

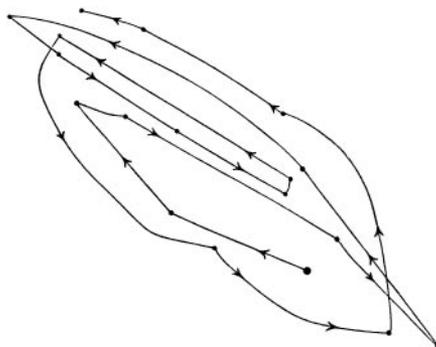
# Up, down, and all around: How plants sense and respond to environmental stimuli

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Although plants are essentially sessile in nature, these organisms are very much in tune with their environment and are capable of a variety of movements. This may come as a surprise to many non-botanists, but not to Charles Darwin, who had a strong interest in plant biology during his multifaceted career. Although it is one of his lesser known works, Charles Darwin, along with his son Francis, published a fascinating book in 1880 entitled *The Power of Movement in Plants* (1). The Darwins studied in great detail the two broad categories of plant movements: the tropisms (directed growth in response to external stimuli) and nastic movements (movements in response to stimuli, but the direction is independent relative to the stimulus source). Examples of tropisms include gravitropism, directed growth in response to gravity (2), and phototropism, growth in response to light (3). Nastic movements include the dramatic leaf movements of the Venus flytrap after a touch stimulus and the less dramatic (but more ubiquitous) “sleep movements,” in which the leaves of some plants (e.g., bean plants) move to a different position at night. The Darwins also studied oscillatory movements (also termed circumnutation; Fig. 1), in which plants rotate around a central axis during their growth. Almost all plant parts exhibit this movement, but vines show an exaggerated circumnutation (4, 5). To date, it is unclear whether these oscillatory movements are an endogenous nastic movement or whether they are coupled to and depend on gravitropism. Although the Darwins (1) were among the first to address these issues, they have been most recently considered by Kitazawa and coworkers (6) in a recent issue of PNAS.

The initial observations by this group (6) published in a previous paper (7) suggested that there was a link between circumnutation and gravitropism because an agravitropic mutant of the Japanese morning glory (*Pharbitis nil*) also was defective in circumnutation. The 2003 paper also reported on a series of gravitropic mutants in the plant *Arabidopsis thaliana*. Those mutants were deficient in the early steps of gravitropism because they had defects in their statocytes, or gravity-perceiving



**Fig. 1.** Drawing from *The Power of Movement in Plants* (1) that illustrates the oscillatory movements (i.e., circumnutation) of the shoot of a young seedling of *Brassica*. The experiment was performed over a period of 10 h and 45 min, and tracings were of the shoot tip as viewed from above.

cells. In roots, the gravity-perceiving statocytes are located in the central columella cells of the root cap, whereas in stems, these statocytes are found in a layer of cells adjacent to the vascular tissue and are termed endodermal cells (Fig. 2). Both columella and endodermal cells have dense amyloplasts (i.e., starch-filled plastids), called statoliths,

## The *SCR* gene regulates circumnutation and gravitropism in *Arabidopsis* and morning glory.

that move in response to gravity (8). Hatakeda *et al.* (7) found that a starchless mutant (thus, with small statoliths) of *Arabidopsis* that had reduced gravitropism also exhibited a decreased circumnutation. Additionally, another *Arabidopsis* mutant (*scr* for scarecrow) lacking an endodermis that was agravitropic in stems had an even more severe lack of circumnutation. [A bit of background: the *SCR* gene belongs to a gene family that encodes putative transcription factors required for asymmetric cell divisions that are essential for endodermal differentiation in roots and shoots (9).] Thus, these results do not

support the hypothesis originally proposed by Darwin and Darwin (1) that circumnutation had an internal driving force and regulating apparatus but add support to the idea that oscillatory movements in plants are directly coupled to gravity sensing.

The present study reported in PNAS (6) builds on the previous 2003 paper (7) in several interesting ways. The hypothesis that the *SCR* protein in morning glory is necessary for the differentiation of the endodermis and gravity responses in stems was supported by complementation tests for *P. nil* *Scr* (PnSCR) using the *scr* mutant of *Arabidopsis*. They also found that mutation of PnSCR causes abnormal shoot circumnutation by studying gravitropism in wild-type morning glory, a morning glory *scr* mutant, and a transgenic *Arabidopsis* line with the mutant *scr* gene. In addition, other *Arabidopsis* mutants that have the endodermis but with abnormal statolith movement (e.g., *sgr2* and *zig/sgr4*; ref. 10) were defective in the oscillatory movements. The results of these studies and the various control experiments clearly demonstrate that the *SCR* gene regulates both circumnutation and gravitropism in both *Arabidopsis* and morning glory, thus clearly linking these two processes.

