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4 Nutation in Plants

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AND STEFANO MANCUSO*

Abstract

This chapter aims to focus on the physiological aspect 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 date for 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, interpreting oscillations as being a continuous series of over-compensatory responses of the plant to the changing orientation of its gravisensory apparatus relative of the Earth's gravity vector. Finally, a revised two-oscillator model is 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.

4.1 Introduction

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 intervals but the organ's instantaneous growth direction usually oscillates slowly about that mean. From a distal viewpoint, the plant organ

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tip, or an elongating cylindrical plant organ, describes an ellipse, a circle or pendulum-like movements about the plumbline, which can alternate between a clockwise and counter-clockwise 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. This oscillating growth pattern was well known to 19th-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. 4.1). Thus, circumnutational oscillations are manifestations of the radially asymmetric growth rate typical of elongating plant organs (Fig. 4.2). These do not include tropic processes induced by external factors such as gravity or light.

Darwin's (1875) close observation of the behaviour of 'climbing plants', of which the 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 occurs not only 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 (Hoiczuk 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 species, the plant organs involved, and the developmental stage of growth. Shoots of climbing plants (e.g. *Dioscorea batatas*, *Ipomoea quamoclit*

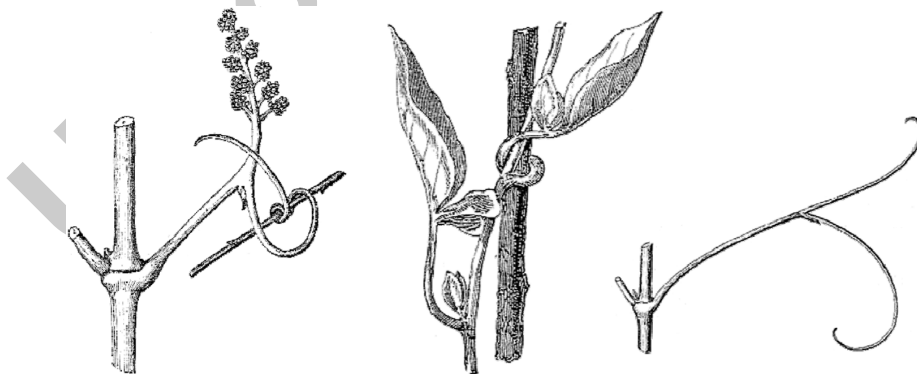


Fig. 4.1 Some sketches illustrating Darwin's close observation of the behaviour of 'climbing plants' (extracted from Darwin 1875)



Fig. 4.2 *Brassica oleracea* and circumnutation of the hypocotyl and cotyledons (extracted from Darwin and Darwin 1880)

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 counter-clockwise (Fig. 4.3). The same organ may stop oscillations 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 μHz (periods of about 20–300 min). Therefore, appropriate methods are needed to fully reveal the high incidence of circumnutational behaviour in growing plant parts. In higher plants, kinematic patterns of circumnutation are unique for each organ of a given plant. Different shoots often do not oscillate in phase and usually have different periods of oscillation.

Various mechanical stimuli can exert a dominant influence on circumnutational behaviour. Pressure (mechanical distortion), mechanical shock, sub-sonic vibrations, and even gentle tactile stimulation can sometimes suppress

