Topic: AUXIN: PHYSIOLOGICAL EFFECTS

Subject: Botany

M.Sc. (Semester II), Department of Botany
Course: MBOTCC- 7: Physiology and Biochemistry; Unit – III

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Effects/ Role of auxin

Effects can be categorized under physiological and development effects. Physiological effects include cell elongation, phototropism, and gravitropism, whereas, developmental effects include apical dominance, formation of lateral and adventitious roots, fruit development, vascular differentiation etc.

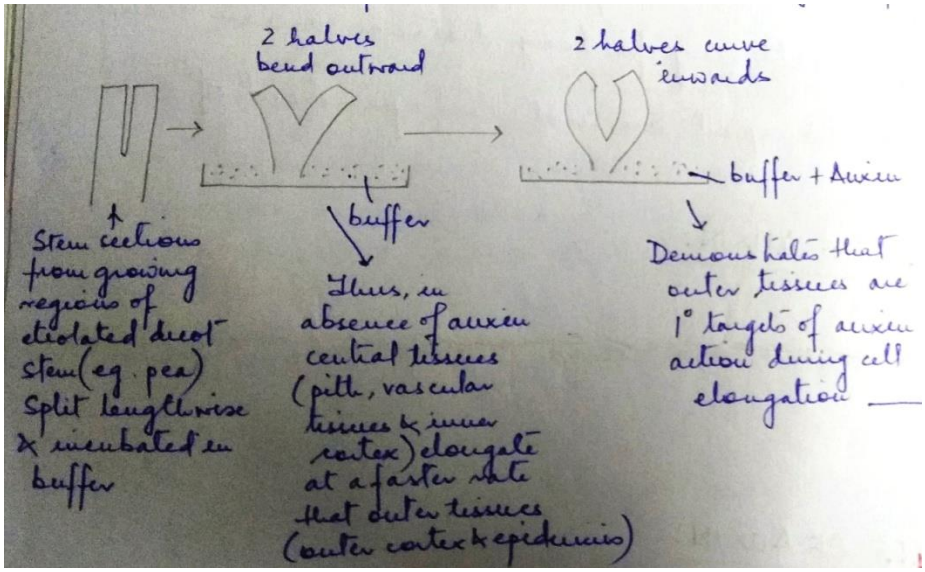
Physiological effects

[I] Cell elongation

Plant cell expansion occurs in the following manner- Osmotic uptake of water across the plasma membrane is driven by the gradient in water potential. This causes turgor pressure which builds up because of the rigidity of the cell wall. After that, biochemical wall loosening occurs, allowing the cell to expand in response to turgor pressure. There is general agreement that auxin causes an increase in the wall extensibility parameter, i.e. it causes biochemical wall loosening.

Auxin is synthesized in the shoot apex and transported basipetally to the tissues below. The steady supply of auxin arriving at the subapical region of the stem or coleoptile is required for the continued elongation of these cells. Auxins promote growth in stems and coleoptiles, while inhibiting growth in roots. Beyond the optimal concentration of auxins, elongation is greatly inhibited due to auxin-induced ethylene biosynthesis. Ethylene inhibits stem elongation in many species. Auxin control of root elongation growth has been more difficult to demonstrate, perhaps because auxin induces the production of ethylene, a root growth inhibitor. However, even if ethylene biosynthesis is specifically blocked, low concentrations of auxin promote the growth of intact roots, whereas higher concentrations inhibit growth. Thus, roots may require a minimum concentration of auxin to grow, but root growth is strongly inhibited by auxin concentrations that promote elongation in stems and coleoptiles.

Outer tissues of dicot stems are the targets of auxin action. When stem sections from growing regions of an etiolated dicot stem, such as pea, are split lengthwise and incubated in buffer, the two halves bend outward. This result indicated that, in the absence of auxin the central tissues, including the pith, vascular tissues, and inner cortex, elongate at a faster rate than the outer tissues, consisting of the outer cortex and epidermis. Thus the outer tissues must be limiting the extension rate of the stem in the absence of auxin. However, when the split sections are incubated in buffer plus auxin, the two halves curved inward, demonstrating that the outer tissues of dicot stems are the primary targets of auxin action during cell elongation.



