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Update on Plant Development

Circumnutations: From Darwin to Space Flights

Allan H. Brown*

Gravitational Plant Physiology Laboratory, University City Science Center, 3401 Market Street, Suite 350, Philadelphia, Pennsylvania 19104-3323

WHAT ARE CIRCUMNUTATIONS?

More than a century ago, plant physiologists were aware that plant organs—roots, hypocotyls, shoots, branches, flower stalks—rarely grow in just one direction. The mean growth direction may be maintained for long intervals, but the organ's instantaneous growth direction usually oscillates slowly about that mean. The plant organ tip, as seen from a distal viewpoint, describes an ellipse. 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 a somewhat irregular helix. That oscillating growth pattern was well known to nineteenth century plant scientists as "revolving nutation" until Darwin (Darwin and Darwin, 1880) introduced the terms "circumnutate" and "circumnutation," which are used today. Thus, circumnutational oscillations are manifestations of the radially asymmetric growth rate typical of elongating plant organs.

HOW UNIVERSAL IS CIRCUMNUTATIONAL BEHAVIOR?

Darwin's (1875) close examination of the behavior of "climbing plants" whose tendrils appeared to "search" for some upright support led him to widen his investigation to include scores of species in which he found no exception to his generalization that circumnutation must be a universal kind of plant movement (Darwin and Darwin, 1880). The widespread occurrence of circumnutations is even greater than Darwin had demonstrated. It occurs not only in dicots and monocots but also is well known in gymnosperms, fungi (*Basidiomycetes*), and algae (*Oscillatoria*). Even some colonial forms of bacteria (*Acetobacter xylinum*) exhibit oscillating growth patterns that kinematically resemble higher plant circumnutations. Circumnutations occur only during organ growth. Whatever interferes with growth inhibits circumnutation. When tissues mature and elongation ceases, so do circumnutations.

Especially within the last three decades, much descriptive information has been acquired to characterize the kinematics of circumnutations and to deduce their mechanisms. My use of the plural may be justified if only to remind us that as Johnsson (1977) said, "Considering the different types of circumnutation encountered among plants, it would be astonishing if there were only one mechanism underlying all types."

BASES FOR SCIENTIFIC INTEREST IN CIRCUMNUTATION

There are four reasons for scientific interest in circumnutation: (a) Any poorly understood general phenomenon warrants a search for an explanation of how it works. (b) Concepts or theories of circumnutational mechanism(s) have been proposed, and, over about half a century, contrasting (but not quite incompatible) concepts have been argued persuasively although inconclusively in the plant physiological literature. (c) For one aspect of the subject, to explain what drives and regulates circumnutation, a biophysical theory (Israelsson and Johnsson, 1967) that would explain circumnutation as a sequence of self-sustaining gravitropic reactions has been available for critical evaluation for more than two decades, although a seemingly conclusive test of its validity had to await developments in spaceflight experimentation before that theory could be put to a definitive test. (d) It has been suggested that a satisfactory explanation of circumnutation might contribute to our general understanding of some other growth processes—a speculation that I believe is not farfetched.

QUANTITATIVE CHARACTERISTICS

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 for several hours, which alternate with periods of vigorous oscillation.

Plant organs may oscillate either clockwise or counterclockwise. 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 eight that accomplishes the reversal. Properly timed, transverse, gravity stimulations also can induce reversal.

Most circumnutational oscillation frequencies are in the range of about 50 μHz (periods of about 20-300 min). Therefore, special methods (e.g. time-lapse cinematography) are needed to appreciate the high incidence of circumnutational behavior by growing plant parts.

In the higher plants, kinematic patterns of circumnutation are unique for each organ of the same plant. Different shoots often do not oscillate in phase and usually have different periods of oscillation.

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* Fax 1-215-818-6258.

Various mechanical stimuli can exert a dominant influence on circumnutational behavior. Pressure (mechanical distortion), mechanical shock, subsonic vibrations, and even gentle tactile stimulation can sometimes suppress the vigor of circumnutations. It may be significant that these effects can occur within a few minutes, often less than the transport time for auxin to move from an organ tip to the growth region. This observation may be used as an argument in favor of a growth-control process that is local rather than in the remote tip region of the growing organ.