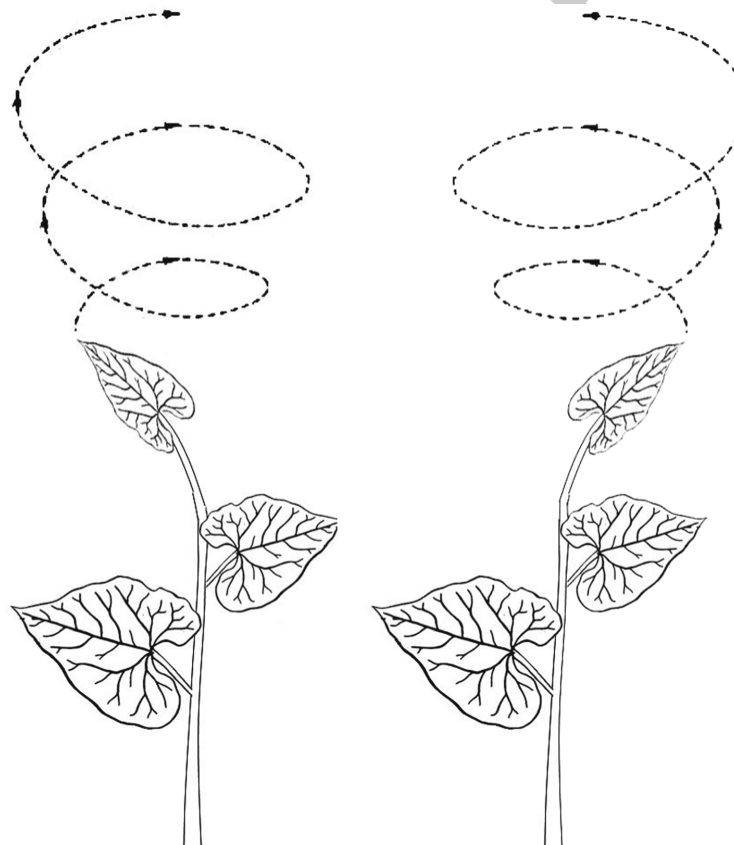


Fig. 4.3 Clockwise and counter-clockwise oscillations of *Phaseolus vulgaris* L.

the vigour of circumnutations. It may be significant that these effects can occur within only a few minutes, often less than that needed for auxin to be transported from an organ tip to the growth region. This observation may be used as an argument in favour of a growth-control process which is local, rather than occurring in the remote tip region of the growing organ.

Beginning about 60 years ago, speculations about how plants grow and respond to tropistic stimulations were dominated by the Cholodny-Went theory (Cholodny 1926; Went 1926), according to which both the plant's environmental gravity-force detectors (statocytes) and the site of production of the growth 'hormone' are located in the apex of the responding organ. As originally proposed, the Cholodny-Went theory was chiefly concerned with the role of a chemical growth regulator in transport and its influence on the growth phases of a plant's tropistic response to a gravitational stimulus. The Cholodny-Went theory served as a guide for several generations of plant physiologists to examine and to revise. More recently, however, other naturally occurring growth regulators have been found, arguing against the 'comfortable' simplicity of views long existing in this research area. As fundamental departure from the simplified Cholodny-Went theory, evidence has been accumulating in support of a local-control theory whereby the tropistically responding region, especially of the shoot, plays a dominant role in determining the kinematics of its own response.

4.2 Theories and Models for Circumnutation

Circumnutation is the consequence of helical growth (Brown 1993) and reversible volume variations occurring in the cells of the moving part of the stem (the bending zone below the apex; Caré et al. 1998). These variations seem to be caused by the difference in water content between the convex and concave sides of the bending zone, associated with turgor and ion concentration differences between opposite sides of the stem (Fig. 4.4; Lubkin 1994). Possibly, a turgor wave rotating around the stem during circumnutation drives a helical, likely acidic growth of the stem (Hejnowicz and Sievers 1995), which we can see as stem bending. The helical growth is hypothesized to be a mechanism which increases the stability of the hypocotyls (Schuster and Engelmann 1997) during cell wall loosening (Cosgrove 2000) accompanying elongation. It has also been suggested that turgor changes are generated by endogenous, spontaneous oscillations. As a consequence, oscillatory growth and movement are generated (Van den Driessche 2000).

The cells of the bending zone communicate via plasmodesmata (Brown 1993), ion channels (Badot et al. 1990) and aquaporins (Comparot et al. 2000). Unlike pulvinary cells which are highly specialized (Engelmann 1996), no particular structure has been identified for cells in the bending zone. Circumnutations occur temporarily in young growing shoots, in the cells at a