It is seen that auxin causes a 5 to 10 fold increase in growth rate in only 10 minutes (minimum lag time) mainly through increase in the extensibility of cell wall. Auxin-induced proton extrusion acidifies the cell wall and increases cell extension. In 1970, **Cleland** and **Rayle** gave a theory to explain auxin stimulated increase in cell wall extensibility. According to them, auxin causes acidification of cell wall environment by stimulating cells to excreate protons. This lowers pH which activates wall loosening enzymes having acidic pH optimum. Hager, further suggested that auxin stimulates H+ excretion by activating a plasma membrane bound ATPase H+ pump. This combined Cleland- Hager proposals are known as '**acid- growth hypothesis**'.

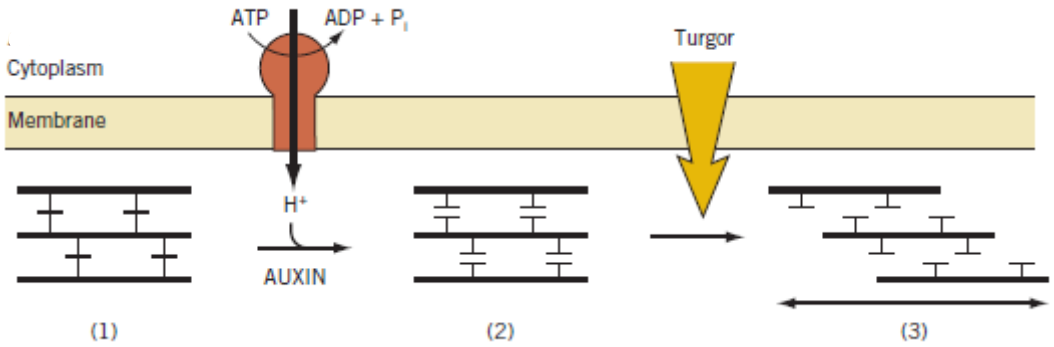


Fig. 1. A schematic demonstrating the role of auxin in the acid-growth hypothesis for cell enlargement. (*A*) Cell wall polymers (cellulose microfibrils) are extensively cross-linked with load-bearing xyloglycans (1), which limits the capacity of the cell to expand. An auxin-activated ATPase-proton pump located in the plasma membrane acidifies the cell wall space by pumping protons from the cytoplasm. The lower pH activates wall-loosening enzymes, such as extensins, that loosen the load-bearing bonds (2). The forces of turgor acting on the membrane and cell wall cause the polymers to displace (3) and allow the cell to enlarge.[1]

[1] Hopkins and Huner (2009)

[II] Phototropism

Phototropism, or growth with respect to light, is expressed in all shoots and some roots. Its primary role is to ensure that leaves receive optimal sunlight for photosynthesis. It is now well known, that, bending in response to light or gravity (as in gravitropism) results from the lateral redistribution of auxin.

Charles and Francis Darwin provided the first clue concerning the mechanism of phototropism by demonstrating that the sites of perception and differential growth (bending) are separate: Light is perceived at the tip, but bending occurs below the tip. The Darwins proposed that some "influence" that was transported from the tip to the growing region brought about the observed asymmetric growth response. This influence was later shown to be indole-3-acetic acid. When a shoot is growing vertically, auxin is transported polarly from the growing tip to the elongation zone. The polarity of auxin transport from tip to base is developmentally determined and is independent of orientation with respect to gravity. However, auxin can also be transported laterally, and this lateral movement of auxin is explained in a model for tropisms originally proposed separately by the Russian plant physiologist, Nicolai Cholodny and Frits Went from the Netherlands in the 1920s.

The **Cholodny-Went hypothesis** states that unilateral illumination induces a *lateral redistribution* of endogenous auxin near the apex of the organ. This asymmetry in auxin distribution is maintained as the auxin is transported longitudinally toward the base of the organ. The higher concentration of auxin on the shaded side of the organ stimulates those cells to elongate more than those on the lighted side. It is this differential growth that causes curvature toward the light source.

