

## 3 Ultradian Growth Oscillations in Organs: Physiological Signal or Noise?

TOBIAS I. BASKIN

### Abstract

This review examines ultradian oscillatory growth in the multicellular organs of higher plants. My objective is to derive insight about the underlying physiological processes powering expansion. If the process of diffuse growth is inherently oscillatory, then it is reasonable to expect entrainment of these cellular oscillators across a tissue and the emergence of coherent macroscopic growth oscillations. After reviewing studies of circumnutation and linear growth, it appears that such entrainment is rare or weak. I argue that rather than reflecting the existence of an inherent oscillation in the process of diffuse growth, ultradian movements of plant organs reflect successive responses to mechanical perturbation.

### 3.1 Introduction

#### 3.1.1 Oscillations as Window into Growth

A growing plant organ comprises thousands of cells. These cells have different shapes, sizes, and states of differentiation. Despite this, the growth of plant organs is coherent, meaning that each cell grows essentially as its neighbor does. How is such uniformity of growth achieved? The cell wall provides a mechanical framework that can constrain the expansion behavior of individual cells by virtue of its continuity. However, cells are able to exert a considerable control over their growth locally, as seen in bulliform cells, trichomes root hairs, and even tropic bending. A common, limiting cell wall is presumably not enough to synchronize growth among a thousand neighboring cells.

An answer is offered theoretically by oscillations. Oscillatory behavior commonly characterizes complex, cellular processes, such as glycolysis or division (Goldbeter 1996). Expansion of a cell is also a complex cellular

---

Biology Department, University of Massachusetts, Amherst, MA 01003, USA, e-mail: Baskin@bio.umass.edu

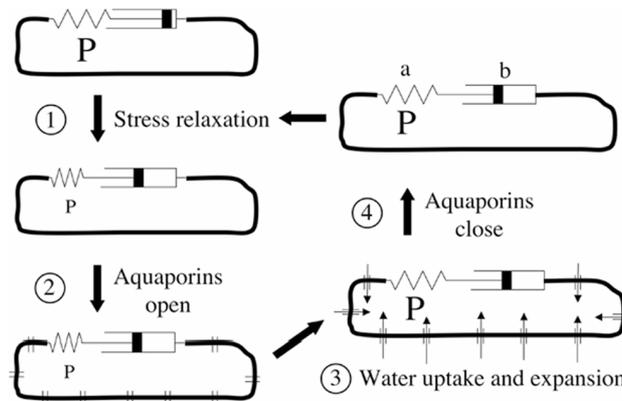
---

S. Mancuso and S. Shabala (Eds.)  
Rhythms in Plants: Phenomenology, Mechanisms, and Adaptive Significance  
© Springer-Verlag Berlin Heidelberg 2007

---

process, comprising steps that could be linked with delayed feedback, a condition for the emergence of a stable oscillation. These steps include water uptake, secretion, incorporation of material into the cell wall, and irreversible (i.e., plastic) as well as reversible (i.e., elastic) deformation of cell wall structure. As an illustration of how expansion could be oscillatory, suppose water uptake were linked to turgor loss, such that aquaporins would open once irreversible (plastic) deformation of the cell wall had decreased turgor sufficiently; the influx of water would raise turgor and hence close the water channels, not to open again until continued plastic deformation had again decreased turgor sufficiently (Fig. 3.1). This hypothetical loop illustrates feedback between steps in the growth process, and many other such loops could be imagined. To the extent that the feedback is delayed, an oscillation becomes stable. When neighboring, individual oscillators share input or output, they are easily synchronized (Goldbeter 1996). Cells of a growing organ have common cell walls and share water; therefore, it is plausible that an organ synchronizes cellular growth oscillations.

This review will examine oscillatory growth behavior. My objective is to derive insight about the underlying physiological processes powering expansion. I will not treat oscillations that are circadian because these are likely to be linked to diurnal rhythms of whole-plant performance, rather than to



**Fig. 3.1** Hypothetical model of diffuse growth giving rise to oscillatory expansion. For a single cell, the mechanical behavior of the cell wall is idealized by an elastic element (*spring*; *a*) and a plastic element (*dash-pot*; *b*) in series. Turgor pressure (*P*) is held by the deformation of the elastic element. Step 1: the elastic element contracts, doing work against the plastic element. This lowers turgor. Step 2: the cell senses lowered turgor and opens water channels (aquaporins). Step 3: the open water channels allow water to move into the cell down the water potential gradient. This rapid water entry stretches the elastic element, thus enlarging the cell's volume and restoring turgor. Step 4: the cell senses restored turgor and closes the aquaporins. The cell then undergoes stress relaxation and the cycle repeats. In a tissue, cell walls are shared and water supply is channeled; therefore, such an oscillation, in principle, could become synchronous over the tissue



growth itself. Also, I will not treat growth oscillations in single cells (the interested reader may consult the review in this volume by Moreno et al., Chap. 2), even though my objective is exemplified beautifully by Castle (1940) who detected an oscillation in the rotary movement of a single-celled, fungal sporangiophore, and argued from the oscillation's amplitude that expansion depends on the discrete insertion into the cell wall of a 7-nanometer brick every 200 milliseconds.