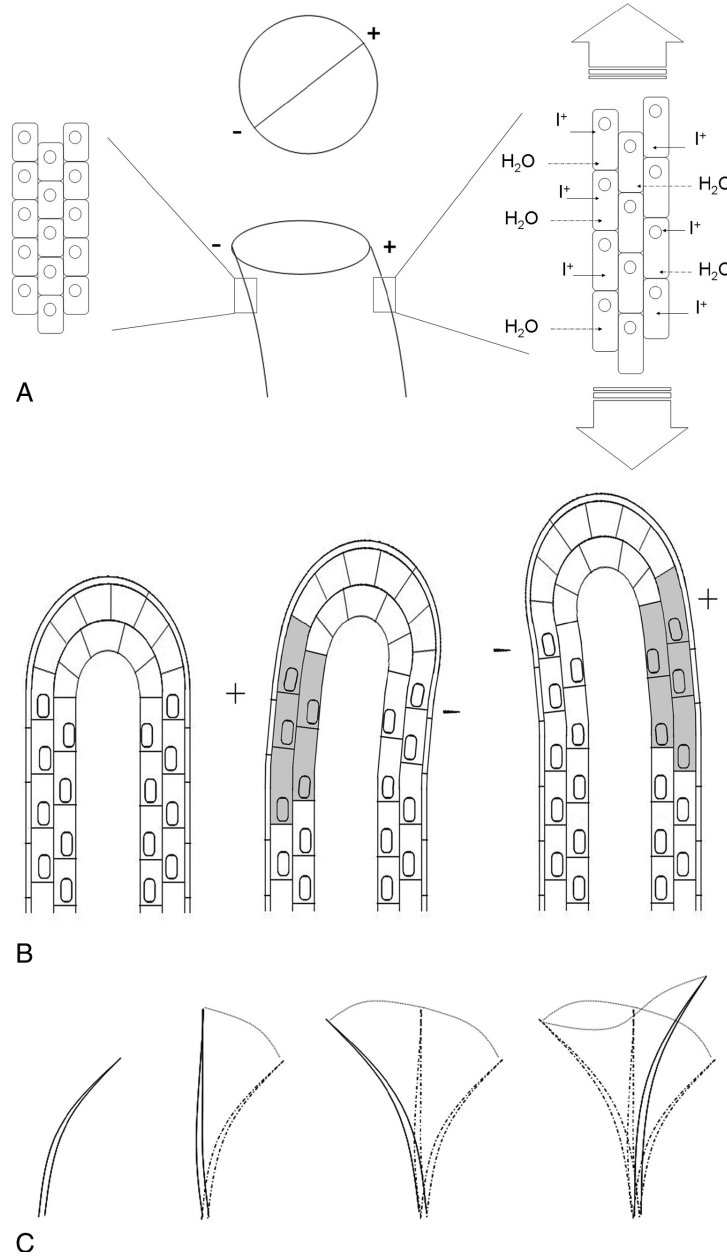
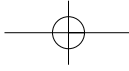


Fig. 4.4 Schematic representation of cellular turgor changes (a), and differential growth rate (b) at two opposite sides of a shoot and its effects on circumnutation (c)

given distance from the apex, or rather in a certain developmental stage (Van den Driessche 2000). The movements also strongly depend on light intensity, photoperiod (Buda et al. 2003), mechanical stress and temperature (Anderson-Bernadas et al. 1997).

To date, two main models for circumnutation have been proposed.

4.2.1 'Internal Oscillator' Model

Charles Darwin and his son Francis suggested that circumnutatory movements are mediated by an endogenous oscillator. Darwin tried to explain (in terms of 19th-century science) why the potential for circumnutating is ubiquitous. He considered that circumnutation is not only universal but also a fundamental process which would "be modified for the good of the plant" to accomplish tropistic or other growth responses. The Darwinian internal oscillator model is more a concept than a model, connected with the biological clock mechanism (Thain et al. 2002). Operationally, this means that the driving and regulating apparatus responsible for circumnutation is internal. Because circumnutation is patently advantageous to the plant only in a small minority of cases, researchers are not inclined to consider that it has endured only because it confers some evolutionarily significant advantage – quite the contrary – there must be something fundamental about the growth process which endows growing plant organs with the ability to circumnutate, an ability commonly displayed.

There are different hypotheses concerning the nature of an endogenous oscillator. Arnal (1953) advanced the argument that the circumnutation of coleoptiles is due to periodic variations in auxin fluxes from the tip. Moreover, Joerrens (1959) proposed that the sensitivity of the elongating cells to auxin changes periodically. Heathcote and Aston (1970) considered a hypothetical 'cellular nutational oscillator', situated in each cell and having a period equal to the periodicity of the circumnutational movement.

