

Stefano Mancuso · Sergey Shabala
Editors

Rhythms in Plants

Dynamic Responses in a Dynamic
Environment

Second Edition

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Preface

Rhythmical behaviour is a quintessential pattern of life itself and is believed to play a key role in cell division and morphogenesis, to mediate all kind of movements, and to provide an advantageous strategy for evolution and adaptation of living organisms. Rhythms have fascinated people for more than 2000 years. As early as the fourth century B.C., Androsthene, scribe to Alexander the Great, noted that the leaves of *Tamarindus indica* opened during the day and closed at night (Bretzl 1903). Some early writers notice single movements of parts of plants in a cursory manner, Albertus Magnus in the thirteenth century and Valerius Cordus in the sixteenth century, thought the daily periodical movements of the pinnate leaves of some *Leguminosae* worth recording. Ray in his “*Historia Plantarum*” at the end of the seventeenth century commences his general considerations on the nature of the plants with a succinct account of *phytodinamical* phenomena mixing up together the movements from irritability and the daily periodical movements; the latter, he says, occur not only in the leaves of *Leguminosae*, but in almost all similar pinnate leaves, and with these periodical movements of leaves, he places also the periodical opening and closing of the flower of *Calendula*, *Convolvulus*, *Cichorium*, and others.

The number of publications on rhythms in plants increased dramatically in the last decades, and the old mystery of the “biological clock” has been tackled from the molecular, genetic, and biochemical perspectives. Yet, most research deals only with measurable rhythms—the so-called hands of the clock mechanism. The clock “pacemaker” still remains a mystery. Many superimposed rhythms are able to coexist in the same cell compartment, all with different periods. How many oscillators does a living cell have? Just one? Or is each of these processes controlled by its own independent oscillator? The situation is similar to that which existed in the physics of elemental particles in the “1960–”1970s, when an avalanche-like increase of discovered particles initiated a revision of theoretical concepts and resulted in the creation of a new paradigm in physics. Innovations in molecular biology, micro- and nanotechnology, and applied mathematics (e.g. hidden patterns, chaos theory) are providing new tools for understanding how environmental

signals and internal clocks regulate rhythmic gene expression and development. Needless to say, this fast, near astounding pace of discoveries shows how extremely the subject has changed and is reflected in the different chapters of the current book which covers aspects of plant physiology neither recognizable nor quantifiable few years ago.

The second edition of this book provides a timely update on a recent progress in this field and comprehensively summarizes current knowledge of molecular and physiological mechanisms behind circadian and ultradian oscillations in plants, and their physiological implications for growth, development, and adaptive responses to dynamic environment. The book is structured around three major topics:

- Ultradian oscillators
- Circadian oscillators
- Theoretical aspects and modelling

Written by a diverse group of leading researchers, this book will surely spark the interest of readers from many branches of science: from physicists and chemists wishing to learn about multifaceted rhythms in plant biology, to biologists and ecologists dealing with state-of-the-art modelling of complex rhythmic phenomena.

Before we close and let the reader enjoy (we hope!) the content of this volume, we would like to acknowledge the Springer's team (Dr. Andrea Schlitzberger and Dr. Christina Eckey) for their idea to proceed with this publication. We would also like to express our sincere gratitude to all contributing authors who have enthusiastically embraced an idea to go for the second edition of this book. Finally, and most importantly, we are truly grateful to all "frontline people" in our institutions and elsewhere in the world for their enthusiasm and patience in revealing one of the greatest mysteries of the life—THE CLOCK.

June 2015

Stefano Mancuso
Sergey Shabala

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Part I
Ultradian Oscillations

Chapter 1

Ultradian Growth Oscillations in Organs: Physiological Signal or Noise?

Tobias I. Baskin

Abstract This review examines ultradian oscillatory growth in the multicellular organs of vascular 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, the regular ultradian movements of plant organs, when they occur, reflect successive responses to mechanical perturbation.