### 3.1.2 Growth Versus Movement

Unfortunately, the word *growth* is used in two distinct ways. On one hand, the length of an entire organ may be measured over time and its rate of increase called a *growth rate*; an equivalent rate is obtained by measuring the position over time of the tip of the organ. On the other hand, a growth rate can refer to relative expansion, often reaching to the level of a single cell, or indeed to the elemental deformation of a unit area of cell wall. The latter is the output of the growth mechanism whereas tip displacement integrates the expansion of the entire growth zone, often many centimeters long and containing cells at different developmental stages. Therefore, the length of an organ, or the position of its tip over time, provides limited information about cellular machinery. For clarity, I will refer to the rate of displacement of an organ tip as a *velocity*, characterizing data of that kind as referring to movement; in contrast, I will use *growth* to denote relative expansion, preferably close to, if not actually on, the cellular scale. Oscillations in movement can provide insight into growth mechanisms, but care must be taken because movement reflects cellular expansion indirectly.

## 3.2 Circumnutation: Growing Around in Circles?

If oscillatory growth behavior among individual cells is entrained, then organs should be characterized by macroscopic growth oscillations. This is believed to be true because it is assumed, first, that the stems and roots of essentially all plants undergo oscillatory movements called circumnutation and, second, that circumnutation is a coherent growth oscillation. Both of these assumptions need to be examined.

The stem tips of some plants undoubtedly move in circles or ellipses with large amplitudes and regular periods for many days (Baillaud 1962). This behavior reflects an obvious circumnutation, clearly adaptive for vines and climbing plants, but happening also in species such as sunflower (*Helianthus annuus*) where synchronization of growth among cells is as good a reason as any other for the behavior. However, the tips of stems and roots of other plants move in erratic trajectories with small amplitude and period far less

regular than that of twining plants (Heathcote and Idle 1965; Spurný et al. 1978; Barlow et al. 1994; Schuster and Engelmann 1997). To claim that all plant organs circumnutate is to assert that the large and regular movements of the French bean (*Phaseolus vulgaris*) stem (Millet and Koukkari 1990) are the same as the tiny and erratic ones of a grass rhizome (Fisher 1964). To be prudent, we should learn more about the mechanism of each type of movement before equating them.

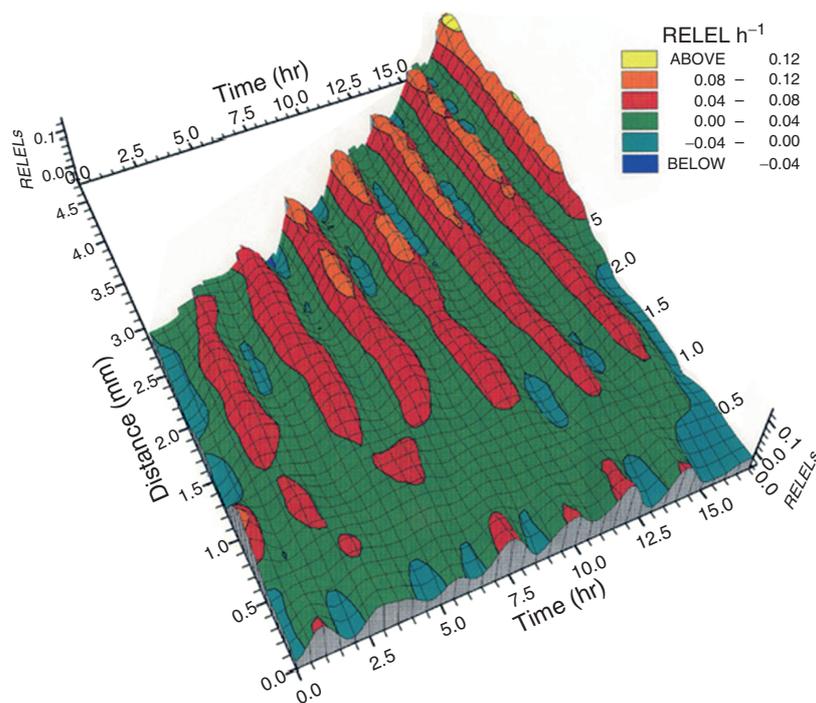
Whether large and regular or small and erratic, circumnutations are widely ascribed to differential growth. But this need not be the case. In many plants, movements of leaves have periods of an hour or two, similar to circumnutations, and are powered by a specialized group of cells, the pulvinus, encircling the petiole at its base: the petiole lifts when adaxial pulvinar cells contract and abaxial cells expand; it lowers when the reverse happens (Satter 1979). The pulvinus moves the leaf by equal increases and decreases in cellular volume on each side, without any net change in volume. Therefore, these leaf movements are reversible and independent of growth.

As if a pulvinus were spread throughout the bending stem, reversible volume changes have been implicated in circumnutations. Pine (*Pinus sylvestris*) hypocotyls continue to circumnutate for a few periods following decapitation and the cessation of net elongation (Spurný 1975). In a tour de force, measurements of the growth of circumnutating French bean stems showed that most of the bending stem enlarges and contracts reversibly, conceptually like a pulvinus (Caré et al. 1998). Consistently, the bending part of the French bean stem undergoes alternating changes in cell length, turgor, ionic composition, and water permeability, reminiscent of those that occur in pulvini (Millet et al. 1988; Badot et al. 1990; Comparot et al. 2000).