A recently proposed model relates to the existence of an intrinsic 'oscillator'. This model is based on the observation of strong correlations between nutation and rhythmical patterns of ion fluxes in the elongation region of corn roots (Shabala and Newman 1997; Shabala 2003). The authors noted that, when maize roots showed rhythmical movements, H^+ and Ca^{2+} fluxes also changed rhythmically, with the same average period and amplitude; when root movement was periodic, so were ion fluxes; moreover, when root growth was absent or very slow, no oscillations in ion fluxes occurred, and no nutation was observed. Shabala (2003) found that correlations between flux oscillations and root circumnutation could also be extended to include K^+ . As K^+ is a major osmotic agent in plant cells and, accordingly, a main factor responsible for differential growth of root cells, an efflux of K^+ results in a loss of turgor within the cell and a consequent 'slumping' of the cell. The non-turgid cells cause asymmetric rigidity in the root, which consequently bends

to the side with less turgor (Shabala and Knowles 2002). This was further supported by direct evidence of K^+ flux oscillations closely associated with root circumnutations (Shabala 2003), the fluxes being in reversed phases when measured from opposite sides of a vertically growing root.

Circumnutation and circadian rhythms have been well studied, and there are some reports of relationships between circumnutation and biological rhythms. Schuster and Engelmann (1997) reported that arabidopsis seedlings showed a very wide range of circumnutation rhythms. In *Helianthus annuus*, circumnutation speed and trajectory length exhibit daily modulation under 16 h light/8 h dark (Buda et al. 2003). Niimura et al. (2005) demonstrated that the modulation of circumnutation speed in arabidopsis inflorescence stems is regulated by a circadian clock, pointing to the existence of an internal oscillator which regulates the speed of circumnutation. Experiments with two loss-of-function mutants, *TOC1* (mutant which shortens the period for all circadian processes analyzed to date) and *ELF3* (mutant which causes arrhythmic circadian outputs under constant white light conditions, with an almost constant nutation speed), demonstrated genetically that the circadian clock controls circumnutation speed. These results strongly confirm the hypothesis that rhythmical membrane transport processes play a key role in plant circumnutation, showing a genetic-based control.

4.2.2 'Gravitropic Overshoot' Model

When Israelsson and Johnsson (1967) proposed a gravity-dependent model to account for circumnutations, their reasoning was essentially consistent with the Cholodny-Went theory, and their theory about circumnutations proved to be an attractive explanation of how oscillations might be driven and controlled specifically by gravity. Basically, they interpreted the 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. By interpreting the oscillations as gravity driven, their model described circumnutation as a special kind of tropistic behaviour (Fig. 4.5). The model also was consistent with the modern version of the Cholodny-Went theory for gravitropic responses, according to which both the plant's gravity detectors (statocytes) and the site of production of IAA are located in the apex of the responding organ. Nevertheless, the localization of gravisensing is much more pronounced in root tips than in shoot tips, which has to be taken into account when we try to explain circumnutations in shoots. Experiments performed under microgravity conditions aboard the Spacelab, however, revealed that gravity is not an absolute requirement either for the initiation or for the continuation of circumnutatory movements in *Helianthus annuus* hypocotyls (Brown 1993).

Kitazawa et al. (2005) demonstrated that gravisensing endodermal cells are required for shoot circumnutation in morning glory (*Pharbitis nil*). They

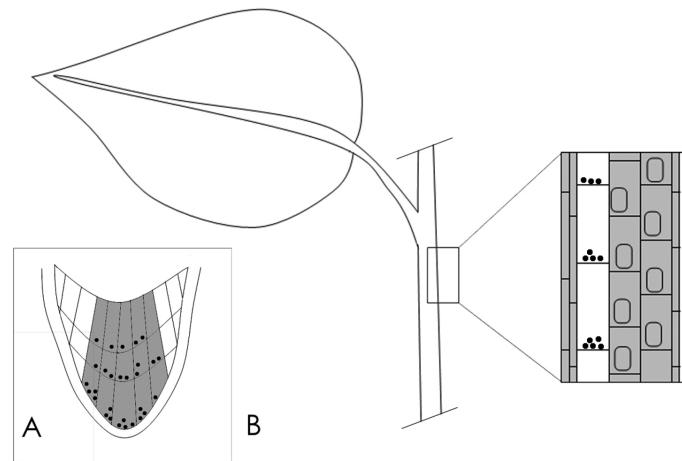


Fig. 4.5 Diagram of a root (a) and a stem (b), illustrating the regions of gravity perception