In maize coleoptiles, auxin is produced in the upper 1 to 2 mm of the tip. The zones of photosensing and lateral transport extend farther, within the upper 5 mm of the tip. The response is also strongly dependent on the light fluence. Two flavoproteins[2], phototropins 1 and 2, are the photoreceptors for the blue-light signaling pathway that induces phototropic bending in *Arabidopsis* hypocotyls and oat coleoptiles under both high- and low-fluence conditions (Briggs et al. 2001). Phototropins are autophosphorylating protein kinases whose activity is stimulated by blue light. The action spectrum for blue-light activation of the kinase activity closely matches the action spectrum for phototropism, including the multiple peaks in the blue region. Phototropin 1 displays a lateral gradient in phosphorylation during exposure to low-fluence unilateral blue light. According to the current hypothesis, the gradient in phototropin phosphorylation induces the movement of auxin to the shaded side of the coleoptile. Once the auxin reaches the shaded side of the tip, it is transported basipetally to the elongation zone, where it stimulates cell elongation. The acceleration of growth on the shaded side and the slowing of growth on the

[2] Flavoproteins are proteins that contain a nucleic acid derivative of riboflavin: the flavin adenine dinucleotide or flavin mononucleotide. Flavoproteins are involved in a wide array of biological processes, including removal of radicals contributing to oxidative stress, photosynthesis, and DNA repair.

illuminated side (differential growth) give rise to the curvature toward light. Consistent with both the Cholodny–Went hypothesis and the acid growth hypothesis, the apoplastic pH on the shaded side of a phototropically bending stem or coleoptiles is more acidic than the side facing the light (Mulkey et al. 1981).

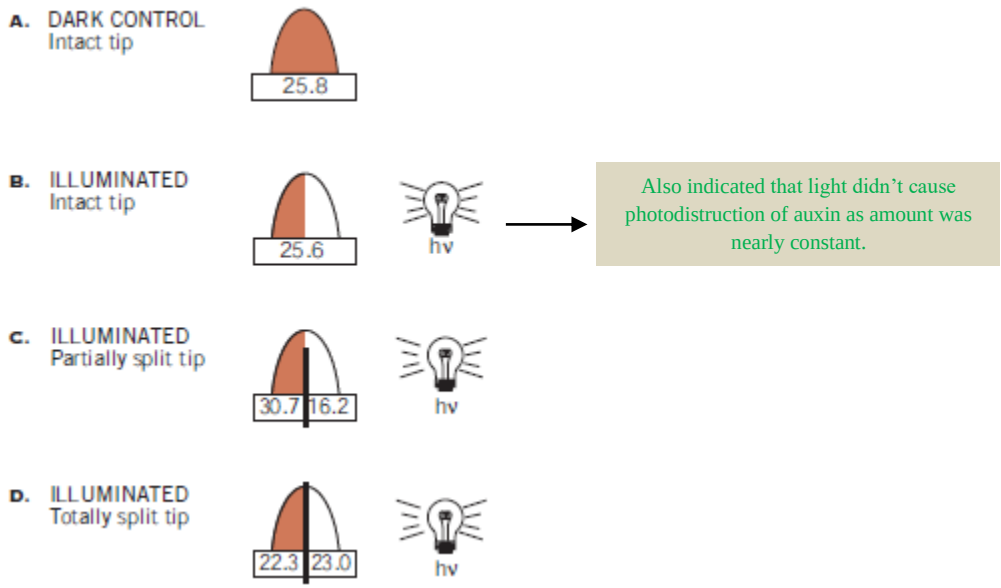


Fig. 2. Phototropic stimulation establishes an asymmetric distribution of diffusible auxin in excised *Zea mays* coleoptile apices. (*A*, *B*) Intact control apices. *A* was maintained in darkness and *B* was provided light unilaterally from the right. (*C*) Tips were partially split, leaving tissue continuity only at the very apex. A microscope cover slip was inserted to provide a barrier to lateral diffusion. The tips were then presented with unilateral light from the right. (*D*) Tips were totally split and the diffusion barrier passed through the apex before being presented with unilateral light from the right. Numbers indicate the amount of auxin collected in the agar blocks over a 3-hour period, based on degrees of curvature in the *Avena* curvature bioassay. Values are for auxin collected from 3 tips (*A*, *B*) or 6 half-tips (*C*, *D*). (Data from Briggs, W. R. 1963. *Plant Physiology* 38:237.)[3]

