Planta (1997) 203: S63–S68

Planta

Plastids and gravitropic sensing

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Received: 27 June 1996 / Accepted: 3 December 1996

Abstract. Data and theories about the identity of the mass that acts in gravitropic sensing are reviewed. Gravity sensing may have evolved several times in plants and algae in processes such as gravitropism of organs and tip-growing cells, gravimorphism, gravitaxis, and the regulation of cytoplasmic streaming in internodal cells of *Chara*. In the latter and in gravitaxis, the mass of the entire cell may function in sensing. But *gravitropic* sensing appears to rely upon the mass of amyloplasts that sediment since (i) the location of cells with sedimentation is highly regulated, (ii) such cells contain other morphological specializations favoring sedimentation, (iii) sedimentation always correlates with gravitropic competence in wild-type plants, (iv) magnetophoretic movement of rootcap amyloplasts mimics gravitropism, and (v) starchless and intermediate starch mutants show reduced gravitropic sensitivity. The simplest interpretation of these data is that gravitropic sensing is plastid-based.

Key words: Gravitropism – Amyloplast – Sedimentation – Gravity sensing – Starch

Introduction

How plants sense gravity is a central question in biology since so much of the world's biomass is oriented with respect to gravity and since the mechanism by which plants do so is still not explained. The classical statolith hypothesis is that dense organelles that sediment, usually amyloplasts, trigger gravitropic sensing (Haberlandt 1900). While revision of this hypothesis is now required, much evidence still supports the idea that amyloplasts function as statoliths (Sack 1991; Poff et al. 1994). Although this idea remains hypothetical in that the actual mechanisms are not known, it is the contention of this review that the mass that functions in gravitropic sensing is most likely to be that of specific plastids. Also discussed is the hypothesis that the mass of the entire cell functions in gravity sensing in cytoplasmic streaming, gravitaxis and in gravitropism.

Several types of gravity sensing probably exist

Plants and algae respond to gravity in many different ways. Gravitropism in organs, such as shoots and roots, is fundamentally different from that in unicellular tip-growing systems such as rhizoids and protonemata (Sievers et al. 1996). Gravity also has many effects on plants and algae in addition to gravitropism, such as reaction-wood formation, development (gravimorphism), cytoplasmic streaming, and gravitaxis. Each of these processes probably involves some specialized form of gravity sensing (Sack 1991).

This is not a trivial or semantic point. If one were asked to explain how light is "sensed" by plants, one might answer that there are several pigments and numerous processes affected by light. Plant physiologists would consider it absurd to describe a *single* mechanism of light sensing. Similarly, it is likely that plants and algae have at least several different mechanisms of gravity sensing, especially since gravity has been such a major and invariant selection pressure throughout plant evolution (Barlow 1995).

This diversity need not imply that gravitropic sensing itself evolved multiple times in higher plants, e.g. in roots vs. shoots. But it is a reasonable possibility that gravitropic sensing in tip-growing cells of algae and in mosses evolved separately from organ gravitropism in plants, as did gravitactic sensing in protists and the control of streaming polarity in algae. Gravimorphic sensing, like gravitropic sensing might be plastid-based (Takahashi 1997, this issue), but much more information is needed in this area.

This review is dedicated to Professor Andreas Sievers for his major and longstanding contributions to our understanding of how plants sense gravity

g-sensing may be overbuilt

Some *g*-sensing systems function at thresholds lower than the unit *g*-level present during their evolution. Spaceflight experiments using the microgravity environment in conjunction with lateral centrifugation have shown that fractional *g*-forces can be sensed. For example, oat coleoptiles can respond gravitropically to 0.1 *g* (Brown et al. 1995). Thus, the gravitropic sensing apparatus could be said to be "overbuilt", i.e. it is constructed to detect *g* levels that the plant normally does not encounter.

But do stimulations lower than 1 *g* produce a noisier response? While *Euglena* orients gravitactically (achieve a particular level in a vertical column) to levels as low as 0.16 *g*, the response is much more variable than at 1 *g* (Häder et al. 1995). But at 0.64 *g* the precision is comparable to 1 *g* indicating that this system is "overbuilt" in integrating signal-to-noise as well as in being able to respond at all to fractional *g* levels. It would be valuable to determine whether gravitropic precision saturates at sub-*g* doses as has been shown for gravitaxis.