1.1 Introduction

1.1.1 *Oscillation as a 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

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(Goldbeter 1996). Expansion of a cell is certainly a complex 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. The following illustrates how expansion could be oscillatory (Fig. 1.1). Suppose water uptake were linked to turgor loss, such that aquaporins would open only when 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. This hypothetical loop illustrates feedback between steps in the growth process. 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 growth mechanisms. Also, I will not treat growth oscillations in single cells, such as pollen tubes or root hairs (the interested reader may consult the review in this volume by Feijo), even though my objective is exemplified beautifully by Castle (1940) who detected an

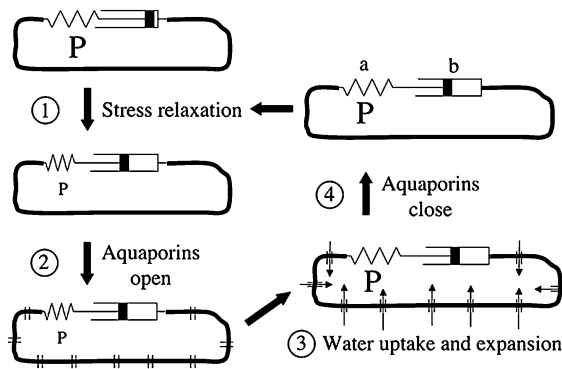


Fig. 1.1 Hypothetical model of diffuse growth giving rise to oscillatory expansion. For a single cell, the mechanical behavior of the cell wall is idealized by an elastic element (*spring*; *a*) and a plastic element (*dash-por*; *b*) in series. Turgor pressure (*P*) is held by the deformation of the 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

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.

1.1.2 Growth Versus Movement

Unfortunately, the word *growth* is used in two distinct ways. On the 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 cellular level, or indeed to the elemental deformation of a unit area of cell wall. The latter is the direct output of the growth machinery, whereas tip displacement integrates the behavior of the entire organ, often many centimeters long. 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 mechanisms indirectly.

1.2 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 widely believed to be true because it is often assumed, first, that an oscillatory movement called circumnutation is undergone by the stems and roots of essentially *all* plants and second, that circumnutation is a coherent oscillation in growth. 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). By *large* amplitude, I mean that the lateral displacement is much greater than the stem diameter. A large amplitude displacement is not required for a regular period (Schuster and Engelmann 1997; Adolfson et al. 1998). This regular behavior reflects an obvious circumnutation, clearly adaptive for vines and climbing plants, but happening also in species such as sunflower (*Helianthus annuus*) and arabidopsis (*Arabidopsis thaliana*) where a plausible reason for the behavior is synchronization of growth among cells.

However, the tips of stems and roots of many plants move in erratic trajectories with small amplitude (i.e. equal or even less than organ diameter) and erratic period (Heathcote and Idle 1965; Spurný et al. 1978; Barlow et al. 1994; Shabala and Newman 1997). To claim that circumnutation is a property of all growing organs is

to assert that the large and regular movements of the *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. Here, I will restrict the word *circumnutation* to movements with a salient and regular period.

Whether large or small, stem movements are widely ascribed to differential growth. But this need not be the case. In many plants, movements of leaves have ultradian periods, similar to those of 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.

Reversible volume changes have been implicated in circumnutation. For example, circumnutation continues for a few periods following decapitation of pine (*Pinus sylvestris*) hypocotyls 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 (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). Conceptually, this is if the pulvinus were spread throughout the bending stem, I will call this arrangement a *diffuse pulvinus*.

That circumnutation 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 equally universal oscillations in growth. In addition, a major topic of research on circumnutation has been to determine to what extent this movement can be explained by gravitropism. One explanation, formulated into an explicit model 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 circumnutation in space flight where gravitational force is all but absent has shown that gravitropism is not essential for circumnutation (Brown et al. 1990), the role of gravitropism in circumnutation continues to be debated (Johnsson 1997; Hatakeda et al. 2003; Tanimoto et al. 2008; Johnsson et al. 2009). Insofar as gravitropic bending is accepted as being based on differential growth, those circumnutations powered by a diffuse pulvinus can be distinguished from gravitropism mechanistically.

