TOPOCAL REVIEW

Motions of leaves and stems, from growth to potential use

To cite this article: Mathieu Rivière et al 2017 Phys. Biol. 14 051001

View the article online for updates and enhancements.
1. Introduction

In this review we start by presenting past works on the motion of aerial parts of plants. Then, we detail how they culminated with the construction of a classification. It is surprising that this scientific problem has had such an extensive lifespan: while it started with the ancient Greeks' observations, it is still a modern subject of investigation, even after extensive work in the 17th and 19th century. Among these investigations, the work of Darwin stands apart as he proposed the global view that movement is already present in any growth of the plant, and that such movements are just deformed and preserved in the mature state in order to fulfill diverse needs (Darwin and Darwin 1880). After presenting the shortcomings of the actual classification, we thus follow Darwin's idea and bring together, in a new perspective, all the motions that can be observed, from the earliest stages of growth to the final reversible ones. Note that although we briefly include in these last movements the carnivorous ones, we consider only alive movements, when the alive plant physiology plays a role. We do not consider the dead movements, when the plant parts are dead or dying, and the variation of water content that sometimes induces some spectacular movements, of rupture, expulsion, or just hygrometric curving movements, which attracted also many recent work such as Reyssat and Mahadevan (2009), Noblin et al (2012), Armon et al (2014).
reproductive soul but lacked a mobile and sensitive soul. That is to say plants, as opposed to animals, did not have the ability to move actively. The emergence of the *scala naturae* (see figure 2) during the Middle Ages, a classification derived from Aristotle’s principles, underlines the persistence of these ideas over time. The study of plant motion for its own sake consequently aroused little interest until the end of the Renaissance (Webster 1966, Whippo and Hangarter 2006). Still, the early observations and considerations on plant motions raised two natural and intricate questions: Are plants sensitive? And what are the mechanisms underlying plant motion?

2.1.2. From external causes...

Early reports associated plant motions with specific external events: for instance day-night cycles, the sun’s position in the sky or external mechanical actions such as wind. Plant motions then appear to be a consequence of these events or, put in other words, plants seem to react to these events. But reactions can be either active or passive: passive reactions occur without any energetic input from the plant; on the contrary, active reactions require an energetic input from the plant, and might also involve receptors or activators, that is to say sensitivity. The study of plant motions is then likely to give insight on plant sensitivity to external cues.

During Antiquity, Aristotle’s ideas about plant insensitivity prevailed. Because of that, passive mechanisms for plant motions were favored. For example, Theophrastus, one of Aristotle’s disciples, explained the slow re-orientation of an organ toward light by the direct action of the sun on the plant. He proposed that the parts more exposed to light would desiccate and this would result in a bending (Whippo and Hangarter 2006). It is interesting to note that the first known explanation of plant motion already relied on a differential mechanism.

The end of the 16th century, with the discovery of the New World, marked a turning point in the study of plant motions. Plant motions were described again—sometimes under spectacular forms—and began to arouse more and more interest. Giambattista della Porta reported that plants were attracted by water. Cristóvão da Costa described for the first time the rapid motions of touch-responsive plants, such as the *Mimosa pudica* which began to be imported from South America in Europe (Whippo and Hangarter 2009) (see figure 3). Prospero Alpini also repeated and extended Androsthenos’ observations of ‘sleep movements’ to other plants (Bell 1959). These striking observations, in particular the sensitive plants, led many botanists to study plant motions. However, most 17th century botanists kept trying to explain plant motions in terms of passive mechanical processes, in a way similar to Theophrastus (Webster 1966).

The 18th and 19th centuries were strongly marked by the study of light and gravity’s influence on plants and associated motions. During these two centuries, proper experiments began to be carried out on plant motions. Passive mechanical explanations for plant motions remained the norm, but Augustin Pyrame de Candolle made an important assumption in 1832. He proposed to explain the slow re-orientation of plants toward light in terms of growth heterogeneities between the illuminated and shaded faces of the bending organ (de Candolle 1832). It was rightly pointed out that the proposed mechanism was ‘a passive developmental’ mechanism (Whippo and Hangarter 2009) and did not imply sensitivity. Henri Dutrochet, who, as de Candolle, was more concerned with the metabolic reasons of plant motions (Bell 1959), proposed a passive mechanism of plant motions based on osmotic-driven turgor pressure changes (Whippo and Hangarter 2009). De Candolle and Dutrochet’s ideas are of great importance in the history of plant motions: by focusing on
plants physiology rather than on the environment, they breached the traditional passive and mechanistic approach of plant motions.

2.1.3. ...To internal mechanisms.
Webster discovered that plant sensitivity had been proposed by British botanists—Sir Robert Browne, Henry Power and Timothy Clarke—during the 17th century, but their ideas had a limited impact at the time (Webster 1966). In addition to that, Robert Sharrock was seemingly the first to interpret plant motions in terms of growth (Sharrock 1660, Webster 1966). Despite their lack of immediate impact, these ideas foreshadowed the fundamental shift that would occur during the 19th century. As already discussed, de Candolle and Dutrochet shifted the debate on plant motions to internal processes within the plant. This approach was further developed by Julius von Sachs and Julius von Wiesner with the additional question of the active/passive character of plant motions (Whippo and Hangarter 2009). Pursuing this route turned out to be fruitful and brought in ideas and results that are at the basis of our current knowledge of plant motions. They proposed that plant motions originated in combined changes of the cell wall extensibility and in turgor pressure (Bell 1959). Julius von Wiesner produced a strong proof that plant motions is an active process. By depriving a plant of oxygen he observed that it did not move anymore (Bell 1959), suggesting that an energetic input from the plant is needed in order to move. At last, in the case of the bending toward a light source, Sachs and Wiesner studied the relationship between the intensity of the stimulus and that of the response (Bell 1959, Whippo and Hangarter 2009). By doing so, they demonstrated that no simple law between these two intensities existed. This actually suggested that plant motions could not be explained in simple mechanical terms and involved some kind of sensitivity (Whippo and Hangarter 2009).

In parallel with this fundamental shift in the study of plant motions, the existence of endogenous rhythms in plants slowly became accepted. Observations of ‘sleep movements’ had been accumulated since Androstenos and Alpini’s reports. Carl von Linné would eventually extend this concept to other plants and to flowers in 1752, creating a flower clock with
species opening and closing their petals at different times of the day (Bell 1959, Somers 1999, McClung 2006). This led scientists to question the origin of these apparent rhythms. These rhythms were first thought to be forced by the day-night alternation (Somers 1999). In 1729, Jean-Jacques d’Ortous de Mairan worked on a sensitive mimosa displaying ‘sleep movements’. He observed these rhythms persisted even in the absence of day-night alternation though (McClung 2006). This was later confirmed by other scientists who additionally showed that temperature and humidity were not responsible for the observed rhythms (Cumming and Wagner 1968, McClung 2006).