[3] Hopkins and Huner (2009)

[III] Gravitropism

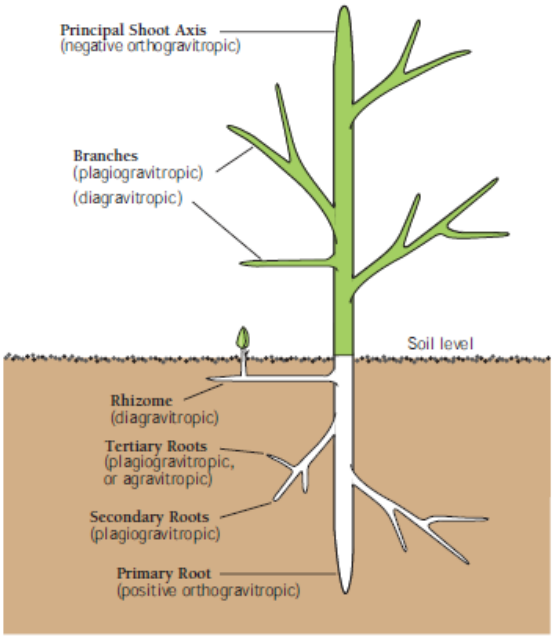


Fig.3. Diagram illustrating the range of gravitropic responses in shoots and roots.[4]

Gravitropism, like phototropism also involves lateral redistribution of auxin. According to the Cholodny–Went model, auxin in a horizontally oriented coleoptile tip is transported laterally to the lower side, causing the lower side of the coleoptile to grow faster than the upper side. Early experimental evidence indicated that the tip of the coleoptile can perceive gravity and redistribute auxin to the lower side.

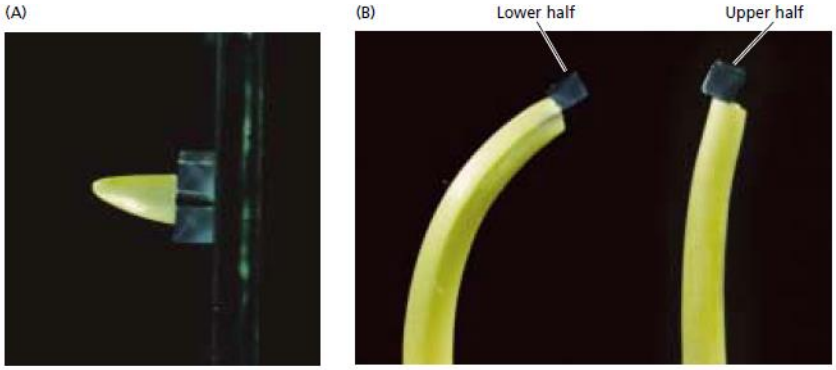


Fig. 4. Auxin is transported to the lower side of a horizontally oriented oat coleoptile tip. (A) Auxin from the upper and lower halves of a horizontal tip is allowed to diffuse into two agar blocks. (B) The agar block from the lower half (left) induces greater curvature in a decapitated coleoptile than the agar block from the upper half (right). (Photo © M. B. Wilkins.)[5]

[4] Hopkins and Huner (2009)
[5] Taiz and Zeiger (2002)

Plant cells detect/ sense gravity through the motion of a falling or sedimenting body, and these intracellular gravity sensors in plants are the large, dense amyloplasts present in their most cells. These specialized amyloplasts are of sufficiently high density relative to the cytosol that they readily sediment to the bottom of the cell. Amyloplasts that function as gravity sensors are called statoliths, and the specialized gravity-sensing cells in which they occur are called statocytes.