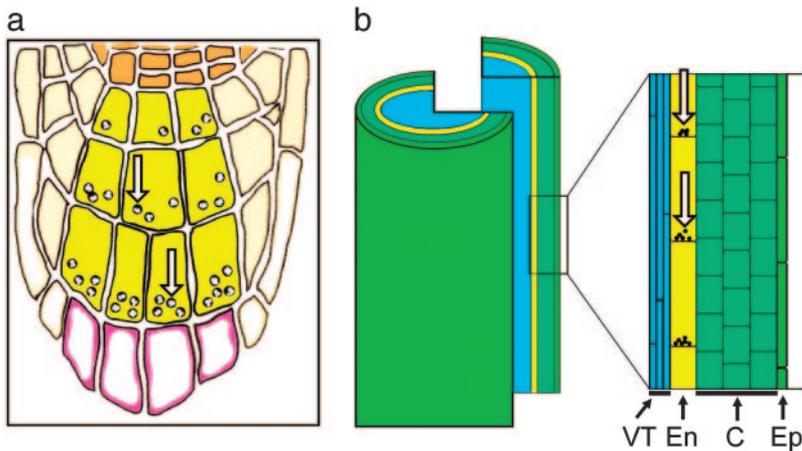
So it seems that the Darwins (1) may not have been right on this issue. However, the results of some experiments (11) on the space shuttle Columbia would no doubt have heartened Charles Darwin. Sunflower seedlings were used in these experiments because these plants exhibit a vigorous circumnutation (see Movie 1, which is published as supporting information on the PNAS web site). Brown and coworkers (11) studied 4-day-old seedlings in microgravity and found that 93% of these plants circumnated compared with 100% of the ground control. The circumnutation of the spaceflight seedlings had a reduced amplitude and period compared with the ground plants. Nevertheless, the spaceflight study seemed to be definitive

Conflict of interest statement: No conflicts declared.

See companion article on page 18742 in issue 51 of volume 102.

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**Fig. 2.** Diagram of a root (a) and stem (b) of *Arabidopsis* to illustrate the regions of gravity perception. (a) Within the root cap at the apex, some cells develop into the gravity-sensing columella cells (yellow), which are the statocytes. These cells contain amyloplasts (arrows) that function as statoliths and move in response to the direction of the gravity (toward bottom). (b) The stem consists of an epidermal layer (Ep), a cortical zone (C), an endodermal layer (En), and vascular tissue (VT). The endodermal cells (En; yellow) are the statocytes with amyloplasts (arrows) functioning as statoliths. Ref. 6 suggests that the endodermal cells also play an important role in circumnutation.

and provides strong evidence that periodic growth oscillations (i.e., circumnutations) persist in the absence of significant gravitational accelerations. Thus, these results are in conflict with the study reported by Kitazawa *et al.* (6).

How do we reconcile these two reports and two hypotheses about the relationship between gravitropism and circumnutation? One unsatisfying suggestion is

that the differences are caused by plant species differences. Alternatively, Kitazawa and coworkers (6) propose that because in these spaceflight experiments (11, 12) the sunflower seedlings were germinated on the ground, the plants sensed gravity before and during the launch. Thus, the oscillatory movement was established on the ground, and then circumnutation continued at

the reduced amplitude and period reported (11). However, in the space experiments, some of the plants studied developed from seeds planted in orbit by the astronauts. Although their studies do not distinguish the results obtained from plants that first developed on the ground from those plants that were completely grown in microgravity, one must assume that most of these seedlings exhibited circumnutation because 93% of the total plants had these oscillatory movements.

Based on the evidence to date, is there more support for the endogenous model of Darwin and Darwin (1) or the hypothesis that suggests that circumnutation depends on gravitropism most recently advocated by Kitazawa *et al.* (6)? Clearly, there is strong support for the latter hypothesis provided for by the elegant study with multiple molecular approaches outlined in ref. 6 and the previous studies from this group that used more structural methods (7). As a space biologist, I hope there will be opportunities to confirm and extend these experiments by using the microgravity environment aboard orbiting spacecraft as a unique research tool (13).

Maria Palmieri and Richard E. Edelman assisted in the preparation of the figures. I thank Roger P. Hangarter for providing Movie 1 and Richard C. Moore and Jack L. Mullen for helpful comments on the manuscript.

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