identified a gene, *PnSCR*, regulating circumnutation: the insertion of a single amino acid into the VHIID motif caused a loss of *PnSCR* function, resulting in an abnormal development of the endodermis required for gravisensing in the shoots of dicotyledonous plants, and suggesting that circumnutation is a gravity-dependent morphogenetic phenomenon. However, it remains obscure whether endodermis-mediated gravisensing is the sole prerequisite for circumnutation. To solve this issue, Kitazawa et al. (2005) analyzed the shoot circumnutation of two agravitropic mutants of arabidopsis, *sgr2* and *zig/sgr4*, which have endodermal cell layers with abnormal amyloplast sedimentation (Kato et al. 2002), finding that inflorescence stems of these mutants were defective in nutational movement. In addition, an earlier study demonstrated that circumnutation in an arabidopsis mutant, *pgrm*, known to show reduced gravitropism caused by the loss of starch granules, was smaller than that of the wild type (Hatakeda et al. 2003). Together, these data corroborate the hypothesis that gravisensing and circumnutation are interlinked, demonstrating also that gravisensing cells or the endodermis-mediated graviresponse is essential for circumnutation in morning glory. The identification of *PnSCR* as the gene responsible for gravitropism in climbing plants has provided a molecular basis for elucidating the detailed mechanism of the relationship between gravisensing/graviresponse and circumnutation.

4.2.3 The 'Mediating' Model

Johnsson et al. (1999) proposed a revised model which combines the two models discussed above: a two-oscillator model to explain the phenomenon of circumnutation. In this model, circumnutational movement involves a

gravitropic reaction which acts as an externally driven feedback oscillator, together with an endogenous or intrinsic oscillator which sends a rhythmic signal to the feedback system. The problem remains that there has been no direct evidence yet for the involvement of the graviresponse as an external oscillator in circumnutation. Indeed, this is rather controversial, as the following discussion demonstrates.

The hypocotyls of space-flown sunflowers show circumnutation in microgravity, although the period and amplitude of the movements are relatively small (Brown 1993). Recently, Yoshihara and Iino (2005, 2006) supported the existence of a close relationship between gravitropism and circumnutation in dark-grown rice coleoptiles: (1) circumnutation was interrupted by a gravitropic response and reinitiated at a definable phase after gravitropic curvature; (2) circumnutation can be re-established by submergence and a brief gravitropic stimulation in coleoptiles which have stopped nutating in response to a red light treatment. Moreover, *lazy* mutants show no circumnutation.

Inconsistent with these results, however, Yoshihara and Iino (2006) report cases in which gravitropism and circumnutation could be separated. Firstly, the non-circumnutating *lazy* coleoptile showed nearly a wild-type level of gravitropic responsiveness in its upper half, although this part was an active site of both gravitropism and circumnutation in wild-type coleoptiles. Secondly, coleoptiles could nutate without overshooting the vertical when developing phototropic curvature. The authors concluded that gravitropism influenced, but is not directly involved in the process of circumnutation. They also suggested that a gravity signal, shared with gravitropism, contributes to the maintenance of circumnutation.

4.3 Root Circumnutation

Although there have been only occasional suggestions in earlier literature that circumnutation may aid underground organs in soil penetration (e.g. Fisher 1964), this idea has more recently gained experimental confirmation in a study on paddy rice (*Oryza sativa*) varieties (Inoue et al. 1999). Rice, an aquatic plant in origin, must have evolved to acquire traits for securing seedling establishment under flooded conditions. However, many modern varieties fail to become established under such conditions. Inoue et al. (1999) demonstrated that varietal differences in seedling-establishment percentage were attributable not to seminal root elongation rate nor apparent weight of the seed in water but rather to differences in the penetrating ability of the seminal root into soil. To examine whether root tip circumnutation could have been a facilitator of soil penetration by the root, a spectrum analysis of the root tip rotations of various varieties of rice seedlings was performed. Those seedlings which circumnutated with a frequency of 2.0–3.4 cycles per

day showed the highest seedling-establishment percentage. From these results, it appears that root tip rotations with large spiral angles are more effective in enabling the root tip to penetrate flooded or very soft soil.

In shoots, the movement has been reported to be irregular (Orbović and Poff 1997) and both right- and left-handed. In roots, by contrast, at least of the commonly studied arabidopsis ecotypes, the movement is helical and right-handed (Simmons et al. 1995). The direction towards which the arabidopsis roots slant during elongation in the wild type is considered to be the right-hand because, when the plant is viewed from above the shoot apex, the root appears to move forwards in clockwise loops – right-handed, as is known in physics. However, it should be remembered that Linnaeus and other scientists (Hashimoto 2002) considered the above movement to be left-handed because they pictured the helix from its interior, in which case the view, logically, is reversed.