A century later, Augustin Pyrame de Candolle went further and showed that the period of ‘sleep movements’ (figure 1 and 4) was not of 24 h. He consequently suggested an endogenous origin to these rhythms (Somers 1999), now called ‘circadian rhythms’ as they remain close to the external cycle of a day. The study of plant motions, which led to the birth of chronobiology, also greatly contributed to its further development since they remained the only known example of internal biological rhythm until the 20th century, when these rhythms and their importance were discovered in humans (McClung 2006).

In a context where the idea of insensitive plants dominated, plant motions were first seen as completely passive and determined by the external environment. This approach allowed a limited diversity of mechanisms to account for plant motions. Most mechanisms would rely on a direct and differential action of the environment on the tissues. The discovery of sensitive plants such as the Mimosa pudica intensified the interest in plant motions and led some botanists to consider the concept of plant sensitivity during the 17th century. The external and mechanic approach to plant motions was slowly abandoned in favor of a more internal and physiological approach. This transition from external causes to internal mechanisms shows through the traditional classification of motions.

2.2. Traditional classification
The wide diversity of motions observed in the Plant kingdom has naturally led to a need of classification. Motivated by the desire to describe the biological functions of these motions (Firn and Myers 1989, Hart 1990), scientists have mostly answered three cleaving questions: Is the motion a directional response to adapt to the outside environment? Is the motion triggered by a signal in the environment? And finally, is the motion linked to growth?

2.2.1. Tropisms versus nastic motions.
The first question distinguishes whether the direction of the movement is dictated by a biased environmental stimulus or by the intrinsic asymmetry of the plant itself. Since this feature is easily observable, it became the main distinction between plant motions. Two main classes of motions were then defined: tropisms and nastic motions (Heller et al 1993, Raven et al 2007).

Stemming etymologically from the Greek word ‘tropos’ meaning ‘a turning’, the term tropism characterizes a re-orientation of the plant in response to an anisotropic signal in the surrounding environment (Gilroy and Masson 2008). Plants can either turn toward or away from this signal. Tropic motions are caused by a differential growth induced by the
differential exposure to external signals in the plant. Among all the possible environmental biases, light is of prime importance for leaves and stems. Phototropism is the re-orientation motion of a plant organ toward a light source (see figure 5(a)). Historically, it has drawn a lot of attention and its study eventually led to the discovery of auxin (Went 1926, Bell 1959, Goyal et al 2013). Many different hypotheses are still debated nowadays, and the study of phototropism remains an active field of research (Coutand et al 2015). However, it is widely accepted that light interacts, directly or indirectly, preferentially with auxin on the most illuminated side of the plant, inducing a greater growth on the other side, to finally bend the plant toward the light source (Whippo and Hangarter 2006).

The second obvious and permanent anisotropy in the environment of plants is the gravitational field. Their response to it, called gravitropism is familiar to the eye as all species display the tendency to realign themselves vertically after any perturbation (see figure 5(b)). This was extensively studied starting from the 18th century (Dodart 1700) and throughout the 19th century (Knight 1806, Hasenstein et al 2013). Sachs observed that the magnitude of the gravitropic response (defined as the rate of reorientation) depended on the orientation of the plant, following ‘a sine law’ (Sachs 1882). The microscopic origin of gravisensing resides in the sedimentation of amyloplasts called statoliths in specific cells (statocysts) (Morita and Tasaka 2004). The coupling between sensing and movement via biomechanics has been formalized by Moulia and Fournier, emphasizing the role of differential growth in the control of gravitropic movement in order to adequately bend the plant toward the vertical (Moulia and Fournier 2009). Gravitropism remains a very active research area. Recently, a unifying model of shoot gravitropism has been proposed explaining the universal kinematics of gravitropic observations. (Bastien et al 2013, Dumais 2013) Some current studies are also investigating the specific mechanisms of gravity perception (Chauvet-Thiry et al 2015, Pouliquen et al 2017).

Physical obstacles can occasionally introduce a bias in the environment. In this case, the sensing of this asymmetry is directly done by contact. This tropism is labeled as thigmotropism (from the Greek ‘touch’). Typically the climbing plants which grow around an obstacle have a rotating motion linked to this asymmetry (Isnard and Silk 2009). Miscellaneous other symmetries can be broken, each one leading to a different kind of tropism. We can cite water availability leading to hydrotropism (Eapen et al 2005, Cassab et al 2013) which mostly concerns roots (subject beyond our scope but addressed in this issue (Kolb 2016)). More generally, if any chemical concentration field is anisotropic, chemotropic motions can be observed as in the case of the pollen tube (Rosen 1961, Higashiyama and Takeuchi 2015). One can finally mention traumatotropism which is linked to spatially localized wounding of a plant (Hart 1990).

By contrast, if an asymmetry is present not in the external environment but in the plant itself, other directed motions can emerge. These are nastic motions and, as tropisms, often consist in the bending of an organ. These internal asymmetries typically originate from anatomical particularities. Thigmonasty is the most striking example of nas-
tic motion, where the leaf curls up at contact. This compaction actually gave the name ‘nasty’ as ‘nastos’ means ‘compact’ in Greek. Sensitive plants like *Mimosa pudica* (Roblin 1979, Braam 2005), *Albizia saman* (Palmer and Asprey 1958) or *Averrhoa carambola* (Bruce 1785) display thigmotropism. These motions are directed by a ‘pulvinus’ (from the Italian ‘cushion’, for their expanded soft tissues). It is a plant articulation which enables a rotation movement of leaflets or leaves. Differences in turgor pressure between the extensor and flexor cells situated on both sides will lead to a motion around the articulation (Gorton 1987). This might also be due to a change in the permeability of the membrane between the two kinds of cells, but the key point is that differential inflation of tissues induces a motion directed by the articulation. The same anatomical specificity rules nyctinasty. This other common nastic motion of the leaves or leaflets that occurs at dawn or dusk (see for example figures 1 and 4 or supplementary data 1: Time-lapse).

If only light is responsible for the motion one can label it as photonasty. The closing mechanisms are different in the spectacular case of the snapping of carnivore plants (Forterre et al 2005), but it is still a thigmotronic behavior in the sense that an external stimulus (here the successive deformation of few hair cells) triggers a motion directed by the organ symmetries.