Nevertheless, circumnutation can involve oscillations in growth. Growth rate oscillations, 180° out of phase on either side of the circumnutating stem, occur in the epicotyl of pea (*Pisum sativum*; Baskin 1986) as well as in the sunflower hypocotyl (Berg and Peacock 1992; Fig. 1.2). 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

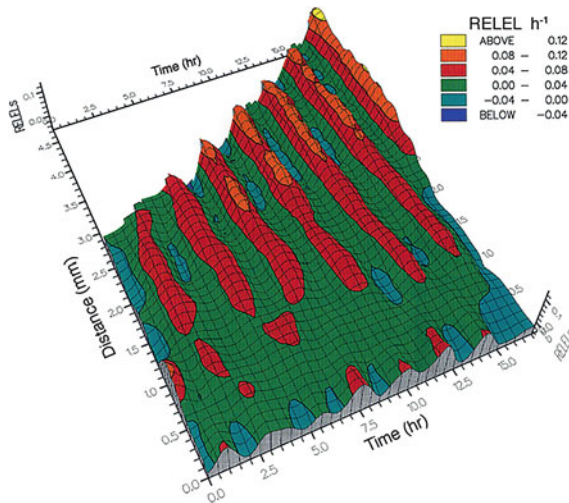


Fig. 1.2 Three-dimensional plot of displacement and elemental elongation versus time for a circumnating sunflower hypocotyl (modified from Berg and Peacock 1992). The hypocotyl was marked at 2-mm intervals and growth rates recovered from marks digitized at 15-min intervals. Data were interpolated to 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

2-mm zones and found that differential expansion is responsible for most of the bending (Fig. 1.2). Interestingly, these authors did record negative elemental elongation rates, implying that contractions (hence reversible volume changes) contribute to the oscillatory movement. Even a total absence of contraction cannot exclude a contribution from elastic changes because reversible and irreversible processes are readily superimposed (Proseus et al. 1999; Fig. 1.1). Therefore, while circumnutation can depend on out-of-phase growth oscillations, as in pea and sunflower, circumnutation can alternatively depend on reversible volume changes (diffuse pulvinus), as in French bean. With so few examples documented, it is unjustified to assume that circumnutation invariably reflects differential growth.

Surprisingly, regular and relatively large amplitude oscillations of organ position can result from underlying processes that are constant. The peduncle of the aquatic angiosperm *Vallisneria spiralis* circumnates with huge amplitude, driven by the interaction of the water surface with the unidirectional (i.e. non-oscillatory) rotation of the stem (Kosuge et al. 2013). When arabidopsis is grown on an inclined and impenetrable surface, the root will grow in a sinusoidal pattern (*root waves*) that has been attributed to circumnutation (Migliaccio et al. 2013) and a regular growth oscillation presumed. However, in an elegant analysis, Thompson and Holbrook (2004) showed that the undulating wavy pattern represents buckling of the root and results from gravitropism and friction between the root tip and the substrate. No

oscillation in growth is needed, and in fact, the tip displacement rate of the root fluctuates erratically, again illustrating how a regular, oscillatory pattern (the shape of the root) can be built up without an oscillation in either reversible or irreversible expansion.

As an aside, 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.

1.3 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 around the circumference. Symmetrical entrainment would give rise to oscillations in tip displacement velocity. I will call these *axial* oscillations, because they are in line with the longitudinal axis of the organ. Additionally, it is common for stems and roots to move laterally through a distance on the order of the organ's diameter. Insofar as entrainment might not be perfectly symmetrical, oscillatory lateral displacements of small amplitude might plausibly indicate synchronized linear oscillations in expansion rate. How prevalent are well-synchronized, ultradian oscillations in movement?

In seeking to answer this question, I will consider first measurements of velocity (both lateral and axial) followed by direct measurements of expansion.