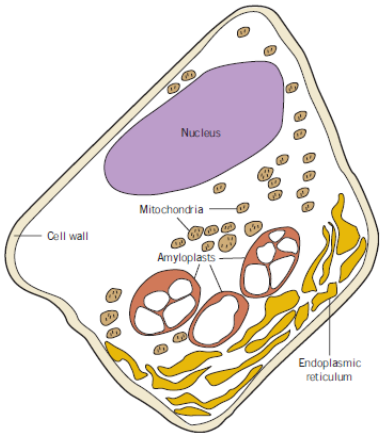


Fig.5. A statocyte (columella cell) containing three statoliths (amyloplasts).
(Based on an electron micrograph of *Lepidium* root, Volkmann and Sievers, 1979. In W. Haupt, M. E. Feinleib (eds.), Encyclopedia of Plant Physiology, NS, Vol. 7, pp. 573–600. Berlin: Springer-Verlag.)[6]

In shoots and coleoptiles, gravity is perceived in the starch sheath, a layer of cells that surrounds the vascular tissues of the shoot. The starch sheath is continuous with the endodermis of the root, but unlike the endodermis it contains amyloplasts. The site of gravity perception in primary roots is the root cap. Large, graviresponsive amyloplasts are located in the statocytes in the central cylinder, or columella, of the root cap. Removal of the root cap from otherwise intact roots abolishes root gravitropism without inhibiting growth.

The starch–statolith hypothesis of gravity perception in roots is supported by several lines of evidence. Amyloplasts are the only organelles that consistently sediment in the columella cells of different plant species, and the rate of sedimentation correlates closely with the time required to perceive the gravitational stimulus. According to one hypothesis, contact or pressure resulting from the amyloplast resting on the endoplasmic reticulum on the lower side of the cell triggers the response. The endoplasmic reticulum of columella cells is structurally unique, consisting of five to seven rough-ER sheets attached to a central nodal rod in a whorl, like petals on a flower. This specialized "nodal ER" differs from the more tubular cortical ER cisternae and may be involved in the gravity response (Zheng and Staehelin 2001).

[6] Hopkins and Huner (2009)