Other motions linked to anatomical anisotropy include epinasty (Palmer 1985) and hyponasty when, respectively, the adaxial or the abaxial face of an organ grows faster than the other. This may result from microscopic differences in the tissue properties like the extensibility of the cell wall for example. Epinasties are associated with blooming while hyponasties are responsible for the leaf motion due to petiole differential growth (Dornbusch *et al* 2014). Tissues might also be affected differently by a change in temperature, as in the case of thermonasty which is a remarkable phenomena observed in flowers like tulip or crocus (Wood 1953) but also in sensitive plants such as the *Mimosa pudica* (Roblin 1979). Opening or closing then seems to be controlled by variations of temperature.

The corresponding mechanisms of sensing as well as the biochemical regulation of the sensing–response leading to these tropisms and nastic motions are beyond the scope of this article, but it is a very active subject evidenced for example by the very recent research concerning mechanical sensing (Peyronnet *et al* 2014, Mouli *et al* 2015, Coutand and Mitchell 2016), osmotic stress sensing (Osakabe *et al* 2013), photo-sensing (Galvão and Fankhauser 2015), gravi-sensing (Blancaflor 2013), autotropism (Peaucelle *et al* 2015) or shape sensing (Hamant and Moulia 2016).

### 2.2.2. Origin of the motion.

When the trigger is the environment, one says that the motion is ‘paratonic’ (Firn and Myers 1989). This is obviously the case for tropisms as it is the environment itself which leads the motion. For nastic motions, the situation is more contrasted. A first subgroup of nastic motions are par tonic, like thigmonasties (also called seismonasties (Vanden Driessche 2000)), photonasties or thermonasties. Following the same terminology, the rest of nastic motions is categorized as ‘autonomic’ to state that the origin of the motion is intrinsic to the plant itself. We find in this subgroup the motions linked to the development of the plant

---

1 Time-lapse videos are accessible online at [www.msc.univ-paris-diderot.fr/plant-dynamics/review/](http://www.msc.univ-paris-diderot.fr/plant-dynamics/review/)
(epinasty/hyponasty) but also those linked to circadian rhythms (nyctinasty)².

### 2.2.3. Irreversibly of growth.

Macroscopically speaking, most plant motions are the kinematic manifestation of a differential dilation of tissues. As discussed above, this was already understood by the 19th century botanists. According to Skotheim and Mahadevan, motions can be classified according to their characteristic timescale and lengthscale (Skotheim and Mahadevan 2005), violent motions occurring faster than a characteristic poro-elastic timescale (Forterre 2013) are driven by the release of previously stored elastic energy.

If only swelling motions are involved they are much slower, the quickest one being that of *Mimosa pudica*.

The particularity of plant cells lies in the presence of an outside cell wall able to resist considerable hydrostatic pressure built from an osmotic origin, the so-called turgor pressure. One could say that turgor pressure is the growth motor force which the plant controls via osmotic pumps (Hill and Findlay 1981). In particular, it is well-known that motions related to circadian rhythms are associated to osmotic variations

²The 'night' in the 'nyctinasty' name does not mean that the night is responsible for the movement. Plants follow their own circadian internal rhythms, as shown by d’Ortous de Mairan and de Candolle. For instance, *Cesalpina sp.* raise their leaves before dawn, and lower them well before sunset, indicating an internal rhythm shorter than 24 h. The internal movement will synchronize with the outside oscillation, with jet-lag periods if suddenly out of sync. Some *Avrithhoa sp.* can nonetheless exhibit both circadian rhythms (nyctinasties) and photonasties. The darkening of the sky from a coming tropical rain induces a fall of the leaves (personal observations). *Albizia saman* present the same behavior, hence its vernacular name 'rain tree'.

(Gorton and Satter 1983). On the other hand, some have argued that the rheology of the cell wall is even more important (Cosgrove 1987). Nowadays, it is commonly accepted that turgor pressure is the mechanical motor of expansion, but the subtle balance between this pressure and the complex rheology of the cell wall is what decides the equilibrium shape and size of the tissue (Geitmann and Ortega 2009).

Although the naïve definition for growth could simply be a geometrical bulk extension of the tissue, there is a consensus to define it as the irreversible transformation in the tissues leading to their extension. This makes a distinction between reversible motions, linked only to temporary changes in osmotic pressures, and irreversible motions, linked to definitive changes in the cell wall mechanical properties.

This irreversibility has been taken into account by adding plasticity in the models (Passioura and Fry 1992, Geitmann and Ortega 2009). Concretely, a threshold is needed to create a biological irreversible growth.

Answering the three former questions for each of the typical motions described above, figure 6 sketches a three dimensional diagram of typical plant motions, the axes being the irreversible nature (or not), the external directionality (or not) and the autonomic or paratonic character.

### 2.3. Issues of this classification and Darwin’s point of view

#### 2.3.1. Criticisms.

While this classification was and remains very useful on pragmatic grounds, one can point out specific issues. Firn and Myers criticized the fact that a given category would embrace very different mechanisms, and pledged for a more reductionist approach (Firn and Myers 1989). This is a controversial criticism as, for example, a recent macroscopical model has
found universal mechanisms in gravitropism (Bastien et al 2013) independently of any microscopic detail, thus proving the usefulness of such approaches.

Historically, tropisms were ordered according to a hierarchy that put forward phototropism, followed by gravitropism and other minor tropisms. One can object that the so-called ‘autotropism’ is too often ignored by plant scientists (Firn and Myers 1989). Autotropism is the observation mechanism whereby most plants have a natural tendency to grow straight, which was shown to be important if one wants to model even only gravitropism (Bastien et al 2013). Referring to the definition of tropism, autotropism is the tendency of the plant to align with itself. As pointed out by Firn and Myers in an interesting note: ‘differential growth is the stimulus for autotropism itself’ (Firn and Myers 1989). In other words, autotropism is a tropism which ‘external’ broken symmetry is actually an internal one!

The following example shows that some movements have an ambiguous position in this classification.