At first sight, ultradian oscillations seem prevalent, reported in many papers. Oscillations in velocity have been claimed with periods of 170 min in rice roots (Iijima and Matsushita 2011), 20–70 min in the arabidopsis inflorescence stem (Degli Agosti et al. 1997; Jouve et al. 2000), 80–120 min in the azuki bean (*Vigna angularis*) stem (Gotô and Chiba 1983), and 60 and 270 min for a maize (*Zea mays*) 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 (*Vigna radiata*) hypocotyls (Prat and Parésys 1995; Prat et al. 1996). In the above examples, although periods were assigned, their significance was rarely tested statistically and the records typically bristle with periods, implying temporal instability. In other examples, the fluctuations were not analyzed temporally but appear aperiodic by eye (Jiang and Staude 1989; Behringer et al. 1990; Yang et al. 1993; Liptay et al. 1995). In general, these fluctuations in axial velocity on a scale of a few hours are far less regular than those seen in circumnutation and arguably represent erratic feedback rather than an endogenous rhythm.

In roots, various types of lateral movement fluctuations have been recorded in the ultradian range, but almost always with small amplitudes, wandering trajectories, and poorly defined periods (Spurný 1966; Spurný et al. 1978; Hasenstein 1991; Barlow et al. 1994; Shabala and Newman 1997; Thompson and Holbrook 2004). For maize roots, small amplitude (few hundred microns) lateral oscillations have been reported with reasonably regular periods of 8 or 90 min (Walter et al. 2003; Vollsnes et al. 2010; Popova et al. 2012), but in other publications, maize roots grow with scarcely perceptible lateral deflections (Erickson and Sax 1956; List 1969). The clearest example I know of sustained lateral oscillations in roots is for rice with about a 1-h period (Hayashi et al. 2004).

Fluctuations in axial velocity might be commonly observed, but they can be separated from growth, at least to some extent. First, erratic fluctuations are often absent, even from high-resolution traces (e.g. Stolarz et al. 2008; Durnham-Brooks et al. 2010). The steady lateral oscillation of the tip of the rice root, mentioned above, vanishes under aluminum treatment, at a concentration that has no discernable effect on growth rate (Hayashi et al. 2004). Erratic oscillations in stem tip velocity occur in 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 *C. rubrum*, tomato (*Solanum lycopersicum*) stems growing under a regular photoperiod and having diurnal oscillations in axial velocity retain erratic higher-frequency fluctuations but only in some individuals (Kerckhoffs et al. 1997). Finally, in a report showing fluctuations in stem tip velocity in the seedlings of five species, with apparent periods ranging from 3 to 120 min, similar fluctuations were detected when the position transducer was attached near the (non-growing) base of the hypocotyl (Kristie and Jolliffe 1986), implying that the source of these fluctuations is distinct from growth.

Turning now to direct measurements of expansion, the story is similar: Fluctuations in expansion rate are usually erratic and are sometimes entirely absent. There is a massive body of work where a position transducer is used to record the growth of excised stem segments. Strictly speaking, this reports the velocity at which one end of the segment is moving relative to the other end; nevertheless, the segments are typically about 1 cm long and contain growing tissue exclusively, attributes that make the reported velocity data reasonably close to an elemental expansion rate, at least compared to data from attaching the transducer to the tip of an intact organ. Growth in these records is usually constant (e.g. Penny et al. 1974), sometimes fluctuates erratically, and only rarely oscillates regularly.

Position transducers involve mechanical attachment and might suppress small fluctuations. Instead, growth is measured more reliably and less invasively from images. In spatial analyses of root growth, elemental elongation rates throughout the growth zone fluctuate erratically (Erickson and Sax 1956; List 1969; Salamon et al. 1973; Chavarría-Krauser et al. 2008; Shih et al. 2014). Sometimes, the spatial profile of elemental elongation in maize is bimodal (Walter et al. 2002, 2003) and that of arabidopsis is multimodal (van der Weele et al. 2003). These bumps might indicate a regular oscillation in elongation rate as a cell traverses the growth zone;

instead, they might indicate a programmatic distinction among regions of the growth zone. Likewise, in the ultradian range, coleoptiles grow without apparent fluctuation (Baskin et al. 1985) and leaf expansion fluctuates erratically (Wiese et al. 2007; Mielewicz et al. 2013). Interestingly, in the later paper, one of the leaves undergoes clear ultradian growth rate oscillations during one night, but these involve substantial contraction, suggesting that they reflect an elastic phenomenon.