In wild-type arabidopsis, root movements are not random at all but rather show a clear right-handedness, i.e. they appear to be animated by a process which could be named ‘chiral circumnutation’. Mullen et al. (1998), investigating the kinetics of the gravitropic response of the *Arabidopsis* mutant *rgr1* (reduced root gravitropism), found that the frequency of the waving pattern and circumnutation was the same in *rgr1* and in the wild type. Thus, the waving/coiling phenomenon is likely governed by circumnutation patterns. The amplitudes of these oscillations may then be selectively amplified by tactile stimulation to provide a directional preference to the slanting.

Recently, arabidopsis root movements were reinterpreted as the combined effect of essentially three processes: circumnutation, gravitropism and negative thigmotropism (Migliaccio and Piconese 2001), albeit with some difficulty in discriminating between these. Piconese et al. (2003), using an RPM (random positioning machine, which subjected the material set at its centre to a general multilateral gravistimulation, approximating space conditions), showed that the observed root pattern depended only on the circumnutating movement, since both gravitropism and negative thigmomorphism had been excluded. Using wild-type ecotypes and different gravitropic mutants (auxin transport mutants such as *aux1* and *eir1*, auxin physiology mutants such as *axr1*, handedness mutants such as *1-6C*), they observed that wild-type arabidopsis roots made large movements of circumnutation only to the right-hand but auxinic mutants, such as *aux1* and *eir1*, showed a lack of regular chiral circumnutation: auxinic mutants are disturbed not only in their gravitropic response (*aux1* and *eir1* are totally agravitropic) but also in their chiral circumnutational movement. The process destroyed in the mutants controls not only gravitropism but also circumnutation: consequently, these seem to have a common basis at the level of signal transduction (Piconese et al. 2003). Indeed, in an earlier paper, Ney and Pilet (1981) concluded that circumnutation and gravitropism had a common basis because, when the roots were responding to gravitropism, they stopped circumnutating and then resumed the movement at the end of the gravitropic response. Similar

results were obtained by the Darwins (Darwin and Darwin 1880) who, on the basis of analogous experiments, stated that gravitropism is a form of modified circumnutation, and that all plant movements have a common origin, evolved from the simple (non-chiral) movement of nutation.

The experiments reported by Piconese et al. (2003), however, limited to arabidopsis roots, cannot fully support the above hypothesis, as they show that chiral circumnutation and gravitropism in arabidopsis primary roots seem to depend on auxin transport and/or physiology. This does not imply that the processes of circumnutation and gravitropism in plants are controlled solely by auxin, which probably would be incorrect (Firn et al. 2000), but simply that this hormone seems particularly highly involved, primarily or secondarily, in the circumnutating and tropic responses of plants, as suggested from the very beginning by the pioneers of auxin research (Went and Thimann 1937).

Although several hypotheses exist as to what triggers root waving, it is clear that auxin transport and signalling are required to propagate the differential growth response once it has been triggered. Historically, auxin was thought to be transported from the shoot tip to the root, but recent evidence shows that the root tip can also synthesize auxin (Ljung et al. 2005). The asymmetric localization of auxin efflux carriers in the plasma membrane determines the polarity of transport (Galweiler et al. 1998). These carriers relocate upon environmental stimulation and subsequently alter the overall growth response of the organ (Friml et al. 2002). Mutants of *WAV6/EIR1/AGR1/PIN2*, which encodes a putative auxin efflux facilitator, have defects in gravitropic responses and do not wave when grown on inclined hard agar plates (Okada and Shimura 1990; Luschnig et al. 1998). Mutants of *WAV5/AUX1*, which encodes a putative auxin influx carrier, are also defective in gravitropic responses but form root coils on inclined hard agar plates (Okada and Shimura 1990). Santner and Watson (2006) found that knockout mutants in the *PK3At* gene, which encodes for protein-kinase, cause aberrant growth of the primary roots of young seedlings, such that they wave. These genes were renamed *WAG1* and *WAG2*, to connote root phenotypes appearing to move to and from an agar surface.

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