2.3.2. The ubiquitous circumnutation.
Two periodic motions of plant organs, circumnutation and nutation, are indeed difficult to fit in the above classification. While the first is a revolution motion (see figure 7(a) and supplementary data 1: time-lapse), the second is an oscillatory motion (see figure 7(b) and supplementary data 1: time-lapse). The circumnutation of climbing plants was already known by British botanists of the 17th century (Webster 1966) and began to be studied by Hugo von Mohl and Ludwig Palm in the first part of the 19th century (Baillaud 1957). It was not until 1880 and the Darwins’ The power of movement in plants that they were popularized. Charles Darwin’s motivations in writing this book were not really centered on plant motions though, but rather on his previously published theory of evolution. He thought that behavior, as living beings, evolved and adapted. He consequently sought general mechanisms in plant motions and evidences of adapted behavior (Whippo and Hangarter 2009). Consistent with these motivations, Darwin proposed that some motions were in fact modified circumnutations (Darwin and Darwin 1880), showing an adaptation of plant behavior to its environment. As a consequence, the book was mainly concerned with ‘modified circumnutation’, and showed that it was widely spread across the plant kingdom. Darwin not only observed that many different species displayed circumnutation motions but also that, for each plant, several organs could undergo circumnutation such as hypocotyls, leaves and stems. He described circumnutation in terms of differential growth between the faces of the moving organ. This differential growth being itself due to combined changes in turgor pressure and cell wall extensibility. It is not clearly stated in The power of movement in plants that nutation is an autonomous motion. It is however implied. Darwin makes clear that circumnutation is occurring in every growing organ but he never refers to any external stimuli.

Since then, (circum)nutation has been extensively studied and is still an active domain of research (Mugnai et al 2015). The exact nature of nutation has been a source of debate for a long time (Baillaud 1957) and is not clearly established yet (Stolarz 2009, Baskin 2015, Mugnai et al 2015). Two of the main questions about nutation are: Is nutation only based on differential and irreversible growth? Is nutation really autonomous or does it result from the interaction with some external cue?

The growth-based mechanism for nutation had first been proposed by Charles Darwin and later found theoretical support with the Cholodny–Went model (Went 1926). Concerted characterizations of growth
rates and nutation show that nutation is indeed linked to growth rate inhomogeneities (Baskin 1986). However, evidences of reversible processes being involved in nutation have accumulated since the end of the 1980s. Contractions have been measured in the bending zone of (circum)nutating organs, both at the organ level (Berg and Peacock 1992, Stolarz et al 2008) and at the cellular level (Caré et al 1998). These contractions suggest a role of turgor in nutation. Therefore, both irreversible and reversible processes appear to be involved in nutation.

The autonomous character of nutation postulated by the Darwins was also soon challenged. It was proposed that nutation was in fact paratonic and the influence of several external cues on nutation was assessed (Baillaud 1957). Among all the cues tested, gravity has drawn most of the attention, and its influence is still debated nowadays (Baskin 2015). A natural idea to test gravity’s influence on nutation is to get rid of the gravity signal. This can be achieved with the use of a clinostat, a slowly rotating device. As soon as 1883, Baranetzky observed the disappearance of nutation in plants placed on a clinostat (Israelsson and Johnsson 1967). Although, the use of the clinostat a century later produced contradictory results, nutation stopping and continuing having both been observed (Johnsson 1997). The limitations of the clinostat were pointed out and space experiments were performed. Brown et al. observed the initiation and the continuation of circumnutation in true microgravity but with a significantly different behavior than observed on the clinostat (Brown et al 1990). Johnsson et al showed that small amplitude nutation persisted in microgravity and that increasing gravity resulted in higher nutation amplitudes (Johnsson et al 2009). Finally, the use of agravitropic Arabidopsis thaliana mutants was made possible these last few years and also suggests a role for gravisensing in nutation (Kitazawa et al 2005, Tanimoto et al 2008).

The position of nutation movements in the traditional classification of motions is unclear. Regarding the irreversible nature of the motion, nutation seems to result from both irreversible growth and reversible length variations linked to turgor variations. On the ‘trigger’ axis, we have seen that gravity is likely to play a role in nutation occurrence (paratonic effect). But it might only be the amplification of an endogenous oscillation (autonomic). This leaves the question of the motion directionality unanswered since it is not clear if gravity triggers nutation or not. In conclusion, nutation is spread everywhere in our graph (see figure 6).
Based on the observation that both nutation and autotropism do not find a coherent position in this classification, we propose to look at plant motions from a different perspective.

3. A vision centered around plant development

[...] For it might have been asked, how did all these diversified movements for the most different purposes first arise? As the case stands, we know that there is always movement in progress, and its amplitude, or direction, or both, only have to be modified, for the good of the plant, in relation with internal or external stimuli (Darwin and Darwin 1880).

In this part we want to develop a new perspective according to which, when the developmental point of view of the plants is taken into account, all the movements naturally find their place and coherence. Foremost, we shift the focus from considering motionless plants which some trigger can put in an abnormal state of motion, toward the idea, following Darwin, that there is movement from the beginning. This must start with a different understanding of what movement is. Instead of saying that there is always (and only) circumnutation, we consider all the movements, and their logic in the progressive development.

3.1. Growth is the first movement

When the plant aerial meristem develops, it produces on its side microscopic bulges of cells (primordia) which differentiates, at a microscopic scale, and then expands considerably to form visible organs (see figure 8(c)).

According to the autodidact Hofmeister’s point of view, the first appearances of primordia, even though the developmental axes are not changed, are already due to inhomogeneous and anisotropic growth (Hofmeister 1868). For instance, the leaf primordium first extends in length, with a smaller extension in width, and an even smaller extension in thickness. Here, two symmetries are already broken: the tip/base and the abaxial/adaxial symmetries.

From a purely physical point of view, this anisotropic growth can be considered as a deformation movement, hence a complex—internal—movement: the position of different elements are changing relative to each other, and cannot simply be ascribed to a change of referential nor to a change of scale. If this viewpoint can be accepted for the beginning of the plant development, it is even less questionable for next step, where the organs (stem, leaves and ‘modified’ leaves in the sense of Goethe) expand considerably, easily by a factor 1000, from 100 μm to 10 cm. This expansion again happens in a very anisotropic way, the leaf and the stem becoming proportionally thinner, the stem in two dimensions and the leaf only in one. These can be called areal or length extension movements.

By just following Darwin, we could already say that these movements are there from the beginning of the plant’s organ life, with their own predefined aims, axes and symmetries. This internally defined growth has been labeled ‘autotropic’ or ‘automorphogenetic’ and described in many cases (Stanković et al 1998). These anisotropic movements are the cornerstone on which all the other movements are going to be constructed.

To guide us we thus have to follow the normal course of the organ development, and see how the various movements unfold.
3.2. Movement is reversing

3.2.1. Hypocotyl/stem.

One can question the use of the term ‘reversal’ by arguing that such motions are not observed in the following extension phases. However, looking at how the development of the plant organs occurs, it is very rare to see a monotonous, homogeneous, expansion from the beginning to the end. The first case of growth, for instance the growth of an hypocotyl from the seeds, often shows a typical hook shape, with the cotyledons pointing toward the ground. This shape seems to remain constant as the hypocotyl expands and the cotyledons rise, especially in dark conditions, in an attempt to escape the ground, outside of which it can finally straighten (see figure 9 and supplementary data 1: time-lapse).