That circumnutations can be powered by reversible changes in volume in the manner of a pulvinus has several consequences. For one, it means that a supposed universal habit of plants to circumnutate cannot be taken to imply an equally universal tendency to growth oscillations. In addition, a major topic of research on circumnutations has been to determine to what extent this movement can be explained by gravitropism. This explanation, formulated into an explicit model 40 years ago (Israelsson and Johnsson 1967), is that a stem responds gravitropically, overshoots its target angle, bends again, and overshoots again, thus creating an oscillation. Although the occurrence of circumnutations in space flight where gravitational force is all but absent has shown that gravitropism is not essential for circumnutations (Brown et al. 1990), the relevance of gravitropic overshoot for the oscillatory movements of stems and roots continues to be debated (Johnsson 1997; Hatakeda et al. 2003). However, gravitropic bending is accepted as being based on differential growth. If so, then those circumnutations powered by a diffuse pulvinus can be, for that reason alone, distinguished from gravitropism mechanistically.

Although circumnutations can involve reversible oscillations in cellular volume, it can also involve growth oscillations. Growth rate oscillations, 180° out of phase on either side of the circumnutating stem, occur in the epicotyl

of Alaska pea (*Pisum sativum*; Baskin 1986) as well as in the sunflower hypocotyl (Berg and Peacock 1992; Fig. 3.2). In both species, the seedling shoot undergoes more or less linear circumnutation, allowing growth to be measured with a single camera. Although Baskin (1986) measured the expansion of 1-cm-long zones and could have missed some contraction, Berg and Peacock (1992) measured 2-mm zones, and found that differential expansion is responsible for most of the bending (Fig. 3.2). Interestingly, these authors did record negative elemental elongation rates; hence, contractions may contribute to the oscillation. While the presence of a large contraction, as seen for the French bean, demonstrates a reversible, non-growth process, even a total absence of contraction cannot exclude a contribution from elastic behavior because reversible as well as irreversible processes are superimposed within the wall (Proseus et al. 1999; Fig. 3.1). Given the difficulty of measuring growth for large-amplitude circumnutation, the relative prevalence of diffuse



**Fig. 3.2** Three-dimensional plot of displacement and elemental elongation versus time for a circumnutating sunflower hypocotyl (modified from Berg and Peacock 1992). The hypocotyl was marked at 2-mm intervals and growth rates recovered from marks digitized at 15-min intervals. Data were interpolated to generate smooth contours. The figure shows one side of the hypocotyl; the other side resembles this but is out of phase by 180°. The peaks of elemental elongation rate occur almost synchronously along the hypocotyl or move rapidly toward the base, and the troughs attain significant negative values (contraction) in the apical part of the organ

pulvini, as in French bean, and out-of-phase growth oscillations, as in pea and sunflower, is likely to remain unknown for a considerable time.

When species with thin roots, such as *Arabidopsis thaliana*, are grown on a surface that is between horizontal and vertical, the root will grow in a sinusoidal pattern that has been attributed to circumnutation ("root waves"; Simmons et al. 1995) and a regular growth oscillation has been presumed. However, in an elegant analysis, Thompson and Holbrook (2004) showed that the undulating pattern represents buckling of the root, and results from gravitropism and friction between the root tip and the substrate. No oscillation in growth is occurring. The tip displacement rate of the root fluctuates erratically. This illustrates how a regular, oscillatory pattern in the shape of the root can be built up without an oscillation in growth rate. Interestingly, the amplitude of root waves varies among rice (*Oryza sativa*) accessions and is correlated with seedling establishment on flooded soil (Inoue et al. 1999), an observation that links the interplay of gravitropism and mechanical responsiveness to successful root penetration. But spiral waves in thin-rooted species cannot be cited in support of the prevalence of growth oscillations.

### 3.3 In Search of Ultradian Growth Oscillations

Under the hypothesis that expansion in plant cells is inherently oscillatory, and hence readily entrained among the many growing cells of an organ, the emergent, master oscillation might most simply be expected to occur symmetrically, rather than as a traveling wave rotating around the circumference. Note that a model for a traveling growth wave has been developed for the lateral movements of maize roots (Shabala and Newman 1997b). Symmetrical entrainment would give rise to oscillations in tip displacement velocity but not to oscillatory lateral movement. I will call these *linear* oscillations, because they are in line with the longitudinal axis of the organ. However, as the symmetry might not be perfect, oscillatory lateral displacements of small amplitude might plausibly indicate synchronized linear oscillations. How prevalent are well-synchronized linear oscillations?

Over the years, the linear displacement of a variety of plant organs, shoots, roots, and leaves has been followed at high resolution and over several hours or even days. Fluctuations are usually but not always reported. According to one of the first botanical applications of position transducers, lupine (*Lupinus perrenis*) stems, intact or excised, grow smoothly (Penny et al. 1974), and high-resolution photographic analysis of elemental elongation of intact, red-light-grown maize coleoptiles failed to find oscillations (Baskin et al. 1985). Nevertheless, fluctuations in growth velocity are common, whether detected with position transducers (e.g., Behringer et al. 1990; Yang et al. 1993) or with optical means that do not involve contact with the organ (Jiang and Staude 1989; Liptay et al. 1995).