Beginning about a half-century ago, speculations about how plants grow and respond to tropistic stimulations were dominated by the Cholodny-Went theory, 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 growth phases of a plant's tropistic response to a gravitational stimulus.

The Cholodny-Went theory was used as a guide for several generations of plant physiologists to examine and to revise. Soon, other naturally occurring growth regulators were found, which destroyed the comfortable simplicity that used to exist in this research area. As a fundamental departure from the simplified Cholodny-Went theory, evidence has been marshalled to support a local-control theory that gives the tropistically responding region, especially of the shoot, a dominant role in determining the kinematic details of its own response.

When Israelsson and Johnsson (1967) proposed a gravity-dependent model to account for circumnutations, their reasoning was basically consistent with the Cholodny-Went theory, and their theory about circumnutations proved to be an attractive explanation of how the oscillations might be driven and controlled specifically by gravity. Basically, they interpreted the oscillations as a continuing sequence of gravitropic responses with overshoots that could become self-sustaining. By interpreting the oscillations as gravity driven, their model described circumnutation as a special kind of tropistic behavior. 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, especially in cereals, the localization of gravisensing is much more pronounced in root tips than in shoot tips, which has to be taken into account as we try to explain circumnutations by shoots.

RESEARCH TECHNIQUES FOR EXPLORING PROPERTIES OF CIRCUMNUTATION

To study the properties of the plant's response to its acquisition of environmental information (called a stimulus), experimenters need to vary the stimulus. They can increase the magnitude of g above that of gravitational acceleration on earth by centrifugation. They can reorient the plant to alter the direction of the gravitational acceleration vector, or they can decrease g by clinostat simulations or by sending the experiment into earth orbit, where the free-fall condition prevails. It is almost immaterial whether, in a space vehicle, the chronic acceleration level is 10^{-3}, 10^{-6}, or 10^{-9} g. We may as well accept NASA's chosen term microgravity and write μg as an approximation of the condition of a space vehicle in near-earth orbit.

By use of centrifuges, the capability for research in hyper-g has been around for a long time. Circumnutation has been studied by centrifugation at accelerations up to about $20g$. However, to explore the effects of the hypo-g condition, in the range 0 to $1g$, space experiments are required. Only by centrifugation on board a spacecraft in orbit is it now possible to create true hypogravity conditions in which experiments can be done at any controlled g value from 0 to $1g$ and above. Exploration of plant responses in all these special test environments involve rotating machines: centrifuges, clinostats, and spacecraft—individually or in combination (Brown, 1992). True (not simulated) μg has only recently become available for plant physiological experimentation.

THEORIES (MODELS) FOR CIRCUMNUTATION

Darwin tried to explain, in terms of nineteenth-century science, why the potential for circumnutating is ubiquitous. He believed that circumnutation was not only universal but also a fundamental process that would "be modified for the good of the plant" to accomplish tropistic or other growth responses (Darwin and Darwin, 1880). The (Darwinian) internal-oscillator model is more a concept than a model. Operationally, it means that the driving and regulating apparatus responsible for circumnutation is internal. Irresistibly, we compare it to the (equally mysterious) internal biological apparatus that controls circadian phenomena—a black box that senses time clues in the environment but may be manipulated experimentally by adjusting those time clues without knowing anything more about the internal biological clock.

Because circumnutation is patently advantageous to the plant only in a small minority of cases, we are not inclined to believe that it has endured only because it confers some evolutionarily significant advantage. We now believe there must be something fundamental about the growth process that endows growing plant organs with the ability to circumnutate (whether they need it or not), an ability that they display most of the time.

Modern theories or at least concepts of circumnutational mechanisms were offered by plant physiologists over the past three decades. Contrasting models were described and evaluated especially by Johnsson and Heathcote (1981). The Darwinian internal-oscillator model, couched in modern terminology, has persisted. However, a special gravity-dependent model, introduced in modern form in 1967 (Israelsson and Johnsson, 1967), has attracted more attention, probably because it could be tested experimentally. The gravity-dependent model attributes circumnutational oscillations to a sequence of gravitropic responses with overshoots. (It is also called a geotropic feedback oscillation model.) The gravity-dependent model has been elaborated by theoretical and experimental work, by tests with computer models and with real plants, and especially by tests in both simulated and real hypogravity. Much of that experimentation elaborated how gravity can be the dominant influence controlling patterns of circumnutation. However, it had not been possible to rule out a contribution from an internal (gravity-independent) mechanism.