From a Darwinian—selection point of view, it is clear that the advantage of such a shape is to protect the apical meristem while going through the ground, as well as protecting the cotyledons from being opened and twisted, if not torn off. One could presume that the same protection benefit makes so many inflorescence stems first grow with this specific hook shape. But while the need of protection is understandable for the first flowers that have to grow through the snow or old leaves (e.g. Galanthus, the snowdrops), the true benefit is less clear in many flower stems where it is still observed (see supplementary data 2: flower stems). It is very common that flower stems present this hook or curved shape at one or several stages of their development, at the expansion, through flowering, or through maturaton. This common occurrence could be the recurrence of the primitive cotyledon hook growth.

This shape formation may again not be seen as a motion, as it is kept constant for a while. However, if the development of the cells of the stem is followed, one observes that cell divisions occur near the cotyledons and apical meristem, and that these cells considerably expand longitudinally to form the hypocotyl. To keep the shape constant in time, and at a fixed distance from the apex, the elongating stem must first curve considerably, to form the hook precisely, and then to uncurve to recover an expanding straight stem. If we follow the cells of the stem, we thus see its result as a reverse motion, leading first to curvature and then to straightness. This oscillation in the material space coordinates is not perceived in time as the shape is kept constant with a flux of new cells (the ’fountain effect’, see figure 9) (Silk & Erickson 1978).

We can thus see that in the history of these cells, during this first early growth, there already is an oscillation of the expansion, with curving and then uncurving. This movement can be seen as the first reversing movement in the plant, and as the basis for the next ones. During this first motion, careful observations show that the curving is first due to the expansion on the outward side, and the uncurving to the expansion of the inward side (Silk and Erickson 1978). In this way this movement, even if reversing in its effect, is not a reverse movement at the cell level (expansion then contraction), but always an expansion, on one side and then on the opposite side of the organ, making it a pure growth movement as discussed above.

3.2.2. Folding-rolling/unfolding-unrolling of leaves.

This basic phenomenon of enhanced expansion on one side, creating a curvature, then followed by the expansion on the reciprocal side, is also very common in the case of leaves. From the early stages after the primordia, when the elongation and lateral expansion first appear, to the final straight petiole and flat leaf, it is easy to make a mental shortcut and imagine that it was simply an expansion, even if slightly anisotropic. However, except for a few cases, this development is far from being so simple, and on the contrary goes through non-straight and non-flat states.

The process is similar to the apical hook’s one, but on the structural parts of the leaf i.e. the veins. The main vein has an asymmetric development, enhanced on the back-abaxial side, which induces a curvature and a displacement of the lamina toward the opposite front-adaxial side, creating a fold (Couturier et al 2012). It can create a simple-fold leaf or leaflet, but if the leaf keeps developing for a long time in a protected enclosed place (the temperate bud or its equivalent), then other folds will appear following the succession of appearance of secondary veins (Royer 2012). Notably, these folds have a direct impact on the shape of the leaf, the first one being the symmetry of the lamina around a fold (Couturier 2009). For leaves with many parallel veins, as in monocotyledons, this asymmetric growth can create the rolling of the whole leaf, on one common roll or on two. This first state of leaf development limited in size, can be seen as the moment when the leaf takes its characteristic shape. This first state, rarely flat, is called 'prefoliation' (Adanson 1763).³

The second movement is a final expansion, outside of the bud, without much change in the global shape of the leaf, even if the magnitude of the expansion is larger. Following Adanson, we can name these movements ‘foliation’. After this expansion, the leaf is eventually flat. This means it has to perform at least all the reverse of the anisotropic growth it experienced during its prefoliation, like the hook has to reverse its curvature. In the case of non-flat leaves however, the reciprocal expansion seldom compensates the first one. Instead, it leads to overshooting and, again, to a non-flat leaf but in the opposite direction. This reverse movement does not always take the exact reverse path, and if folded leaves often simply unfold, or rolled leaves unroll, it happens that folded leaves open by rolling in

³ Adanson invented this description during his first trip in Africa as he did not have the possibility to see all the plants in their reproductive state, e.g. with flowers, following Linne’s tradition. So he tried to describe all the other possible characteristics, prefoliation being one. Since then, it has been regularly referred as a particularity, but never really used nor studied.
the opposite direction (see figure 10 and supplementary data 3: reversing), or that rolled leaves unfold (see supplementary data 1: time-lapse).

3.3. Movement within the tropisms

The first expansion of leaves—prefoliation—does not show any sign of dependence on the physical surroundings, protected as they are in the bud or bud-equivalent, and following the stem axis. Conversely, the movement of the hypocotyl hook growth is a first example of dependence on the environment, the first cue being gravity. In the rise through the upper layer of the soil (snow, leaves), gravity gives a good cue for the successful direction of growth. The global movement of the expanding stem is defined as ‘negative gravitropism’ (against the direction of gravity). However, we can see that the apex and the cotyledons are always tilted downward, so we could say that the stability of this shape (the hook) is due to a ‘positive gravitropism’ (same direction as gravity) of the apex. The oscillation of curving/uncurving presented by the cells of the stem can thus be ascribed to a shift from positive to negative gravitropism during their development.

Reversal of gravitropism throughout development is quite general, and can be seen in many plants and organs. For instance, during their foliation, leaves can...
first point out upward or downward (as in figures 8, 10 or 11), before adopting their final orientation. Some authors call it plagiogravitropism (Heller et al 1993). For compound leaves the same can be observed for the rachis: curved at the apex, but perfectly straight at the stem junction. In the latter case, it is not certain if gravity is important in the final position as perfectly straight secondary stems are observed in rice (Oryza sativa L.) and Arabidopsis thaliana grown in the absence of gravity (space station) (Hoson et al 1999). This last study shows that autotropism dictates the straightening of the plant while gravity only seems to influence the stem junction angle. It is clear from these first examples that the surrounding physical world in which the plant is immersed is an important clue—rather than cue—for its development, hence movement. We could say, as Firn and Myers, that it is part of the growth system (Firn and Myers 1989).

A surprising effect could be to see how the stem succeeds to be perfectly straight after the gravitropism reversing oscillation. One interpretation is that gravitropism is so efficient that it not only leads to the right direction, but also to a perfectly straight stem. However, Bastien et al recently refuted this hypothesis (Bastien et al 2013). They tilted plant organs and observed their gravitropic motions. These motions could not be reproduced with a pure gravitropic model including an active term for the tendency of each stem part to align with the gravity direction. The trajectories were recovered thanks to an additional term accounting for the tendency of the stem to grow straight (even in the absence of gravity). This term covers what previous studies have combined as autotropism, and whose importance has been underlined in many observations (Hoson et al 1999).