Cell mass may be used in gravity sensing for streaming and gravitaxis

Sedimentation of internal organelles appears to be absent from most gravitactic cells and from the internodal cells of *Chara* (Wayne et al. 1990; Machemer and Bräucker 1992). Instead, in both systems the mass of the entire cell has been implicated in gravity sensing.

In *Chara* internodal cells, the polarity of cytoplasmic streaming appears to be influenced by gravity (Wayne et al. 1990; Staves 1997, this issue). The failure of some methods to reveal this polarity (Ackers et al. 1994) has been explained by the need to measure the specific focal planes in the cell with the fastest rates of streaming (Staves et al. 1995). Since the polarity of streaming in vertical cells reverses when the density of the medium is artificially raised to exceed the density of the cell, Wayne et al. (1990) hypothesized that the mass of the cell functions in gravity sensing. Tension at the top of the cell and compression at the bottom are thought to act via "integrin-like" molecules in the plasma membrane to regulate calcium uptake differentially and thus influence the polarity of streaming (Staves et al. 1995).

Polar regulation of streaming seems to prevent a gravity-induced accumulation of cytoplasm in the bottom of the cell by increasing the thickness of upward-streaming cytoplasm (Staves et al. 1995). It is not clear whether the effect of gravity on streaming has any other consequences for internodal cells, e.g. whether this effect contributes to the negative gravitropism of the *Chara* "shoot" ("Sprossteil": Schröder 1904). Interestingly, other cells of *Chara* with well-documented gravitropism, such as rhizoids and protonemata, do have probable statoliths that are barium sulfate vesicles that sediment (Sievers et al. 1996). Thus the same organism seems to have two different methods of gravity sensing for two different processes, gravitropism and polar streaming.

In gravitaxis, when the density of the medium exceeds that of the *Euglena* cell, the direction of gravitaxis reverses (Lebert and Häder 1996; Häder and Hemmersbach 1997, this issue). These data, along with theoretical calculations (Machemer and Bräucker 1992) suggest that the mass of the cell itself, rather than an intracellular statolith, functions in gravitactic sensing in *Euglena*.

But at least for some other protists, gravitaxis is hypothesized to be statolith-based (Fenchel and Finlay 1986). The ciliates *Loxodes* and *Remanella* have dense, intracellular Müller vesicles that contain barium or strontium. These bodies are positioned by gravity and have specialized connections to the cytoskeleton and to the motile apparatus. Thus two different methods of gravity sensing may exist for the same process (gravitaxis) in different organisms.

These data reinforce the idea that there are several different types of gravity sensing. And data supporting the possibility of the cell mass functioning in at least some types of gravity sensing are novel and merit more intensive study.

The location of cells containing sedimentation is highly regulated

In contrast to the *Chara* internode or gravitactic *Euglena*, gravitropic organs contain amyloplasts that sediment. This sedimentation is found only in cells in specific locations at distinct developmental stages, i.e. when and where sedimentation occurs is precisely regulated (Sack 1991). In stems, amyloplast sedimentation occurs in the endodermis primarily in elongating regions (Sack 1987). In roots, amyloplast sedimentation only occurs in the central (columella) cells of the root cap; as these cells mature into peripheral cap cells, the amyloplasts no longer sediment (Fig. 1; Sack and Kiss 1989; Sievers and Braun 1996). The roots of *Equisetum* and *Limnobium* are exceptional in that sedimentation also occurs in the elongation zone, but again, sedimentation only takes place in cells of a specific stage and location (Ridge and Sack 1992; Sack et al. 1994).

In gravitropic tip-growing cells, sedimentation occurs in a specific part of the cell. In moss protonemata, most amyloplast sedimentation takes place in a subapical zone even though amyloplasts are distributed throughout the length of the cell (Sack et al. 1997). In *Chara* rhizoids and protonemata, the sedimentation of barium sulfate vesicles also occurs in a specific zone which is the sole location of this organelle in the cell (Sievers et al. 1996).

