

The Hot and the Classic

CIRCUMNUTATION

Time-lapse measurements of rapidly elongating plant organs reveal that the growing tips of most organs, including roots, shoots, and coleoptiles, grow helically about the plumb-line (Johnsson, 1985). This month's "The Hot and the Classic" examines some recent developments in our understanding of these poorly understood circumnutatory movements.

Agricultural Importance of Circumnutation

Although circumnutatory movements are of obvious use to twining plants seeking mechanical support, in many cases the movements appear to serve no useful purpose. Many researchers have regarded them simply as oddities of plant growth or perhaps an outward manifestation of some important processes involved in the elongation of plant organs. Although there have been occasional suggestions in the literature that circumnutation may aid underground organs in soil penetration (e.g. Fisher, 1964), this idea has recently gained experimental confirmation in a study of paddy rice (*Oryza sativa*) varieties (Inoue et al., 1999). Although rice, an aquatic plant in origin, must have evolved to acquire traits for securing seedling establishment under flooded conditions, most 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 or apparent weight of the seed in water, but 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, Inoue et al. (1999) performed a spectrum analysis of the root tip rotations of various varieties of rice seedlings. Those seedlings that circumnutated with a frequency of 2 to 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 allowing the root tip to penetrate flooded or very soft soil.

A Role for Gravity Revisited

Charles Darwin and his son Francis suggested that circumnutatory movements were mediated by an endogenous oscillator (Darwin and Darwin, 1880). A later school that attracted some adherents envisaged nutatory movements as being a continuous series of over-compensatory responses of the plant to the changing orientation of the its gravisensory apparatus relative of the Earth's gravity vector (see Israelsson and Johnsson, 1967). Part of the attraction of this gravitropic model stemmed from the observation that the percentage of seedlings exhibiting nutation is greatly enhanced by brief gravitropic stimulation. Experiments performed under conditions of microgravity aboard the Spacelab, however, revealed that gravity is an absolute requirement neither for the initiation nor the continuation of circumnutatory movements in *Helianthus annuus* hypocotyls (Brown, 1993). Thus, the prevailing opinion once again became that circumnutatory movements are endogenously regulated.

More recent experiments by Hatakeda et al. (2003) emphasize that that role of graviresponsiveness in amplifying circumnutational movements is not trivial. These authors examined the nutational movements of a number of gravitropically impaired *Arabidopsis* mutants. The inflorescences of wild-type *Arabidopsis* showed relatively large circular movements. The *pgm-1* mutant, which is defective in starch synthesis, showed reduced circumnutation. Even more seriously affected were two mutants that were defective in endodermal cell differentiation. Circumnutation also was not apparent in the auxin-resistant *axr2-1* mutant. It is important to emphasize, however, that these agravitropic mutants did show nodding movements just not the broad

sweeping movements typical of circumnutation.

The Role of Auxin

It is apparent that circumnutation is linked to the movement of indolyl,3, acetic acid (IAA). Indeed, there is a strong temporal correspondence between circumnutation and the transport of auxin in both *Triticum aestivum* coleoptiles (Arnal, 1953) and *Phaseolus vulgaris* hypocotyls (Heathcote, 1965); the point of maximum curvature of the organs migrates basipetally during nutation at approximately the same rate as the basipetal transport of IAA. The auxin transport inhibitor naphthylphthalamic acid (NPA) has been found to abolish the nutatory movements in *Pisum sativum* stems (Britz and Galston, 1983). Classic experiments demonstrated that the nutations of grass coleoptiles cease following decapitation of the apex, the site of auxin release, or following removal of the seed, the source of the bound auxin released in the apex. Nutatory movements can be reawakened by the application of agar blocks containing diffusible auxin to the cut surface (Jorrens, 1959; Anker, 1972; Britz and Galston, 1983). These findings indicate that oscillations in IAA synthesis or release are not responsible for the movements and, more generally, that the apex is not the site of the oscillator. Although these studies do indicate a role for IAA in nutation, it would be a mistake simply to assume that if auxin is present, then nutation will follow. Indeed, Anker (1972) found that the feeding of free IAA to the transpiration stream of decapitated oat coleoptiles failed to restore nutation: the mere presence of free IAA is in itself insufficient to elicit nutatory movements. Rather, nutatory movements appear to depend on the natural polar movement of IAA through the plant.

Ionic Changes during Circumnutation

Circumnutatory movements are caused by spirally propagating changes

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in the extension rate of the organs' elongation (motor) zones (Berg and Peacock, 1992). Changes in K^+ distribution underlie the nutatory movements of *Phaseolus vulgaris* shoots (Badot et al., 1990). These data are supported by pharmacological studies that have shown that tetraethylammonium (TEA), a well-known K^+ channel antagonist, increases the period of the nutatory movements of *Phaseolus* shoots without affecting their elongation rate. Li^+ ions also inhibit circumnutation (Millet et al., 1978; Zachariessen and Johnsson, 1988). Although the pharmacology of Li is unclear, Li is a well-known inhibitor of phosphoinositide turnover (Gillaspy et al., 1995). In such cases, the effects of Li^+ can be reversed by the addition of much lower concentrations of myoinositol. Given that phosphoinositide turnover and intracellular Ca^{2+} release often give rise to propagating Ca^{2+} waves, it would be interesting to determine whether the effects of Li^+ on circumnutatory movements can also be reversed by myoinositol.

Oscillations in H^+ and Ca^{2+} fluxes in the elongation zone of *Zea mays* roots have been linked to circumnutation (Shabala and Newman, 1997a), and these authors have proposed a new model of circumnutation (Shabala and Newman, 1997b). The hy-

pothesis supposes that a lowered growth rate on one side of a root could occur in response to a local stimulus. This inhibition of growth is proposed to propagate in opposite directions and at different speeds from the site of initial stimulation, and to circumnavigate the circumference of the root.

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