Here we propose that a natural hierarchy of tropisms lies in their temporal succession during the development. The first would be autotropism, existing from the very beginning of the development. The second would be gravitropism, so obvious and universal, for the direct evolutionary reason of going above to spread spores then leaves. Finally would come phototropism, and all the other possible tropisms influencing the development movements. All these influences are simultaneous with their respective weight, depending on the plant and also its state of development (with possible inversions as seen above), history, etc.

It would be strange to consider growth without the influence of these tropisms, or to consider that the movement of the plant would be only a response to an external stimuli, as implied by the notion of ‘tropism’.

One question that arises from this description, of both expansion movement and autotropism, is to know how this can be achieved. Namely, how can the anisotropically developing plant perceive its own shape, to the point of having regulations to bring it back to the target shape? In other words, what ‘ proprioception’ (perception of self) enables autotropism? In order to answer this question, some physical studies focus nowadays on the possible role of hydraulic signaling (Louf et al 2014).

3.4. Oscillatory movements
These first reversing movements, often guided by gravity’s external cue, already show a reversion, as the plant goes locally from curving to uncurving, and also changes direction, from upward-downward to roughly horizontal. Note that the word ‘movement’ is often understood in our animal world as ‘reversible movement’, that can be repeated several times without much change in the organism. This happens later in the plant’s development, in the famous case of nutation (including circumnutation). In this case, the hypocotyl, once outside of the dark and straightened vertically, as the later stem, can nutate, oscillating around its vertical position in an often irregular manner. Its trajectories range from perfectly circular, through elliptic and to planar oscillations (see figure 7) (Yoshihara and Iino 2005, Stolarz et al 2008). The nutation’s oscillation frequency can also be modulated on a circadian basis (Buda et al 2003, Charzewksa and Zawadzki 2006). Notably, the frequency is always much higher than the circadian rhythm, supporting the hypothesis of an internal clock. Nutation also appears in compound
leaves’ rachis, with oscillations in the horizontal plane from left to right (see figures 7(b) and 12 or supplementary data 1: time-lapse).

More generally, all the movements of the leaf before it becomes flat present some degree of oscillation. Most of the leaves originally develop in a folded or rolled compact shape; this is the ‘prefoliation’. Next, they perform the reverse movement in their expansion phase, before eventually becoming flat. All these movements may present diverse degrees of oscillation. For instance, the curvature associated with the unrolling can oscillate (figure 11 (7, 8, 9) or supplementary data 1: time-lapse). Despite their diversity, oscillatory motions are unified by some common features. They are observed just before the end of the organ expansion. Since the organ oscillates around its final shape, in particular for straight and vertical stems, we propose that these movements are a way to enhance the perception of the alignment with gravity, similar to photography where one reaches a more precise focus by going out of focus on both sides. More generally, these movements happen not only for the plant to perceive the alignment with gravity, but also for the rachis to straighten out (possibly inclined with respect to gravity), or for leaves to become flat, it is tempting to think that they are part of perceiving not only the position with respect to gravity (gravitropism), but also with respect to the shape of the organ itself (autotropism). In a way, oscillatory motions could be an answer to the problem of proprioception. By moving one part, with respect to another, the plant could feel the corresponding deformation, as a response to a known solicitation, and finally deduce its original shape from it.

3.5. Movements within the symmetries
All these oscillatory movements have particular symmetries that can be traced back to the symmetry of the organ itself, as in the case of nastic motions. For instance, a hypocotyl or a stem are supposed to be radially symmetric. Hence, their movement tends to be circular (see figure 7). On the contrary, the abaxial and adaxial faces of a rachis are not symmetric, but the lateral faces are. This results in a left–right oscillatory motion (see figures 12 and 7(b)). These quick nutation oscillations can then be simply related to the preserved symmetry of the organ.

However, the slower reversion of movement, which lasts for the whole development, reveals broken symmetries. The bending of the leaves is simply related to their different front and back (adaxial - abaxial sides): it first curves backward, with adaxial upward, then points downward (see supplementary data 3: reversing and supplementary data 1: time-lapse). Doing so the adaxial part of the leaf is turned upward while the abaxial part of the leaf is turned downward (as in figures 10 and 11). However, stems and hypocotyls, which are supposed to be symmetric, can also bend downward to one side (figures 8 and 9). A priori, the bending direction could be thought to be arbitrary, given by the amplification of some fluctuation (noise). But if we look at the tip of hypocotyls, there are two cotyledons that break the circular symmetry into two orthogonal symmetry planes: front/back of the cotyledons, or left/right. These two directions can then be privileged for bending (see figure 9 or (Abbas et al. 2013)). Since bending along the front/back of the cotyledon breaks the symmetries between them, and that one is exposed to the earth while the other one is protected, it is more reasonable to think that in the ground the bending happens on left/right side of the cotyledons, as this favors neither of them. It also allows the stem to point out quicker between the cotyledons (see figure 9).

The stem symmetry can also be broken in the specific case of folded leaves with an alternate distichous phyllotactic pattern. In some instances, one can observe that the folded leaves are turned horizontally on alternating sides so that they present their folding main vein on the same side of the stem (Charlton 1998). This particular prefoliation usually produces leaves with asymmetric sides, the outer side growing further down near the petiole, with alternating sides from leaf to leaf. In such a situation, it seems that the whole stem reacts as the main folding veins of the leaves, so it bends globally downward, with its back turning to the bottom, and its front turning up (see figure 8 and supplementary data 4: leaf stem hook). In many curving flower stems, we have the same symmetry breaking phenomenon. However the symmetry is already broken for secondary stems starting from the axillary buds, between a previous stem and a leaf base. This attachment gives an asymmetry similar to the adaxial/abaxial one of a leaf, and thus leads to very similar shapes (see supplementary data 2: flower hook).

3.6. Reversible movements are regressions
Among reversible movements, we can see a difference between the quick alternating movements, i.e. the nutations, and the slow reversing movements. The former seem to appear only near the end of the expansion, just before it stops, for instance in the oscillating curving of the compound leaf localized at the end of the growing part. The latter start from the very beginning of the organ expansion, with its gravitropism, and last until the end of its extension. Another difference is that we can recognize reversing movements in the movements that are still observed in the mature organ, such as the reversible movements of circadian rhythm and sensitivity.