In roots, various types of movements have been recorded, almost always with small amplitudes, wandering trajectories, and poorly defined periods, ranging from minutes to hours (Spurný 1966; Spurný et al. 1978; Hasenstein 1991; Barlow et al. 1994; Thompson and Holbrook 2004). In some cases, roots grow with scarcely perceptible lateral deflections (Erickson and Sax 1956; List 1969), whereas in others, lateral position fluctuates with both short (8 min) and long (90 min) periods (Shabala and Newman 1997a; Shabala 2003; Walter et al. 2003). In spatial analyses of maize root growth, the tip displacement velocity (of straight-growing roots) as well as elemental elongation rates throughout the growth zone fluctuate erratically (Erickson and Sax 1956; List 1969; Salamon et al. 1973). More recently, image processing methods have been applied to map the spatial profile of elemental elongation at high resolution, in maize (*Zea mays*; Walter et al. 2002, 2003) and arabidopsis (van der Weele et al. 2003). The zone of rapid elongation in maize is often bimodal, whereas several peaks are seen for arabidopsis, patterns that may indicate a regular oscillation in elongation rate as a cell traverses the growth zone.

In stems, besides the large-amplitude circumnutations discussed above, oscillations in lateral movement are often reported that may be temporally regular but are nevertheless of small amplitude. For example, species of soybean (*Glycine soja* and *G. max*) differ in whether the stem tip executes large- or small-amplitude movements but a similar period is found for each (Adolfson et al. 1998). In contrast, runner bean (*P. multiflorus*) seedling stems wander, with small-amplitude excursions (less than 5 mm) and poorly defined period (Heathcote and Idle 1965). Analysis of small-amplitude movements in the inflorescence stem of arabidopsis has shown that, although modified diurnally in period and amplitude, the movements as such are independent of the main circadian pacemaker: the diurnal modifications quickly disappear when entrained plants are moved into constant conditions (Buda et al. 2003), and arrhythmic mutants circumnutate at a constant and stable period (Dowson-Day and Millar 1999; Niinuma et al. 2005).

In contrast to the lateral movement trajectory, the linear tip velocity of stems usually fluctuates but seldom with long-lived regularity. Oscillations in displacement speed have been detected with periods of 20 to 70 min in the arabidopsis inflorescence stem (Degli Agosti et al. 1997; Jouve et al. 2000), 80 to 120 min in the azuki bean (*Vigna angularis*) stem (Gotô and Chiba 1983), and 60 and 270 min for a maize coleoptile (Liptay et al. 1995) and runner bean stems (Heathcote and Idle 1965), respectively. Oscillations so short they were termed micronutations (12- to 30-min periods) were found in runner bean tendrils, in most but not all individuals (Heathcote 1966), and even faster growth oscillations (3- to 10-min periods) occur in 1-cm-long segments of mung bean (*V. radiata*) hypocotyls (Prat and Parésys 1995; Prat et al. 1996). Both short and long oscillations in stem tip velocity, ranging from 3 to 120 min, have been observed for the seedlings of five species; surprisingly, oscillations could be detected when the position transducer was attached near the base of the hypocotyl, suggesting that elastic oscillations may also occur

(Kristie and Jolliffe 1986). In these examples, although periods are assigned, the records are noisy, and the emergence of a stable period is short lived, if it happens at all.

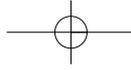
Erratic oscillations in stem tip velocity occur in the stems of red goosefoot (*Chenopodium rubrum*) grown under constant conditions but, under a regular photoperiod, stem velocity oscillates with a 24-h period and the erratic, higher-frequency signals vanish (Ruiz Fernandez and Wagner 1994). In contrast to the dutiful entrainment of *C. rubrum*, 3- to 4-week-old tomato (*Solanum lycopersicum*) stems grown under a photoperiod could behave more erratically: Kerckhoffs et al. (1997) recorded some (albeit not all) stems showing noisy oscillations in velocity superimposed on the regular diurnal changes.

Taken altogether, this survey suggests that highly synchronized growth oscillations, as reported for pea epicotyls (Baskin 1986) and sunflower hypocotyls (Berg and Peacock 1992), may be the exception, rather than the rule. Organs do undergo lateral movements of minor amplitude and have fluctuations in their overall extension rate, but these growth fluctuations seldom have a stable period. Admittedly, better synchrony might be visible were (elemental) growth characterized; however, given the proposed concept of facile entrainment of neighboring oscillators, one expects the entrainment to pervade the growth zone. To my knowledge, there is no example among stems or roots of a linear growth oscillation (i.e., not out of phase on different sides of the stem) demonstrated to have the temporal stability characteristic of circumnutation in twining plants.

### 3.4 The Power of Bending in Plants

Pronounced, ultradian growth oscillations, although not ubiquitous, do occur and require explanation. The well-characterized growth oscillations in pea and sunflower stems take place on opposite sides of the stem, out of phase, and cause the stem to deviate appreciably from vertical. Therefore, these oscillations could be driven by gravitational overshoot. In 1973, Johnsson and Heathcote laid out the evidence pro and con for models of circumnutation based on gravitational overshoot, and concluded that gravitational overshoot was well supported. Since then, experiments in space (Brown et al. 1990) and on Earth (e.g., Hejnowicz and Sievers 1995; Obrović and Poff 1997; Yoshihara and Iino 2005) tend to suggest that circumnutation and gravitropism are separate phenomena, although able to interact.