The most recent theory, which for want of a better term we may call a growth-affected symplastic-communication model, was proposed in 1991 (Brown, 1991). It exploits some recent concepts of "local control" of tropistic growth responses, in contrast with the Cholodny-Went theory. It is not incompatible with the gravity-dependent model but has a different way of accounting for nutational oscillations. It is quite consistent with the local-control theory that localizes the "command posts" for nutational oscillations within the tropistically responding tissues.

TEST RESULTS AND INTERPRETATIONS THAT SUPPORT THE GROWTH-AFFECTED SYMPLASTIC-COMMUNICATION CONTROL MODEL

Two observations support the growth-affected symplastic communication control model. First, circumnutations persist on a centrifuge. According to the gravity-dependent model, nutational activity would be expected to be very responsive to increased *g*. Over the range that has been carefully explored (1–20*g*), the vigor of circumnutations of sunflower hypocotyls was not greatly increased (Chapman et al., 1980). It appeared that above 1*g* the process was not very responsive to an increase in *g*.

Second, in simulation tests the vigor of circumnutation was lowest at simulated 0*g*. It increased very rapidly as the simulated *g*-level was raised incrementally to a few tenths of *g*. Then it began to level off toward 1*g*, after which it increased only very slowly up to about 15 or 18*g* (Chapman et al., 1980). A somewhat more pronounced enhancement of nutational parameters by an incremental increase of centripetal acceleration in the hyper-*g* range was observed using the same apparatus but with a different cultivar of *Helianthus annuus* (Zachariassen et al., 1987). Whatever model for circumnutation one favors, it should be compatible with those observations. Taken alone, those results supported the gravity-dependent model that predicted that gravity should influence circumnutations, but the critical test of a putative requirement for gravity to drive nutation was accomplished in 1983 on the first NASA Spacelab mission, during which sunflower circumnutations were initiated and continued in *μg* (Brown et al., 1990). That result was not predicted by the gravity-dependent model as the exclusive explanation for circumnutational oscillations.

The vigor of oscillations observed in true *μg* was intermediate between that observed at 1*g* and that observed at clinostat simulated 0*g*. The most straightforward interpretation of those results is that gravity does influence both the amplitude and period of nutational oscillations but that it is not a mandatory requirement for circumnutation. Accordingly, acceleratory forces enhance the oscillations whether on earth, on a centrifuge, or in *μg*, but, even without a significant *g*-force, circumnutations proceed. The gravity-dependent model that explained how gravity could influence circumnutational parameters was not thereby disproven, but it was shown to be only a partial explanation for nutational oscillations because circumnutation can be internally driven, without any help from gravity.

A NEW MODEL

To make the most of what we know as we try to peek into the black box, the salient features of seedlings' circumnutational behavior are as follows. (a) Circumnutations can originate and will continue in a *μg* environment; therefore, *g* is not an essential requirement for circumnutation. (b) Circumnutations are responsive to gravity forces especially in that part of the range of chronic *g*-levels we call hypo-*g* (0–1*g*). Accordingly, whatever drives the oscillations can be influenced by a superimposed acceleration. (c) Mechanical perturbations often have an immediate effect on the oscillations (and also on growth). (d) Circumnutations are absolutely growth dependent.

From the above statements it can be shown that the local control theory, conceived only to explain organ elongation and bending, also is applicable to growth oscillations. I proposed (Brown, 1991) that circumnutations have the following origin. (a) Consistent with the local-control theory, morphological sites of the control process are where the gating avenues of lateral (radial) transport of growth-enabling substances occur. Those sites are the plasmodesmata that connect adjacent cells en route to growth-controlling external tissues. Accordingly, transport is confined to the symplast rather than the apoplast, where effectively selective gating would be very difficult to explain.

(b) During cell elongation as new walls become established, many plasmodesmata are functionally disrupted and restored (either repaired or replaced), and new plasmodesmata are formed. Measurements of repair time vary from 10 min (Erwee and Goodwin, 1984) to several hours (Meiners et al., 1988). Disruption may interrupt symplastic transport of critical growth substances and locally inhibit organ elongation until after restoration of functional plasmodesmata in the region of cell elongation.