It is perhaps premature to take the absence of evidence as evidence for absence; research on growth rhythmicity has focused all but exclusively on diurnal rhythms (Walter et al. 2009). As a result, most published growth data are averages over individuals, an expedient used to reinforce and hence identify the phase relation between growth and an external cycle (typically light). Unfortunately, averaging will smooth out ultradian rhythms insofar as they are endogenous and hence out of phase among individual plants.

Taken altogether, this survey suggests that unmistakable, ultradian growth oscillations, as reported for pea epicotyls (Baskin 1986) and sunflower hypocotyls (Berg and Peacock 1992), are the exception, rather than the rule. Organs do undergo lateral movements of minor amplitude and have fluctuations in their overall extension rate, but these fluctuations are erratic and possibly due to processes other than growth. Some organs grow without a trace of ultradian fluctuations. Admittedly, distinct oscillations might emerge from a dedicated study using high-resolution methods; however, given the guiding concept of facile entrainment of neighboring oscillators, one expects a robust output. To my knowledge, there is no example of an ultradian growth oscillation shown to be symmetric (i.e. not out of phase on different sides of the stem) and having the temporal stability characteristic of circumnutation.

1.4 The Power of Bending in Plants

Pronounced, ultradian growth oscillations, although not ubiquitous, do occur and require explanation. The aforementioned 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 the 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 liable to interact.

Nevertheless, the overshoot model was recently supported 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; Tanimoto et al. 2008). Furthermore, circumnutation in *Arabidopsis* stems is strongly if not absolutely

suppressed in microgravity (Johnsson et al. 2009). However, in many environments, circumnutation, though having a well-defined period, is small in amplitude and hence unlikely to generate a significant gravitropic signal (e.g. Hatakeda et al. (2003) report wild-type amplitudes of $\sim 200 \mu\text{m}$ for the circumnutation of the arabidopsis inflorescence). Furthermore, despite lacking the ability to reorient when rotated, these mutant stems, as well as stems in microgravity, grow vertically (the morning glory stems eventually fall over and adopt a lazy habit). One would expect the non-gravitropic stems to meander when subject to the random deviations needed to initiate an overshoot cycle. That a plant can respond by suppressing circumnutation has been documented for the etiolated rice coleoptile in response to red light (Yoshihara and Iino 2005). Conceivably, a similar response occurs in morning glory stems and arabidopsis inflorescences when gravitational responsiveness has been diminished genetically or by travel beyond the pull of the Earth.

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. Darwin and Pertz (1892) constructed a clinostat that would rotate a plant by 180° and then stop for a specific interval before making another 180° rotation. The interval between 180° 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, when after many rotations, 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. 1.3). In some cases, the stems reversed a second time, again as if the alternating stimuli had continued. Gravitropic (or phototropic) overshoot cannot explain these results because stopping the clinostat rhythm led to the stems bending down (or away from the light); instead, it suggests that the stems were also 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. 1.2). Likewise, the peduncle of the cyclamen (*Cyclamen hederifolium*) fruit 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