The nucleus is the only other organelle that is known to sediment in gravitropic organs. In those few cases where the nucleus sediments, it does so in cells which also show amyloplast sedimentation (Sack 1991; Ridge and Sack 1992; Sack et al. 1994). More often, nuclear position is regulated so that it is at the top of root cap cells containing sedimentable amyloplasts (see below).

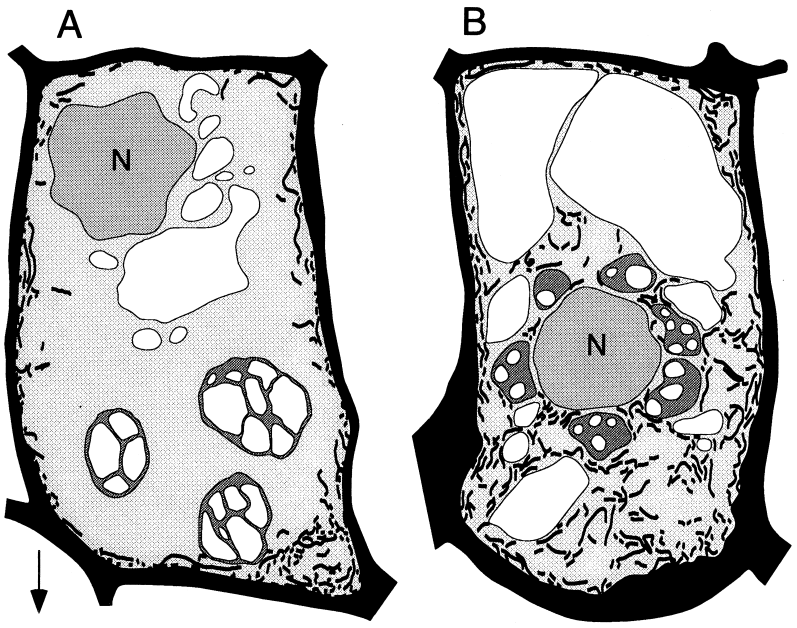

Fig. 1A,B. Diagram showing the cytology of a columella cell (**A**) and a peripheral root cap cell (**B**) based upon tracings of electron micrographs from *Arabidopsis* (Sack and Kiss 1989). In the columella, the ER (*black lines*) is peripheral, the nucleus (*N*) is proximal, and the amyloplasts are filled with starch (*white regions surrounded by darker gray*). These features favor unobstructed amyloplast sedimentation. When a columella cell subsequently differentiates into a peripheral cap cell, the ER becomes distributed throughout the cell, the nucleus moves to the center, the starch is mobilized, and the plastids cluster around the nucleus. The bottom walls (*thick black regions*) of the peripheral cell are thick due to the accumulation of mucilage. Vacuoles are represented by *white regions surrounded by thin black lines*. Other organelles are omitted to emphasize the features shown. The *arrow* (lower left) shows the gravity vector. × 3800

Clearly, the tight developmental and spatial regulation of where sedimentation occurs implies that such cells are specialized in function as well as in structure.

Columella cells contain other adaptations favoring sedimentation

Rootcap columella cells have several cytological features in addition to the presence of sedimented amyloplasts that indicate that they are highly specialized (Sack and Kiss 1989; Sack 1991; Sievers and Braun 1996; Perbal et al. 1997, this issue). These features can all be interpreted as adaptations that favor amyloplast sedimentation. As mentioned, often nuclear position is maintained at the proximal end of the cell (top of cell in vertical roots; Fig. 1). Also, the endoplasmic reticulum (ER) is largely peripheral in location (Figs. 1–2) and often more abundant in the distal end of the cell. The cell is not filled with amyloplasts since their number is restricted, and they are not as large as in storage organs such as a potato tuber. All these features, including plastid sedimentation, are lost when columella cells mature into peripheral cap cells (Fig. 1).

Collectively these features of columella cells allow amyloplasts to sediment relatively unimpeded by other organelles. There are enough amyloplasts to provide orientational information, but not so many as to block access to possible receptors such as in the peripheral ER. If sensing were triggered by amyloplast contact with ER, then the distal accumulation of ER provides more sensitive surfaces where sedimentation usually occurs.

