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GRAVITROPISM IN PLANTS: HYDRAULICS AND WALL GROWTH PROPERTIES OF RESPONDING CELLS

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INTRODUCTION

Gravitropism is the asymmetrical alteration of plant growth in response to a change in the gravity vector, with the typical result that stems grow up and roots grow down. The gravity response is important for plants because it enables them to grow their arial parts in a mechanically stable (upright) position and to develop their roots and leaves to make efficient use of soil nutrients and sunlight. The elucidation of gravitropic responses will tell us much about how gravity exerts its morphogenetic effects on plants and how plants regulate their growth at the cellular and molecular levels.

PATTERNS OF ALTERED GROWTH

Marker studies of the gravitropic response of various young plants have shown that the curvature results from a reduction of growth on the upper surface and a stimulation of growth on the lower stem surface (Gordon, Macdonald, Hart & Berg, 1984; Digby & Firn, 1979; Carrington & Firn, 1983). In my studies (Cosgrove, in press), young cucumber seedlings show a lag of ten minutes before the upper stem surface ceases elongation entirely and the lower surface doubles its expansion rate. Although the curvature appears to originate at the apex and migrate basipetally, in fact the response occurs simultaneously along the length of the stem. The appearance of the "wave propagation" results from the diminishing growth rate and magnitude of growth response in more basipetal parts of the stem.

GROWTH BIOPHYSICS

Expanding plant cells are highly vacuolate (perhaps 95% of the cell volume is vacuolar), they are constrained by a tough, fibrous, polymeric cell wall, and they are pressurized to a value of about 4-8 atmospheres (Cosgrove, 1986). As a result, the wall is under considerable tension (equivalent to thousands of pounds per square inch) and a major problem for expanding cells is how to yield to these wall stresses and enlarge the cell without rupturing the wall and thus cell. Beside wall expansion, cell enlargement also requires uptake of water, since the volume increase occurs principally by enlargement of the vacuole, which is filled with a watery solution. The requirements of wall expansion and water uptake have been put together in a biophysical model of plant growth (Cosgrove, 1986; Lockhart, 1965), which envisions two coupled processes: (a) cell turgor pressure generates the mechanical driving force for wall expansion via shearing and expansion of the constituent wall polymers and (b) wall expansion and relaxation reduces cell turgor pressure and water potential, thus creating the driving force for water uptake and volume expansion.

During gravitropism, the changes in cell expansion correspond to changes in water uptake, and in principle they could be caused by changes either in the water uptake properties of the expanding cells, or in their cell wall growth properties. Using the pressure probe to measure cell turgor pressure directly, I found that turgor of the cells remained nearly constant during the gravitropic response of cucumber stems. Other measures of the osmotic and hydraulic characteristics of the cells also showed little if any alteration during gravitropism. Thus, the altered growth appeared to be the result of altered cell wall properties. The mechanism of wall relaxation and its alteration during gravitropism is not yet understood, but hypotheses center around enzymatic loosening of the cell wall, with control via alteration of the ionic environment of the extracellular space.

IONIC CHANGES IN THE CELL WALL.

Recent studies have accumulated evidence that gradients in hydrogen and calcium ions in the cell wall free space (apoplast) are intimately connected with the gravitropic growth response. At present the role of such ionic changes in the wall has not been adequately deciphered: they may have direct effects on cell wall extensibility, on auxin and solute transport, and/or on membrane function.

Mulkey, Kuzmanoff and Evans (1981) visualized pH asymmetries in gravitroping roots and stems by placing the seedlings on agar containing a pH indicator. In this and related studies, gradients in wall pH were not directly measured, but were implied from the pattern of acidification of the external medium. Other studies have shown that this pH asymmetry is apparently essential for the expression of growth asymmetry (Wright & Rayle, 1982; Schurzmann & Hild, 1980; Wright & Rayle, 1983). Such observations are in line with the acid-growth hypothesis which proposes that auxin stimulates growth by acidifying of the cell wall space (Rayle & Cleland, 1977; Cleland & Rayle, 1978). The acidic pH in turn promotes loosening of the wall which consequently extends more readily under the influence of the cell's hydrostatic pressure (turgor pressure). In agreement with this concept is the observation that horizontal sunflower segments fail to curve upward when treated with neutral buffers (Wright & Rayle, 1982). Also, when a lateral pH gradient is imposed on cucumber stems, they are induced to curve (Iwami & Masuda, 1973). It is easy to imagine, then, that an asymmetry in auxin (or other hormone) leads to an asymmetry in pH of the cell wall, and consequently an asymmetry in growth.

A major unanswered question regarding this acid-growth mechanism is whether the changes in pH are sufficient to account for the observed changes in growth rate. Recent reports from two different laboratories have questioned whether proton efflux induced by auxin is sufficient to account for auxin stimulation of growth (Vesper, 1985). However, no direct measurements of wall pH were made in these studies, and since the large ion-exchange capacity of the walls can alter exchange with the external medium, a compelling test of the hypothesis is still lacking. It is remarkable that so little direct information is available concerning the pH of the wall under various conditions.

In addition to hydrogen ions, calcium ions are also believed to play an essential role in gravitropism. In coleoptiles, calcium appears to accumulate in the walls of the upper side, that is, on the inhibited side (Slocum & Roux, 1983). Calcium acts as an inhibitor of wall expansion and chelation of calcium promotes wall expansion (Baker & Ray, 1965a; Cleland & Rayle, 1977; Cooil & Bonner, 1957; Tepfer & Cleland, 1979). Moreover, chelators of calcium and calmodulin antagonists block gravitropism with little or no inhibition of elongation (Daye, Biro & Roux, 1984; Lee, Mulky & Evans, 1983). However, the mechanism by which calcium modulates gravitropism is still uncertain (58,34). Calcium appears to have direct effects on the wall and on putative wall loosening enzymes (Cleland & Rayle, 1977; Jarvis, Logan & Duncan, 1984; Cooil & Bonner, 1957; Moll & Jones, 1981; Baker & Ray, 1965b). Moreover, because auxin transport and calcium are interlinked (DeLa Fuente, 1984) and calcium mediates many cell functions, it is likely that calcium functions in more than one fashion during gravitropism.

In summary, the majority of the evidence indicates that gravitropic asymmetry in growth arises from an alteration of the cell wall growth properties on the two sides of the stem. Although wall pH and pCa are implicated in the growth response, further quantitative work is necessary to assess the magnitudes of the ionic changes in the wall during gravitropism and their significance to the altered wall properties.

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