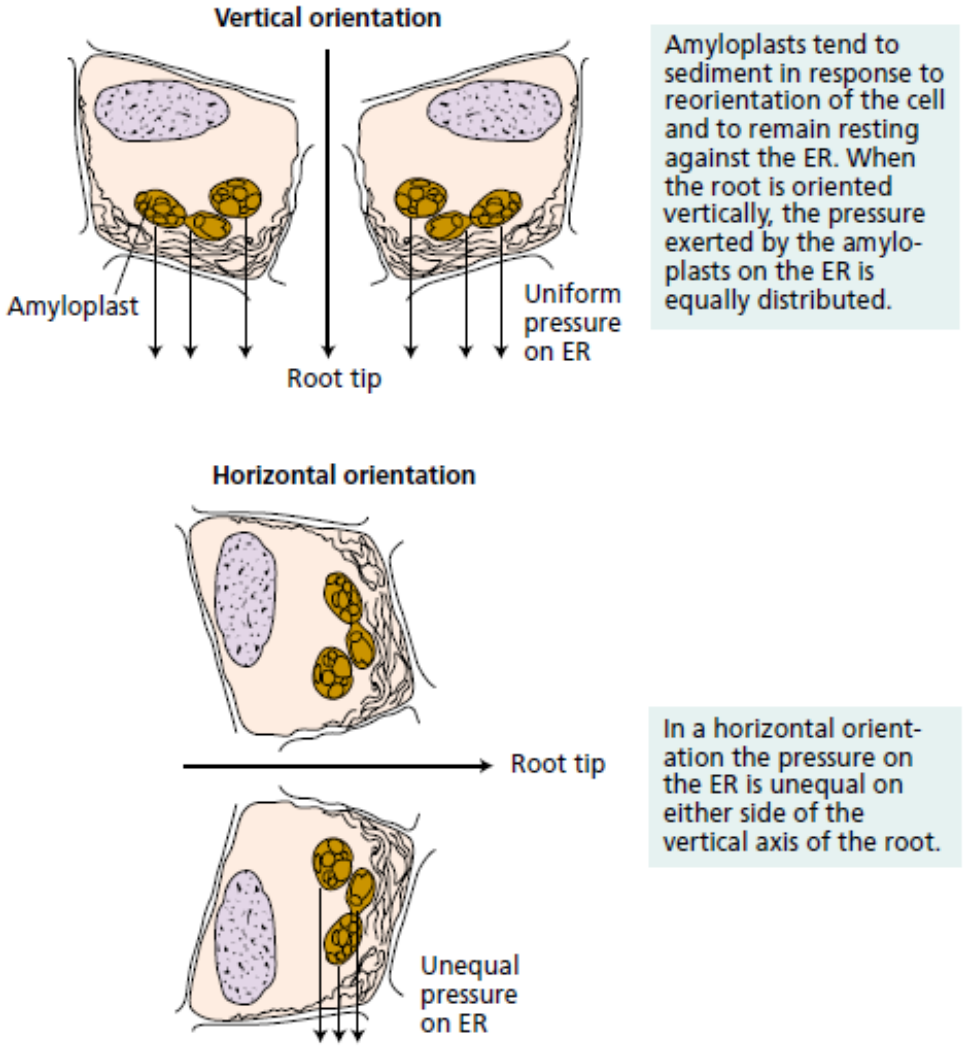


Fig.6. The perception of gravity by statocytes of Arabidopsis. Diagram of the changes that occur during reorientation from the vertical to the horizontal position. (based on Sievers et al. 1996 and Volkmann and Sievers 1979.)[7]

A comparatively new model for gravitropism called as **tensegrity model**, is proposed by Andrew Staehelin et al (Yoder et al. 2001). *Tensegrity* refers to structural integrity created by interactive tension between the structural components like meshwork of actin microfilaments that form part of the cytoskeleton of the central columella cells of the root cap. The actin network is assumed to be anchored to stretch-activated receptors on the plasma membrane. Stretch receptors in animal cells are typically mechanosensitive ion channels, and stretch-activated calcium channels have been demonstrated in plants. According to the tensegrity model, sedimentation of the statoliths through the cytosol locally disrupts the actin meshwork, changing the distribution of tension transmitted to calcium channels on the plasma membrane, thus altering their activities.

[7] Taiz and Zeiger (2002)

In roots, auxin is redistributed laterally in the root cap as demonstrated by the microsurgery experiments in which half of the cap was removed showed that the cap produces a root growth inhibitor. This finding suggests that the cap supplies an inhibitor to the lower side of the root during gravitropic bending. Although root caps contain small amounts of IAA and abscisic acid (ABA), IAA is more inhibitory to root growth than ABA when applied directly to the elongation zone, suggesting that IAA is the root cap inhibitor.

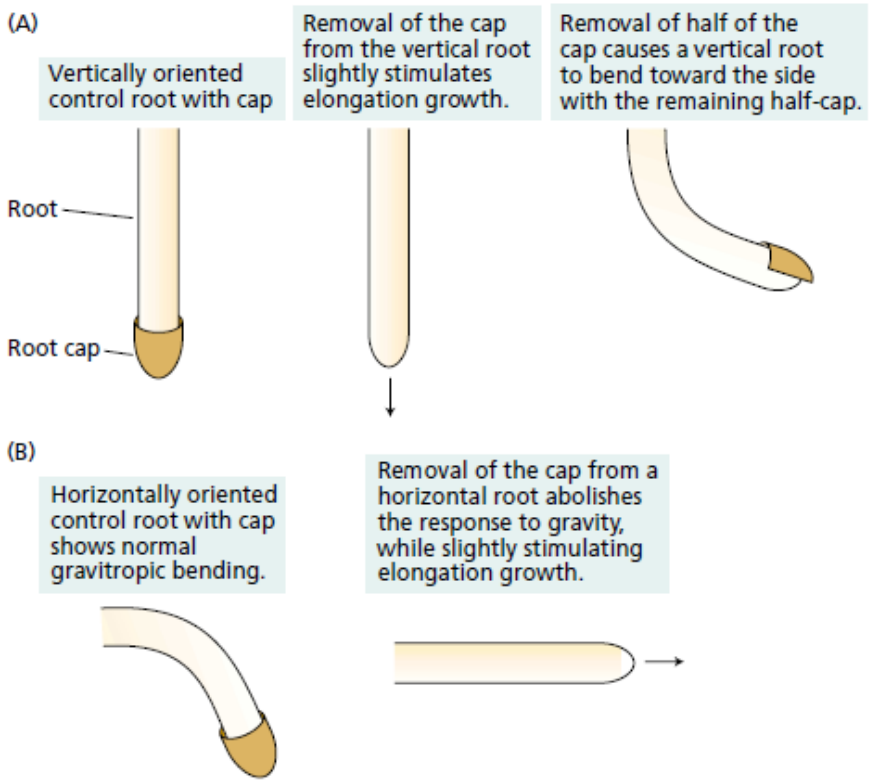


Fig. 7. Microsurgery experiments demonstrating that the root cap produces an inhibitor that regulates root gravitropism. (After Shaw and Wilkins 1973.)[8]