Recently, however, support of the overshoot model was inferred by finding that circumnutation is suppressed if not eliminated in mutants of arabidopsis and morning glory (*Parbitis nil*) that lack gravitropic responsiveness in the inflorescence or main stem (Hatakeda et al. 2003; Kitazawa et al. 2005). Still, another interpretation is possible. Circumnutation in the inflorescence

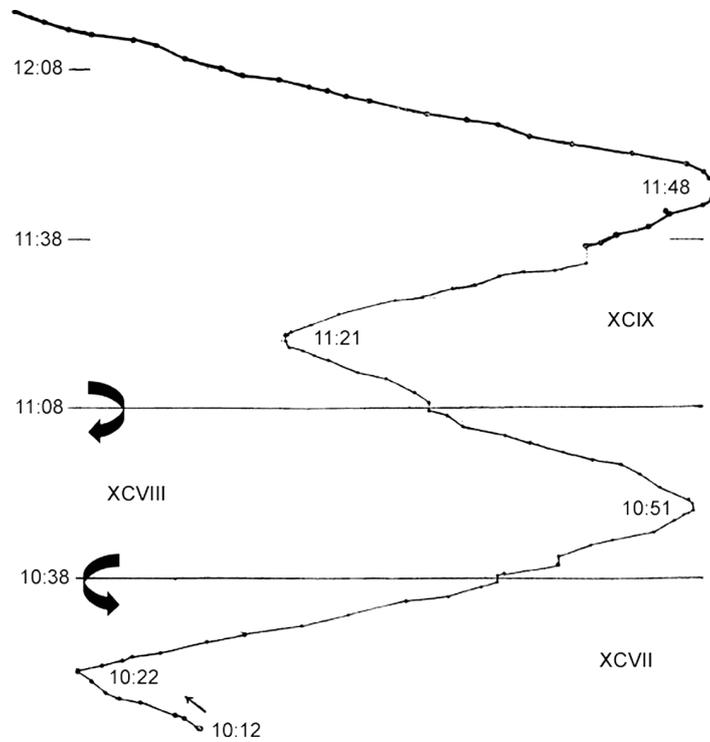


stems of *arabidopsis*, though having a well-defined period, is small in amplitude and hence not likely to generate a significant gravitropic signal (Hatakeda et al. 2003 report wild-type amplitudes of  $\sim 200 \mu\text{m}$ ). Despite lacking the ability to reorient when rotated, these mutant stems nevertheless grow vertically (the morning glory stems eventually fall over and adopt a lazy habit). One would expect random deviations (of the kind that presumably initiate an overshoot cycle) would lead the non-gravitropic stems into a wandering habit. Instead, in the absence of a gravitropic signal, it could be adaptive for the plant to suppress circumnutation. That a plant can respond by suppressing circumnutation has recently been documented for the etiolated rice coleoptile in response to red light (Yoshihara and Iino 2005), and sunflower seedlings grown in space circumnutate with diminished amplitude, and sometimes not at all (Brown et al. 1990). Conceivably, a similar response occurs in morning glory stems and *arabidopsis* inflorescences when gravitational responsiveness has been diminished genetically.

An alternative to oscillations based on gravitational overshoot are oscillations based on mechanical overshoot (Brown 1991; Peacock and Berg 1994). A curving stem has its convex side in compression and its concave side in tension, stresses that could in principle be sensed by the plant. And, just as the response to gravity could overshoot, so too could the response to being bent. Indeed, if an oscillating trajectory is advantageous for a growing organ, then a mechanical overshoot could be deliberate.

Remarkably, a series of experiments in favor of this idea were published over 100 years ago. Francis Darwin and Dorothea Pertz (1892) constructed a clinostat that would rotate a plant by  $180^\circ$  and then stop for a specific interval before making another  $180^\circ$  rotation. The interval between  $180^\circ$  rotations was usually 30 min. They used a horizontal axis of rotation to give opposite gravitropic stimuli, or a vertical axis to give opposite phototropic stimuli. The apparatus ran for many hours, and they noted the position of the stem tip every minute. Not surprisingly, this procedure set up a rhythmic bending, entrained to the alternating rotations, with phase dependent on the lag time for the gravitropic or phototropic response. But very surprisingly, after many rotations, when they deliberately failed to rotate the clinostat, the stems reversed direction anyway, just as if the apparatus had been rotated (Darwin and Pertz 1903; Fig. 3.3). In some cases, the stems reversed a second time, again just as if the alternating stimuli had continued. These results cannot be explained by gravitropic (nor phototropic) overshoot because stopping the clinostat rhythm led to the stems bending down (or away from the light); instead, it suggests that the stems were responding to the alternating mechanical flexure.