For compound leaves, reversible movements are of two types: either the leaflets come forward (and slightly upward) against each other, or they go down (also against each other). In both cases we can recognize the movements exhibited by growing leaflets. Most of the folded leaflets will first head downward, open, and then rise horizontally (figures 3, 8, 10 and 11). When the leaflets are downward, before rising up, the sensitive/circadian movements is a reversing downward movement (figures 3 and 11). On the contrary, most leaf-
lets that are first flat just open during their maturation. Their sensitive/circadian movements is a reversing closing movement (figure 13). Of course, some exceptions exist, as some folded leaflets can open without heading downward. But their sensitive/circadian movements is just a closing regression (see supplementary data 5: Reversible movements). Looking at the development thus explains the origin of the two possibilities (closing straight or downward) shown in figure 1.

We can thus formulate that the reversing growth motions are the basis of future reversible sensitive/circadian movements, or more precisely that these sensitive/circadian movements are regressions among the normal growth movements.

As stated above, these movements are now driven by a reversible change of turgor pressure in cells with soft walls, typically localized at the base of the principal or secondary petiole, forming an enlarged section called the ‘pulvinus’. This means that the movement that was then linked to irreversible growth and through the whole body of the organ, becomes reversible but also localized to a particular place, essentially at the base, where it can act as a joint.

In sensitive plants, sensitivity movements are generally similar to those associated to circadian rhythms. It seems to be the case when sensitivity movements are protective movements, to protect the leaf from mechanical (animal) aggression for example. Then the 'sleep move-
ment’ can also be considered a protection movement, as proposed by Darwin and Darwin, protecting against thermal or hygrometric stress (Darwin and Darwin 1880). However, there are cases in which sensitivity movements are not protective but aggressive, as for carnivorous plants. In this particular case, they do not need a protection at night and do not present the same movements on a circadian rhythm. Whether these movements are truly reversible is a subject of debate. Although they involve physical phenomena quicker than water movements and typically do not require pulvini, they might also involve growth in the process. Nevertheless, these motions also appear to be regression of growth movements (supplementary data 5: reversible movements).

3.7. Partial conclusion
We thus see that, starting from the earliest stages, the development of stems and leaves can be decomposed into several successive movements. The first one, the prefoliation, is an anisotropic expansion without any change of axis and where the shape of the organ is settled. The second one, the foliation, involves the environmental clues, in particular gravity. We prefer ‘clues’ to ‘cues’, as the plant is integrating information rather than being subjected to an order from the environment. This second movement displays large asymmetric movements and reversals before reaching the final target state. The final state is mainly horizontally flat but turned toward the light, for the leaf, or straight for the petiole and the stem. But before this final state, one observes rapid symmetric oscillations (the nutations). These might exist in order to make the final convergence more precise, thus helping the proprioception of the plant. In opposition to Darwin, we see that nutations come last, and are thus not strictly speaking at the basis of the other movements. The fact that they are between the pure growth movements, and the final reversing movements, indicates that they could present both characteristics as current debates suggest. Interestingly, we also see that the mature movements (sensitive, carnivorous or circadian movements), the most fascinating to a first observer, are partial regressions of the second phase of movements (foliation). Paraphrasing Darwin, we again stress that development motions appear prior to their possible use in maturity for whatever may be ‘the good of the plant’ (Darwin and Darwin 1880). An indication of this is their ubiquity and similarities (see supplementary data). It is striking that some second development motions (within the tropisms) remain in mature states, either because they are not too costly, in particular in tropical environment, or because they can be useful, but for as many different reasons as there are different environments.

If undisturbed, the plant follows its natural growth path and some effects may seem non-existent. For instance, the alignment with gravity may seem spontaneous without the appearance of any special regulation, or gravitropism. On the contrary, if the plant is disturbed, these regulations become clearly visible. But it does not mean that it is only then that the plant is reacting to an external signal, as a hasty observation can lead to believe. Rather we emphasize that the development of the plant always takes place in presence of external clues, and along the internal symmetries of the organ. When the external signals are changed, the plant has to adapt anew, and it does so by reactivating its previous growth and regulations (figure 14).

4. Global conclusion
Instead of following the traditional classification presented in section 2, segregating the plant movements into different categories, we can recover a continuity and a coherence if movement is cast in the logic of plant development (figure 14). We can then distinguish essentially three phases. The first phase is a pure

*Figure 14. A scheme of the development of aerial organs of plants. From the initial state (apex/primordia), the developing organ first follows an expansion following its own internal axis (‘autotropism’, 3.1). The plant uses more and more external clues (‘tropisms’) to direct asymmetric and reversing growth movements (3.2 and 3.3). Finally, before reaching the mature state, one observes the appearance of nutations (3.4), rapid oscillations along the symmetries (3.5) of the organ. A disturbance during this process, for instance a change in the external clues (gravity, light) will induce a reversion to a previous state, evidenced by a renewed anisotropic growth.*
expansion within the organ symmetries, (prefoliation). The second consists in implementing this expansion within the tropisms (essentially using the gravity cue, foliation). The third one, with some oscillations before converging toward the final state, (mutation, see figure 14). The first state could be ascribed to some autotropism, the plant developing anisotropically, and converging toward its shape, without any visible influence of external cues.

In the second phase, the plant uses the external clues to guide its movements. In particular, its reversions ensure that the unfolding/straightening of the plant organ is complete and that the right orientation is achieved relatively to the environment. In this way tropisms are there to help the plant reach its position and shape.

Similarly, the last phase, the mutation, could be ascribed to proprioception, or the fact that, after the distorting first and second phases, by moving quickly the plant organ while preserving symmetries, is able to better feel its changing shape, and to better converge toward its final symmetric straight/flat state.

In this optic all the growth movements are there to help the plant to reach its final state. Following a Darwinian selection principle, we could say that this is the reason why they were selected/preserved.

We also propose that the most famous reversible movements observed in the mature plant, i.e. sensitive or circadian movements, are regressions of the second development phase. In this sense, we follow Darwin, saying that the mature movements were already present (during the development) and that they are sometimes preserved, for many different purposes. However, we observe that it is the movements of the second phase (foliation, development within the tropisms), rather than the movements of the third phase (mutations) that are reversed and used for various purposes.

During development, these movements can come from different mechanical origins, in different plants or organs, and at different times (Finn and Myers 1989). For instance, the nature of the movement from the second phase, based on differential growth, is very different from the mature reversible movements, originating in the pulvinus. However, the fact that there is a continuity of these movements, namely that the reversible movements are partial regressions of the development, is the key to understand the origin of these otherwise surprising movements. During maturation, there is just a localization of the movement and transition of the biological mechanisms, possibly from constant turgor pressure and irreversibility in the plasticity of the expanding cell walls, to purely elastic cell walls with changing turgor pressure. The position in the whole development (beginning/end) giving the proportion of which effect (irreversible/reversible) should be observed.