(c) If growth just happens to be exactly equal on all flanks of the elongating organ, the pattern of disruption and restoration of growth-controlling plasmodesmata will be radially symmetrical and growth should be exactly straight. However, if a small asymmetry develops, the organ will bend. On the convex side of the bend peripheral tissues are stretched, and on the concave side they are compressed.

(d) In the case of gap junctions in animal cells, functionally analogous with plasmodesmata, some junctions are known to be stretch activated, others stretch inactivated. Although this trait has not yet been established convincingly for plasmodesmata, we speculate that it may be so and we can extend the argument by a prediction that (even without plasmodesmatal breakage and restoration) compression of the concave side of a bend and stretching on the convex side (or both) may introduce a functional asymmetry in symplastic transport exactly in the zone of most rapid organ growth. If by chance some asymmetry develops, the organ will bend, which will enhance the transport asymmetry and will set off a succession of self-sustaining oscillations.

(e) In the relatively quiet, weightless space laboratory, circumnutations started and stopped seemingly capriciously. In the one flight experiment where this could be observed, sunflower hypocotyls circumnutated 40% of the time. On earth, the incidence of circumnutation occurred almost 100% of the time. Such a difference is what one would expect, since a slight bend that would reorient the growing organ in a 1-*g* field would add a *g* component and so could provide an added stimulus to bend farther. The result would be that even a slight bending could more easily set off a sequence of oscillations in the 1-*g* "control" plants than in weightless plants.

(*f*) In ground-based experiments on clinostats with the same experimental material, plants circumnutated on average 21% of the time, an incidence of circumnutation only half of that observed in space. We interpret the difference as evidence that the clinostat does not perfectly simulate the μg condition. In other words, clinorotation partially inhibits circumnutation.

None of the above is incompatible with the growth-affected symplastic-communication model. A more detailed explanation and further support for this model can be found elsewhere (Brown, 1991).

Circumnutations are the inevitable consequence of specific features of the growth mechanism common to probably all elongating plant organs. Perhaps we have hit upon the explanation for their ubiquity, which was what inspired Darwin to study them as if they had to confer some evolutionarily significant advantage. If our model is correct concerning the way circumnutations work, then why they are ubiquitous is only because the elongating plant organ's growth machinery is designed in a way that makes growth-dependent oscillations highly probable.

Observations of circumnutations during space flight confirmed that the oscillations are basically nastic movements, because there was no directional stimulus that could generate a tropistic response. Given an environment with a significant *g* level, a tropistic influence may dominate.

FUTURE RESEARCH

One prediction we can propose with confidence is that future studies on circumnutations will be pursued in laboratories both on earth and in space. As with many kinds of plant behavior that could be influenced in some way by *g*, research on circumnutation will be taking advantage of opportunities to experiment without complications from earth's gravity.

It would be especially helpful to know the *g*-threshold for a detectable influence of an acceleration (loosely called a *g*-force) on circumnutation. Will it be the same as the *g*-threshold for the gravitropic response to a lateral stimulus? Neither of those thresholds has yet been measured unambiguously and probably cannot be except in a space experiment.

For theoretical reasons it would be useful to know with precision how rapidly an imposed *g*-force can perturb an ongoing sequence of circumnutations. Such tests could be important and probably will be attempted. Some cultivars of familiar test plants are ageotropic. Do they all circumnutate on earth? In space?

Vibration in the sonic range affects plant growth by mechanisms not yet elucidated. Only a few laboratories are doing exploratory studies in this area under the rubric of thigmomorphogenesis, but progress is being made and eventually we may learn why circumnutations are so easily affected by mechanical stimuli. Such experiments also will provide "ground control" information that will be useful for the design of space experiments in which selected parts of the vibration frequency spectrum will be designated as especially appropriate for testing the relation of plasmodesmatal function to growth inhibition and to altered nutational behavior.

Some kinds of flight apparatus suitable for studies such as those referred to above are already available, but relevant technologies are developing rapidly and even more useful flight-qualifiable apparatus will become available.

Space flight opportunities will continue to be far less than enough to accommodate all good research proposals in this general area of plants' physiological behavior. Research on circumnutation is still largely in the exploratory stage and, for most objectives, further descriptive studies of kinematics of circumnutations will be needed.

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