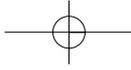
We are far more advanced in our understanding of how plants respond to light or gravity than to their mechanical status, but this status is arguably crucial to the plant. Consistent with out-of-phase growth oscillations being a response to stress in the bent region, in the circumnutating sunflower stem, growth along the entire side increases and decreases nearly synchronously (Berg and Peacock 1992; Fig. 3.2). Likewise, the peduncle of the cyclamen



**Fig. 3.3** Trajectory showing the existence of a response to bending (redrawn from Darwin and Pertz 1903). Time flows from the *bottom* to the *top*, indicated in hours:minutes by Arabic numerals. The horizontal coordinate shows the position of the stem tip in arbitrary units. A mustard (*Raphanus* sp.) seedling was placed horizontally in the custom-made clinostat, and rotated by 180° every 30 min (*thick curved arrows*). The rotation required less than 10 s, thus giving a gravitropic stimulus that changed sign every 30 min. Rotations began the day before, their total number being given by the Roman numerals. At 11:38 the clinostat was not rotated, but at 11:48 the seedling reversed direction anyway. The trajectory is drawn to show continuous movement of the plant even though the direction changed sign at each rotation. The short *vertical steps* in the trajectory at rotation times reflect the need to adjust the traveling microscope used to read the position of the stem tip. Spontaneous reversals were obtained with phototropic or gravitropic stimuli and with rotations at either 15- or 30-min intervals, and after as few as four periods. In some experiments, two reversals occurred after the clinostat stopped

(*Cyclamen hederifolium*) plant curves rapidly toward the ground as part of its dispersal mechanism, and this involves a migration of a bending growth zone at many centimeters per hour (MacDonald et al. 1987). These changes seem too rapid to reconcile with the movement of auxin, as would presumably be required for a mechanism based on gravitropism.

Responses to bending have been reported. For example, in dandelion (*Taraxacum officinale*) peduncles, a modest and transient (5 to 10 min) lateral stress elicits a vigorous growth response (Clifford et al. 1982). Recently, an ingenious series of experiments were conducted on tomato stems where the



non-growing, basal part of the stem was bent in a controlled way, and the consequent growth response in the apical part could be attributed precisely to the integrated stresses built up by the bending (Coutand and Moulia 2000; Coutand et al. 2000). To my knowledge, this is the first demonstration that plants are able to respond specifically to being bent, as opposed to a more general perturbation consequent on bending, and supports the idea that out-of-phase growth oscillations could be generated by successive responses to stem flexure.

### 3.5 Conclusion and Perspectives

I began with the proposition that if the growth mechanism of single plant cells within an organ is inherently oscillatory, then one expects to see those oscillations entrained and large-scale oscillations to result. This survey has shown that such oscillations in some cases are not due to growth, and in other cases are spatially and temporally erratic. From this one may suggest that either the ability to entrain the cellular oscillators is obscured by a feature of the tissue or that diffuse growth itself is not inherently oscillatory, and hence the erratic fluctuations at the organ level result from the imperfect regulation of growth among cells.

To settle this issue, measurements of relative elongation at essentially cellular resolution are crucial. Also useful would be to look for growth oscillations in single plant cells in culture that grow by diffuse growth. It might be interesting to make local perturbations, such as spot application of auxin or cellular ablation, and examine how any associated change in expansion behavior propagates through a tissue. Finally, the subject of mechanical responses requires more attention. Just as the interaction between circumnutation and gravitropism has been probed, so too the mechanical status of the organ can be manipulated and its effects on growth oscillations quantified. This endeavor would benefit from continued collaboration with engineers to develop an appropriate framework for experiments and interpretations. In this way, the power of movement in plants can eventually be understood.

*Acknowledgements.* Work in the author's laboratory on morphogenesis is supported by the U.S. Department of Energy (grant no. 03ER15421 to T.I.B.), which does not constitute endorsement by that department of views expressed herein. I thank Jacques Dumais (Harvard University) for scintillating comments on the manuscript, and Arthur R. Berg (University of Aberdeen) for a color version of his figure.

### References

- Adolfson KA, Sothorn RB, Koukkari WL (1998) Ultradian movements of shoots of two species of soybeans *Glycine soja* (Sieb. and Zucc.) and *Glycine max* (L.) Merr. *Chronobiol Int* 15:1–11
- Badot P-M, Melin D, Garrec J-P (1990) Circumnutation in *Phaseolus vulgaris*. II. Potassium content in the free moving part of the shoot. *Plant Physiol Biochem* 28:123–130