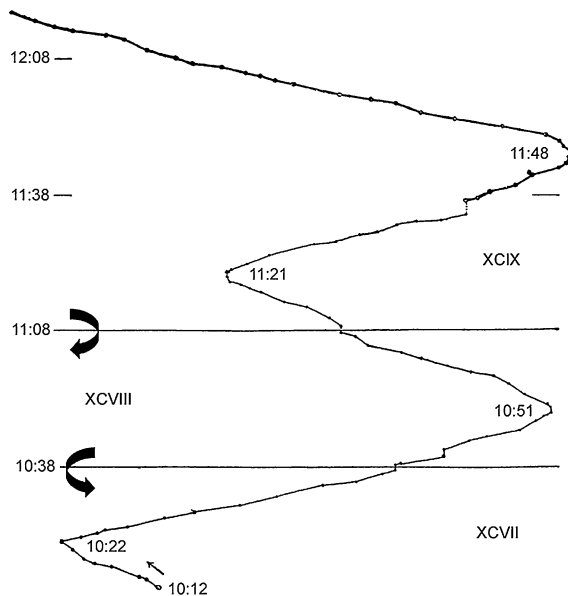


Fig. 1.3 Trajectory showing the existence of a response to bending (redrawn from Darwin and Pertz 1903). Time flows from the *bottom* to the *top*, indicated in hours:minutes by *Arabic numerals*. The *horizontal coordinate* shows the position of the stem tip in arbitrary units. A mustard (*Raphanus* 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

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 documented. For example, in dandelion (*Taraxacum officinale*) peduncles, a modest and transient (5–10 min) lateral stress elicits a vigorous growth response (Clifford et al. 1982). An ingenious series of experiments was 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). This work demonstrates 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.

1.5 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 are uncommon and those that occur in some cases are not due to growth and in others are too erratic to be called oscillations. 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, or the superposition of elastic changes related to water flow.

To settle this issue, measurements of relative elongation at cellular and sub-cellular resolution are crucial. Also useful would be to look for growth oscillations in single 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.

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Chapter 2

Nutation in Plants

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Abstract This chapter aims to explore and describe the physiological aspects of oscillating growth patterns in rapidly elongating plant organs, such as roots, hypocotyls, shoots, branches and flower stalks. After a brief description of the phenomena, the theories and models proposed to explain circumnutation are reported, focusing largely on the internal oscillator model and the gravitropic overshoot model. The former is derived from the intuition of Charles Darwin, the first to suggest that circumnutatory movements are mediated by an endogenous oscillator, i.e. the driving and regulating apparatus responsible for circumnutation is internal. By contrast, the latter theory proposes a gravity-dependent model to account for circumnutations, essentially consistent with the Cholodny-Went theory, thus interpreting oscillations as being a continuous series of over-compensatory responses of the plant to the changing orientation of its gravisensory apparatus relative to the Earth's gravity vector. A revised two-oscillator model is also reported, which is based on a combination of the above-mentioned two models. In this combined model, circumnutational movement involves a gravitropic reaction acting as an externally driven feedback oscillator, together with an endogenous or intrinsic oscillator which sends a rhythmic signal to the feedback system. The role of hormones will be finally discussed, with particular attention to the effect of ethylene in controlling nutation.

2.1 Overview of Nutations: Definition and Kinematic

More than a century ago, plant physiologists were already aware that rapidly elongating plant organs—roots, hypocotyls, shoots, branches, flower stalks—rarely grow in only one direction. Mean growth direction may be maintained for long

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intervals, but the organ's instantaneous growth direction usually oscillates slowly around that mean. From a distal viewpoint, the plant organ tip, or an elongating cylindrical plant organ, describes an ellipse, a circle- or pendulum-like movements about the plumb line, which can alternate between a clockwise and counterclockwise direction. The axes of the ellipse can vary: at one extreme, the ellipse approximates a line and, at the other, a circle. As the organ grows, its tip advances and (in three dimensions) traces an irregular helix (Migliaccio et al. 2009). This oscillating growth pattern was well known to nineteenth-century plant scientists as 'revolving nutation' until the Darwins (father and son, Darwin and Darwin 1880) introduced the term 'circumnutation', used to this day (Fig. 2.1). Thus, circumnutational oscillations are manifestations of the radially asymmetric growth rate typical of elongating plant organs (Fig. 2.2). These do not include tropic processes occurring in response to a directional cue, such as gravity or light, or nastic movements, which occur in response to external factors but are independent of the position, i.e. the closing of leaves at night. These various forms of movements usually occur together; for example, it has been shown that gravity amplifies the circumnutatory response in *Arabidopsis thaliana* (Johnsson et al. 2009).

