals performed by the author.

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