Thus, columella cells are not only the sole site of sedimentation in roots, but also contain a unique and highly specialized cytology that favors amyloplast sedimentation and that presumably functions in gravitropic sensing.

Amyloplast sedimentation correlates with gravitropic competence

The many correlations between amyloplast sedimentation and gravitropism have been extensively documented and discussed (Sack 1991). In short, there is no wild-type gravitropic cell or organ known which lacks amyloplast (or barium sulfate vesicle) sedimentation. Similarly, when starch is depleted through experimental manipulation, gravitropism is eliminated or severely reduced (Sack 1991). The effect of starch depletion through mutation is discussed in the next section. A correlation for gravitropic tip-growing cells (rhizoids of *Chara* and protonemata of the moss *Ceratodon*) is that the recovery of gravitropism after basipetal centrifugation coincides with the return of organelle sedimentation (Sievers et al. 1996; Braun 1997, this issue; Sack et al. 1997).

Recently Kuznetsov and Hasenstein (1996) provided additional correlational evidence for the importance of amyloplast mass in higher-plant roots. High-gradient magnetic fields (HGMF) induce a magnetophoretic force which repels amyloplasts due to the difference in the diamagnetic susceptibilities of starch and the cytoplasm. Application of such a field across rootcaps caused both amyloplast displacement (magnetophoresis) and curvature of *Linum* and wild-type *Arabidopsis* roots away from the denser magnetic field. Significantly, starchless (TC7) *Arabidopsis* roots did not curve away from the HGMF, showing that the field was acting solely on the diamagnetic starch. The specific displacing of columella amyloplasts by magnetophoresis thus appears to mimic gravitropism. These data provide yet another line of evidence supporting the starch-statolith hypothesis.

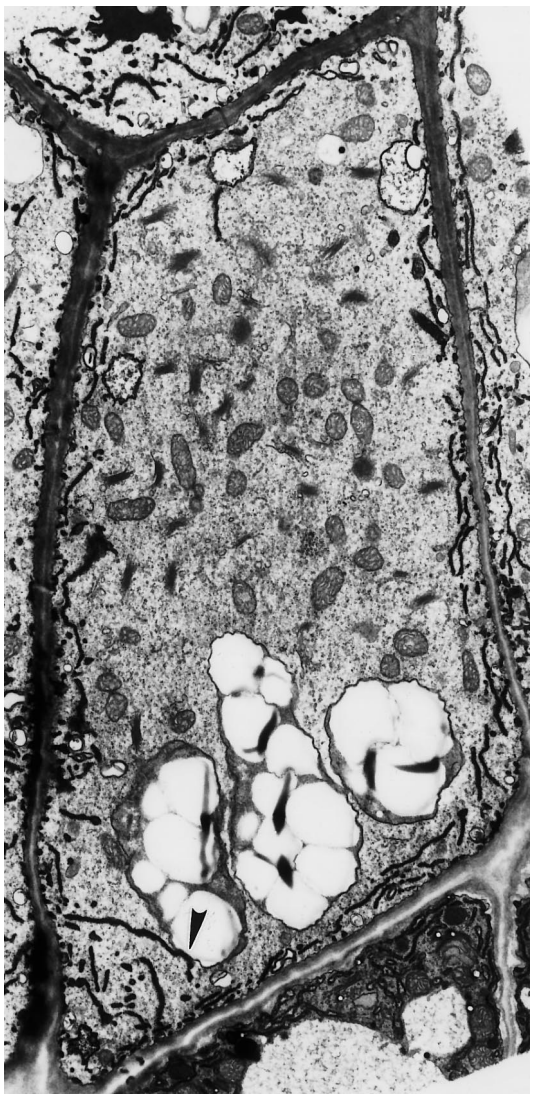

Fig. 2. Electron micrograph of columella cell of *Arabidopsis*. The ER is impregnated with osmium ferricyanide (Sack and Kiss 1989) and is black. Almost all the ER is located in the cell cortex rather than in the cell interior. Note the contact (*arrowhead*) between a sedimented amyloplast and ER. The nucleus is out of the plane of the section. × 6100