- Baillaud L (1962) Mouvements autonomes des tiges, vrilles et autres organes à l'exception des organes volubiles et des feuilles. In: Handbuch der Pflanzenphysiologie, vol 17 part 2. Springer, Berlin Heidelberg New York, pp 562–634
- Barlow PW, Parker JS, Brain P (1994) Oscillations of axial plant organs. *Adv Space Res* 14(8):149–158
- Baskin TI (1986) Redistribution of growth during phototropism and nutation in the pea epicotyl. *Planta* 169:406–414
- Baskin TI, Iino M, Green PB, Briggs WR (1985) High-resolution measurements of growth during first positive phototropism in maize. *Plant Cell Environ* 8:595–603
- Behringer FJ, Davies PJ, Reid JB (1990) Genetic analysis of the role of gibberellin in the red light inhibition of stem elongation in etiolated seedlings. *Plant Physiol* 94:432–439
- Berg AR, Peacock K (1992) Growth patterns in nutating and nonnutating sunflower (*Helianthus annuus*) hypocotyls. *Am J Bot* 79:77–85
- Brown AH (1991) Gravity perception and circumnutation in plants. In: Bonting SL (ed) *Advances in Space Biology and Medicine*, vol 1. JAI Press, Kidlington, UK, pp 129–153
- Brown AH, Chapman DK, Lewis RF, Venditti AL (1990) Circumnutations of sunflower hypocotyls in satellite orbit. *Plant Physiol* 94:233–238
- Buda A, Zawadzki T, Krupa M, Stolarz M, Okulski W (2003) Daily and infradian rhythms of circumnutation intensity in *Helianthus annuus*. *Physiol Plant* 119:582–589
- Caré A-F, Nefed'ev L, Bonnet B, Millet B, Badot P-M (1998) Cell elongation and revolving movement in *Phaseolus vulgaris* L. twining shoots. *Plant Cell Physiol* 39:914–921
- Castle ES (1940) Discontinuous growth of single plant cells measured at short intervals, and the theory of intussusception. *J Cell Comp Physiol* 15:285–298
- Clifford PE, Fenson DS, Munt BI, McDowell WD (1982) Lateral stress initiates bending responses in dandelion peduncles: a clue to geotropism? *Can J Bot* 60:2671–2673
- Comparot S, Morillon R, Badot B-M (2000) Water permeability and revolving movement in *Phaseolus vulgaris* L. twining shoots. *Plant Cell Physiol* 41:114–118
- Coutand C, Moulia B (2000) Biomechanical study of the effect of a controlled bending on tomato stem elongation: local strain sensing and spatial integration of the signal. *J Exp Bot* 51:1825–1842
- Coutand C, Julien JL, Moulia B, Mauget JC, Guitard D (2000) Biomechanical study of the effect of a controlled bending on tomato stem elongation: global mechanical analysis. *J Exp Bot* 51:1813–1824
- Darwin F, Pertz DFM (1892) On the artificial production of rhythm in plants. *Ann Bot* 6:245–264
- Darwin F, Pertz DFM (1903) On the artificial production of rhythm in plants. With a note on the position of maximum heliotropic stimulation. *Ann Bot* 17:93–106
- Degli Agosti R, Jouve L, Greppin H (1997) Computer-assisted measurements of plant growth with linear variable differential transformer (LVDT) sensors. *Arch Sci Genève* 50:233–244
- Dowson-Day MJ, Millar AJ (1999) Circadian dysfunction causes aberrant hypocotyl elongation patterns in arabidopsis. *Plant J* 17:63–71
- Erickson RO, Sax KB (1956) Elemental growth rate of the primary root of *Zea mays*. *Proc Am Philos Soc* 100:487–498
- Fisher JE (1964) Evidence of circumnutational growth movements of rhizomes of *Poa pratensis* L. that aid in soil penetration. *Can J Bot* 42:293–299
- Goldbeter A (1996) *Biochemical oscillations and cellular rhythms*. Cambridge University Press, Cambridge, UK
- Gotô N, Chiba Y (1983) Oscillation in the growth rate and shortening of the lag time for IAA response by cotyledons, gibberellic acid and sucrose in bean hypocotyls. *Plant Cell Physiol* 24:1297–1303
- Hasenstein KH (1991) Measurement of circumnutation in maize roots. *Microgravity Sci Technol* 4:262–266
- Hatakeda Y, Kamada M, Goto N, Fukaki H, Tasaka M, Suge H, Takahashi H (2003) Gravitropic response plays an important role in the nutational movements of the shoots of *Pharbitis nil* and *Arabidopsis thaliana*. *Physiol Plant* 118:464–473