Darwin's (1875) close observation of the behaviour of 'climbing plants', which tendrils appeared to 'search' for some upright support, led him to widen his investigation to a large variety of species in which, however, he found no exception to his generalization that circumnutations must be a universal kind of plant movement (Darwin and Darwin 1880). Indeed, today we know that the widespread occurrence of circumnutations is even greater than Darwin had ever suspected. It not only occurs in dicots and monocots (Brown 1993) but also is well established for gymnosperms, fungi (*Basidiomycetes*), bryophytes (*Ceratodon purpureus*, Kern et al. 2005) and algae (*Spirogyra*, Kim et al. 2005). Even some colonial forms of bacteria (*Acetobacter xylinum*) exhibit oscillating growth patterns which kinematically resemble higher plant circumnutations (Hoiczzyk 2000).

Although circumnutatory movements are of obvious use to twining plants seeking mechanical support, in other cases the movements appear to have no useful purpose. The amplitude, period and shape of circumnutation depend on the plant

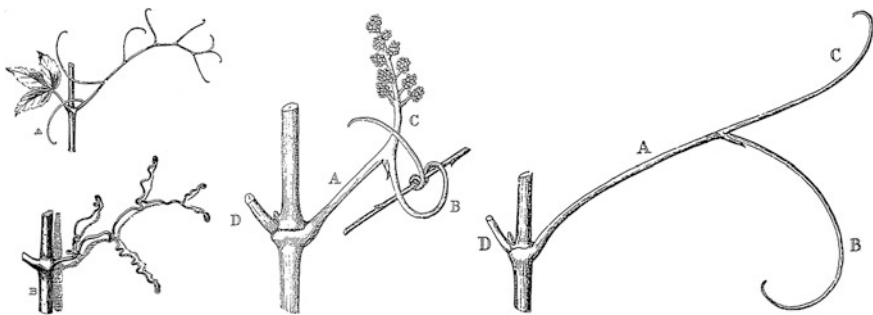


Fig. 2.1 Some sketches illustrating Darwin's close observation of the behaviour of 'climbing plants' (extracted from Darwin 1875)

Fig. 2.2 *Brassica oleracea* and circumnutation of the hypocotyl and cotyledons (extracted from Darwin and Darwin 1880)



species, the plant organs involved and the developmental stage of growth. Shoots of climbing plants (e.g. *Dioscorea batatas*, *Ipomoea quamoclit* and *Phaseolus vulgaris*) circumnutate very regularly in circular orbits (Baillaud 1962; Millet et al. 1984). By contrast, such regular circumnutation can rarely be found in more common non-climbing plants such as *Arabidopsis* (hypocotyls, Schuster and Engelmann 1997), rice (Yoshihara and Iino 2005), *Triticum* (coleoptiles, Joerrens 1959) and tulip (peduncles, Hejnowicz and Sievers 1995).

Researchers have regarded these phenomena both as oddities of plant growth and also as an outward manifestation of some important processes involved in the elongation of plant organs. Circumnutation is a growth movement, its expression depending closely on growth: whatever interferes with growth reduces or inhibits circumnutation—when tissues mature and elongation ceases, so do circumnutations. Moreover, circumnutations do not necessarily persist throughout the entire time course of organ growth. The oscillations may be interrupted by periods of straight growth, some lasting several hours, alternating with periods of vigorous oscillations. Plant organs (shoots and roots) may oscillate either clockwise or counterclockwise (Fig. 2.3). The same organ may stop oscillating while continuing to elongate; later, it may resume circumnutating but in the opposite direction or, without any pause, its tip may trace a figure of eight which accomplishes the reversal. Most circumnutational oscillation frequencies are in the range of 50 μ Hz (periods of about 20–300 min). In some cases, the oscillating rhythm is connected with circadian cycles, as shown in *Helianthus* (Niimura et al. 2005; Stolarz et al. 2008; Stolarz 2009). Therefore, appropriate methods are needed to fully reveal the