Starchless and starch-deficient mutants have reduced gravitropic sensitivity

Two starchless mutants (TC7 and ACG 21) of *Arabidopsis* have been tested for gravitropic sensitivity (Caspar and Pickard 1989; Kiss et al. 1989, 1996). These allelic mutants were isolated independently by ethyl methanesulfonate (EMS) and T-DNA insertional mutagenesis respectively, and are defective in plastidic phosphoglucomutase (*pgm*). Strikingly, the roots of both mutants are gravitropic. However, their gravitropism is substantially reduced as measured by all parameters. Thus, mutant sensitivity is significantly decreased when root responses to threshold doses (short periods of reorientation) are determined. But also, the long-term responses of mutant roots are much noisier than wild-type roots; mutant roots grown for an extended period in one orientation are further from the vertical and have a much greater standard deviation than wild-type roots.

Three other mutants with varying degrees of starch have also been analyzed (Kiss and Sack 1989; Kiss et al. 1996). The NS 458 mutant of *Nicotiana sylvestris* is almost starchless, while the ACG 27 and 20 mutants of *Arabidopsis* have about 60% and 51%, respectively, of the starch in wild-type root caps. All three mutants show varying degrees of depressed gravitropism. The sensitivity of both *Arabidopsis* intermediate starch mutants is closer to the wild-type than to the starchless mutant, and ACG 27, which has slightly more starch, is closer to the wild-type than ACG 20.

In a preliminary report, Poff and Bullen (1992) argued that gravitropism is reduced and starch is absent in TC7 due to two separate, but closely linked mutations. However, as mentioned, other independently isolated starchless (ACG 21) or almost starchless (NS 458) mutants also show depressed gravitropism (Kiss and Sack 1989; Kiss et al. 1996). Thus it is very likely that the reduced gravitropism in starch-deficient plants is primarily attributable to the starch phenotype rather than to second mutations.

All starchless and starch-deficient mutants tested have reduced sensing in response to both threshold and long-term stimulations. These reductions are probably not related to alterations in carbohydrate metabolism (Caspar 1994) that might affect, for example, differential growth, since growth rates are normal and mutant roots show a much noisier response even to long-term stimulations. Thus the reduced gravitropism in these mutants probably reflects reduced sensing rather than secondary effects. This leads to the conclusion that starch plays a role in sensing when present and that starch is necessary for full gravitropic sensitivity.

However, it is significant that some gravitropic sensing can occur without starch and thus that starch is not absolutely required for sensing. This residual gravitropism could be explained if sensing were plastid-based (see below).

Does gravitropic sensing utilize the mass of the entire cell?

It has been argued that the mass of the starch in columella cells contributes to gravitropic sensing by increasing the weight of the cell, rather by functioning as statoliths that act upon an intracellular receptor (Fig. 3; Wayne et al. 1990). The hypothesis that gravitropic sensing relies upon cell mass, is based, in part, upon extrapolation from published data on gravitaxis and streaming (Wayne et al. 1990; Pickard and Ding 1992; Konings 1995). These data derive from cells that are up to a million times larger than columella cells. Wayne et al. (1990) calculated that a columella cell has enough mass to trigger stretch-sensitive channels since the starch provides "ballast" that makes the cell heavier so that sensing can occur at or outside the plasma membrane.