- Heathcote DG (1966) A new type of rhythmic plant movement: Micronutation. *J Exp Bot* 17:690–695
- Heathcote DG, Idle ERIC (1965) Nutation in seedling *Phaseolus multiflorus*. *Ann Bot* 29:563–577
- Hejnowicz Z, Sievers A (1995) Proton efflux from outer layer of the peduncle of tulip in gravitropism and circumnutation. *Bot Acta* 108:7–13
- Inoue N, Arase T, Hagiwara M, Amano T, Hayashi T, Ikeda R (1999) Ecological significance of root tip rotation for seedling establishment of *Oryza sativa* L. *Ecol Res* 14:31–38
- Israelsson D, Johnsson A (1967) A theory for circumnutations in *Helianthus annuus*. *Physiol Plant* 20:957–976
- Jiang Z, Staude W (1989) An interferometric method for plant growth measurements. *J Exp Bot* 40:1169–1173
- Johnsson A (1997) Circumnutations: results from recent experiments on Earth and in space. *Planta* 203:S147–S158
- Johnsson A, Heathcote D (1973) Experimental evidence and models on circumnutations. *Z Pflanzenphysiol* 70:371–401
- Jouve L, Greppin H, Degli Agosti R (2000) Floral stem growth of arabidopsis ecotypes. II. Short time scale events and evidence for ultradian rhythms. *Arch Sci Genève* 53:215–224
- Kerckhoffs LHJ, Sengers MMT, Kendrick RE (1997) Growth analysis of wild-type and photomorphogenic-mutant tomato plants. *Physiol Plant* 99:309–315
- Kitazawa D, Hatakeda Y, Kamada M, Fujii N, Miyazawa Y, Hoshino A, Iida S, Fukaki H, Morita MT, Tasaka M, Suge H, Takahashi H (2005) Shoot circumnutation and winding movements require gravisensing cells. *Proc Natl Acad Sci USA* 102:18742–18747
- Kristie DN, Jolliffe PA (1986) High-resolution studies of growth oscillations during stem elongation. *Can J Bot* 64:2399–2405
- Liptay A, Barron JL, Jewett T, van Wesenbeeck I (1995) Oscillations in corn seedling growth as measured by optical flow. *J Am Soc Hort Sci* 120:379–385
- List A Jr (1969) Transient growth responses of the primary roots of *Zea mays*. *Planta* 87:1–19
- MacDonald IR, Gordon DC, Hart JW (1987) Cyclamen coiling – the migration of a growth response. *Plant Cell Environ* 10:613–617
- Millet B, Koukkari WL (1990) Ultradian oscillations of three variables in the circumnutation movements of shoots. *Chronobiologia* 17:53–58
- Millet B, Melin D, Badot P-M (1988) Circumnutation in *Phaseolus vulgaris*. I. Growth, osmotic potential and cell ultrastructure in the free-moving part of the shoot. *Physiol Plant* 72:133–138
- Niinuma K, Someya N, Kimura M, Yamaguchi I, Hamamoto H (2005) Circadian rhythm of circumnutation in inflorescence stems of arabidopsis. *Plant Cell Physiol* 46:1423–1427
- Obrović V, Poff KL (1997) Interaction of light and gravitropism with nutation of hypocotyls of *Arabidopsis thaliana* seedlings. *Plant Growth Regul* 23:141–146
- Peacock K, Berg AR (1994) Effect of mechanical stress on sunflower (*Helianthus annuus* L.) hypocotyl growth. *Ann Bot* 74:661–666
- Penny D, Penny P, Marshall DC (1974) High resolution measurement of plant growth. *Can J Bot* 52:959–969
- Prat R, Parésys G (1995) High resolution study of plant cell growth kinetics. *Plant Physiol Biochem* 28:123–130
- Prat R, Kellershohn N, Ricard J (1996) Aperiodic ('chaotic') behavior of plant cell wall extension. II. Periodic and aperiodic oscillations of the elongation rate of a system of plant cells. *Chaos Solitons Fractals* 7:1119–1125
- Proseus TE, Ortega JKE, Boyer JS (1999) Separating growth from elastic deformation during cell enlargement. *Plant Physiol* 119:775–784
- Ruiz Fernandez S, Wagner E (1994) A new method of measurement and analysis of the stem extension growth rate to demonstrate complete synchronization of *Chenopodium rubrum* plants by environmental conditions. *J Plant Physiol* 144:362–369
- Salamon P, List A Jr, Grenetz PS (1973) Mathematical analysis of plant growth. *Zea mays* primary roots. *Plant Physiol* 51:635–640

- Satter RL (1979) Leaf movements and tendril curling. In: Haupt W, Feinleib ME (eds) Encyclopedia of Plant Physiology, New Series, vol 7, Physiology of Movements. Springer, Berlin Heidelberg New York, pp 442–484
- Schuster J, Engelmann W (1997) Circumnutations of *Arabidopsis thaliana* seedlings. Biol Rhythm Res 28:422–440
- Shabala S (2003) Physiological implications of ultradian oscillations in plant roots. Plant Soil 255:217–226
- Shabala SN, Newman IA (1997a) Proton and calcium flux oscillations in the elongation region correlate with root nutation. Physiol Plant 100:917–926
- Shabala SN, Newman IA (1997b) Root nutation modelled by two ion flux-linked growth waves around the root. Physiol Plant 101:770–776
- Simmons C, Söll D, Migliaccio F (1995) Circumnutation and gravitropism cause root waving in *Arabidopsis thaliana*. J Exp Bot 46:143–150
- Spurný M (1966) Spiral feedback oscillations of growing hypocotyl with radicle in *Pisum sativum* L. Biol Plantarum 8:381–392
- Spurný M (1975) Elongation and circumnutation oscillations of hypocotyl of pine seedlings (*Pinus sylvestris* L.). Biol Plantarum 17:43–49
- Spurný M, Koutná R, Čížková R, Konečná D (1978) Growth and nutation parameters of primary root of pedunculated oak (*Quercus robur* L.). Biol Plantarum 20:167–172
- Thompson MV, Holbrook NM (2004) Root-gel interactions and the root waving behavior of arabidopsis. Plant Physiol 135:1822–1837
- van der Weele CM, Jiang H, Palaniappan KK, Ivanov VB, Palaniappan K, Baskin TI (2003) A new algorithm for computational image analysis of deformable motion at high spatial and temporal resolution applied to root growth: roughly uniform elongation in the meristem and also, after an abrupt acceleration, in the elongation zone. Plant Physiol 132:1138–1148
- Walter A, Spies H, Terjung S, Küsters R, Kirchgessner N, Schurr U (2002) Spatio-temporal dynamics of expansion growth in roots: automatic quantification of diurnal course and temperature response by digital image sequence processing. J Exp Bot 53:689–698
- Walter A, Feil R, Schurr U (2003) Expansion dynamics, metabolite composition and substance transfer of the primary root growth zone of *Zea mays* L. grown in different external nutrient availabilities. Plant Cell Environ 26:1451–1466
- Yang T, Law DM, Davies PJ (1993) Magnitude and kinetics of stem elongation induced by exogenous indole-3-acetic acid in intact light-grown pea seedlings. Plant Physiol 102:717–724
- Yoshihara T, Iino M (2005) Circumnutation of rice coleoptiles: its occurrence, regulation by phytochrome, and relationship with gravitropism. Plant Cell Environ 28:134–146