This continuous point of view along the whole plant development thus helps understand the different characteristics of the plant movements. It shows that they can be mixed, and can change during development.

All in all, there should be more studies on the prefoliation and foliation, as fundamental movements before the latter ones (mutations, reversions). Because looking at it globally allows to give a consistent picture of this otherwise puzzling and confusing diversity. In particular, this point of view could guide modeling. The effects should be considered all together, all the time. Their impact being only different depending on the state of the organ along its development (Bastien et al 2015).

In conclusion, with the necessary caveats about differences in details and particular cases, we propose following Darwin, global vision of plant movements that we hope make them more understandable. We also hope that this new understanding of plant movements leads to many practical applications for their modeling and their measurements. It is indeed essential for a good measurement or model to have a precise a priori conception of the various movements involved and their respective symmetries.

Acknowledgments

The authors are grateful to Arezki Boudaoud and the editorial board for the invitation to contribute to this special issue, and to the CNRS-Guyane for supporting their stay in the CNRS Station of Nouragues (French Guiana) where movies were shot. MR is thankful to ‘École Doctorale Frontières du Vivant (FdV) Programme Bettencourt’ for financial support. Special thanks to Jacqueline Donnelly author of the blog ‘Saratoga woods and waterways’5 for sharing her marvelous pictures (see supplementary data 2: Flower hook), to Christophe Golé for his precious reading of the manuscript, and to Étienne Couturier for initiating this research by his ingenious observations.

References

Abbas M, Alabadí D and Blázquez M A 2013 Differential growth at the apical hook: all roads lead to auxin Frontiers Plant Sci. 4 441
Adanson M 1763 Familles des Plantes (chez Vincent, imprimeur-libraire de Mgr le Comte de Provence) (https://doi.org/10.5962/bhl.title.271)
Armon S, Yanai O, Ori N and Sharon E 2014 Quantitative phenotyping of leaf margins in three dimensions, demonstrated on KNOTTED and TCP transgenics in Arabidopsis J. Exp. Bot. 65 2071–7
Baillieul J 1957 Recherches sur les mouvements spontans des plantes grimpantes PhD Thesis Université de Besançon
Baskin T I 1986 Redistribution of growth during phototropism and mutation in the pea epicotyl Planta 169 406–14

5 http://saratogawoodswaters.blogspot.fr/
Blancalor E B 2013 Regulation of plant gravity sensing and signaling by the actin cytoskeleton Am. J. Bot. 100 143–52
Braam J 2005 In touch: plant responses to mechanical stimuli New Phytol. 165 373–89
Bruce R 1875 An account of the sensitive quality of the tree atheroa carobala. In a letter from Robert Bruce, md to sir joseph banks, bart. prs. Phil. Trans. R. Soc. 75 356–60
Charlton W 1994 The rotated-lamina syndrome. IV. Relationships between rotation and symmetry in magnolia and other cases Can. J. Bot. 72 35–38
Charzewskia A and Wawrzkzi T 2006 Circadian modulation of circumnutation length, period, and shape in Helianthus annuus J. Plant Growth Regul. 25 324–31
Chauvet-Thiry H, Pouliquen O, Forterre Y, Legué V and Mouilla B 2015 On the role of gravity in shoot gravising 8th Plant Biomechanics Int. Conf. (Nagoya University) p 253
Coggrove D J 1987 Wall relaxation and the driving forces for cell expansive growth Plant Physiol. 84 561–4
Coutand C and Mitchell S J 2016 Editorial: Mechanical signaling in plants: from perception to consequences for growth and morphogenesis (thigmomorphogenesis) and ecological significance Frontiers Plant Sci. 7
Darwin C and Darwin F 1880 The Power of Movement in Plants (London: John Murray)
Hicks R D 2015 (Cambridge: Cambridge University Press)
Hoson T et al 1999 Morphogenesis of rice and arabidopsis seedlings in space J. Plant Res. 112 477–86
Isern S and Silk W K 2009 Moving with climbing plants from Charles Darwin’s time into the 21st century Am. J. Bot. 96 1205–21
Israelsson D and Johansson A 1967 A theory for circumnutations in Helianthus annuus Physiol. Plantarum 20 957–76
Johansson A 1997 Circumnutations: results from recent experiments on Earth and in space Planta 203 S147–58
Knight T A 1806 On the direction of the radicle and germen during the vegetation of seeds Phil. Trans. R. Soc. 96 99–108
Kitazawa D et al 2019 Morphogenesis of rice and arabidopsis seedlings in space J. Plant Res. 112 477–86
Hicks R D 2015 Aristole De Anima (Cambridge: Cambridge University Press)
Higashiyama Y and Takeuchi H 2015 The mechanism and key molecules involved in pollen tube guidance Annu. Rev. Plant Biol. 66 393–413
Hoson T et al 1999 Morphogenesis of rice and arabidopsis seedlings in space J. Plant Res. 112 477–86
Isern S and Silk W K 2009 Moving with climbing plants from Charles Darwin’s time into the 21st century Am. J. Bot. 96 1205–21
Israelsson D and Johansson A 1967 A theory for circumnutations in Helianthus annuus Physiol. Plantarum 20 957–76
Johansson A 1997 Circumnutations: results from recent experiments on Earth and in space Planta 203 S147–58
Johnson A, Solheim B and Iversen T H 2009 Gravity amplifies and microgravity decreases circumnutations in arabidopsis thaliana stems: results from a space experiment New Phytolog. 182 621–9
Knight T A 1806 On the direction of the radicle and germen during the vegetation of seeds Phil. Trans. R. Soc. 96 99–108
Llul R 1304 Llibre de descens i descens intelectus (Valencia: Jorge Costilla) (published 1512)
McClung C R 2006 Plant circadian rhythms Plant Cell 18 792–803
Forterre Y 2013 Slow, fast and furious: understanding the physics of plant movements J. Exp. Bot. 64 1745–60
Forterre Y, Skotheim J M, Dumas I and Mahadevan L 2005 How the venus flytrap snaps Nature 433 421–5
Gledhill D 2008 The Names of Plants (Cambridge: Cambridge University Press) (https://doi.org/10.1017/cbo9780511550898)
Gorton H L 1987 Water relations in pulvini from samanea saman i. Intact pulvini Plant Physiol. 83 945–50
Hart J W 1990 Plant Tropisms and other Growth Movements (New York: Springer)
Hicks R D 2015 Aristole De Anima (Cambridge: Cambridge University Press)
Higashiyama Y and Takeuchi H 2015 The mechanism and key molecules involved in pollen tube guidance Annu. Rev. Plant Biol. 66 393–413