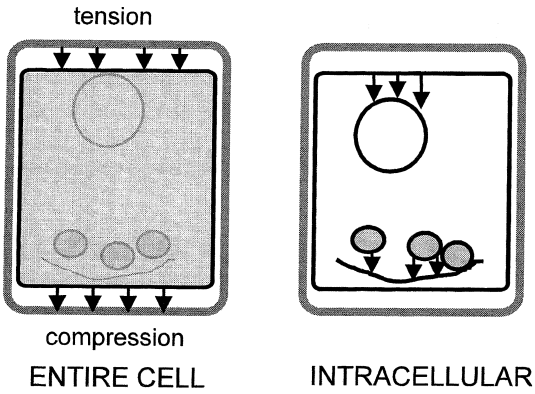

Fig. 3. Diagram of hypotheses about the mass that acts in gravitropic sensing. The *left-hand figure* illustrates the model of Wayne et al. (1990) where the mass of the entire columella cell provides a signal in the form of compression at the bottom of the cell and/or tension at the top (*arrows*). In this model, the sedimented amyloplasts provide "ballast" and only function by adding to the weight of the cell overall. The *right-hand figure* illustrates hypotheses about how an intracellular mass might function in gravitropic sensing. An organelle (here shown as a nucleus, *large circle at top of cell*) could exert tension on a receptor in the plasma membrane via the cytoskeleton (*top arrows*) or plastids (here shown as sedimented amyloplasts) might compress endoplasmic reticulum (one version of the starch statolith hypothesis)

But Björkman (1992) calculated that differences in the tension of the plasma membrane between the top and the bottom of a columella cell would not be high enough to differentially regulate channel activity. And if starch were functioning solely as ballast, selection pressures should have favored the evolution of large cells filled with amyloplasts and starch, instead of columella cells which have fewer amyloplasts and cytological specializations favoring sedimentation. The magnetophoresis data discussed above also argue that it is the amyloplast and not the cell mass that is critical for sensing since curvature was triggered by amyloplast repositioning to the side wall, whereas the cell mass acted on the bottom wall since the roots were vertical (Kuznetsov and Hasenstein 1996).

Cell mass may function in gravity sensing in streaming and in gravitaxis, but there are few direct data for this role in gravitropism (see preliminary data in Staves et al. 1991). Thus, claims for a role for cell mass in gravitropic sensing rest largely on theoretical grounds whereas, in contrast, there is a substantial body of data consistent with the idea that gravitropic sensing is plastid-based.

Plastid-based gravitropic sensing

It is likely that, during evolution, starch-filled plastids acquired a role in gravitropic sensing and became a "susceptor", the mass that gravity acts on in sensing. This probably occurred in concert with the evolution of a "receptor", a structure which converts the orientational signal from the susceptor into a meaningful physiological output (Sack 1991). Presumably, the evolution of a susceptor-receptor pair increased the signal-to-noise ratio so as to allow efficient sensing that upon further specialization became overbuilt, i.e. sensitive to g levels less than 1. If so, this could explain the finding that a mutant (ACG 27) with 60% of the starch of the wild type has almost the same degree of sensitivity as the wild type (Kiss et al. 1996). It could also explain why starchless mutants can still sense gravity, although more poorly than the wild type. A receptor capable of specifically detecting plastid mass might still obtain enough signal from a starchless plastid to produce a response, but this response would be noisier than if a heavier, starch-filled plastid were present. This reasoning supports the hypothesis that only one mass acts in gravitropic sensing, that of plastids. But it cannot be ruled out that a second unidentified mass also functions in gravitropic sensing in addition to (not instead of) that of plastids.

The nature of the receptor that interacts with plastids is unclear. The possibility that the cytoskeleton mediates gravitropic sensing is reviewed in Sievers et al. (1991), and in Sievers and Braun (1996). An alternate receptor could be the endoplasmic reticulum (Fig. 3). Sedimented amyloplasts do not appear to contact the plasma membrane, but do contact endoplasmic reticulum, contacts which can be visualized when special staining protocols for the ER are employed (Figs. 1–2; Sack and Kiss 1989; Fig. 3B in Satiat-Jeunemaitre et al. 1996). As mentioned, the unique presence of distally enriched ER in columella cells could constitute an adaptation which both presents a high concentration of receptors to sedimenting amyloplasts and could be a signal amplification mechanism (Sack 1991).

Since gravitropism may have evolved several times in parallel, such as in organs vs. in tip-growing cells, there may be different receptors in different systems, just as there appears to be a unique susceptor (barium sulfate vesicles) in *Chara* gravitropism. Similarly, there may be other types of susceptors and receptors in other forms of gravity sensing. This diversity suggests that studies in this area should be broad-based and hints at the range of sensory transduction systems yet to be revealed.

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