Basipetal auxin transport in a vertically oriented root is equal on all sides. When the root is oriented horizontally, however, the cap redirects the bulk of the auxin to the lower side, thus inhibiting the growth of that lower side. Consistent with this idea, the transport of [^{3}H]IAA across a horizontally oriented root cap is polar, with a preferential downward movement (Young et al. 1990). Gravity sensing may also involve calcium and pH as second messengers.

[8] Taiz and Zeiger (2002)

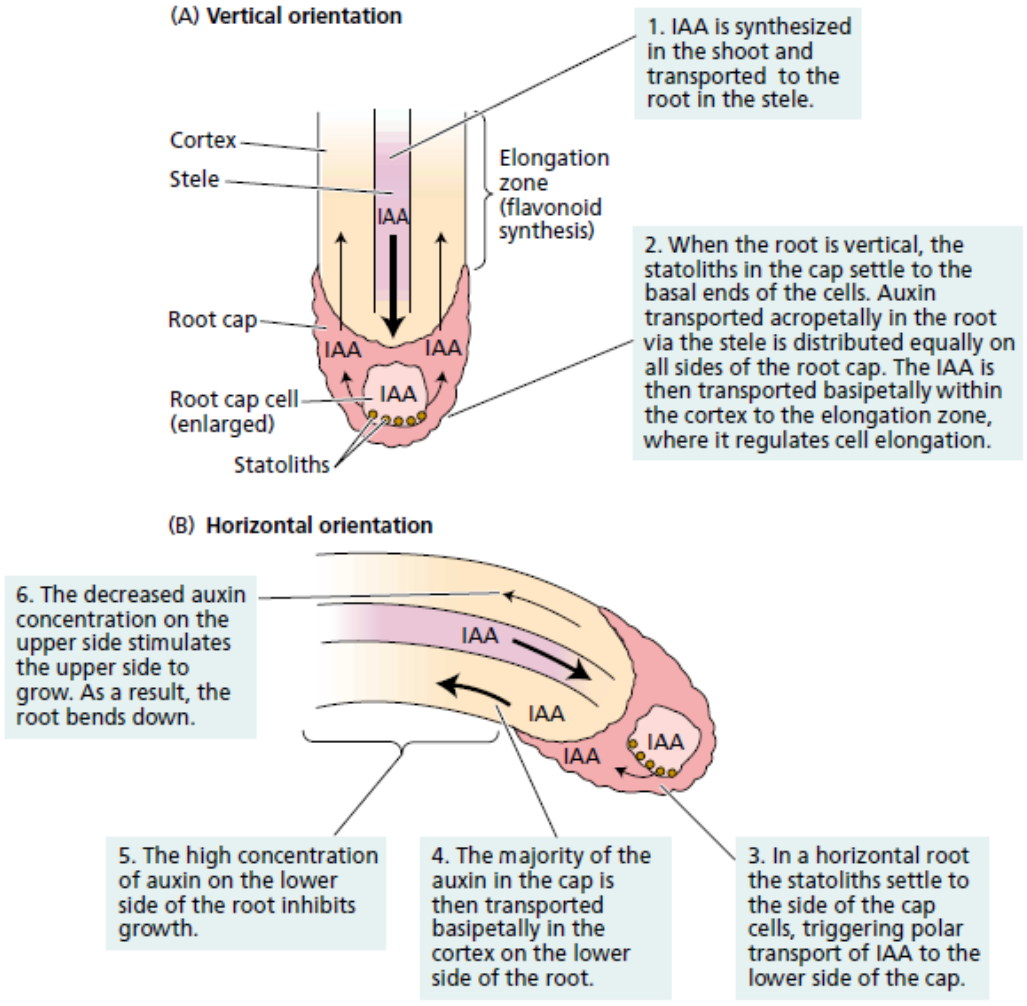


Fig. 8. Proposed model for the redistribution of auxin during gravitropism in maize roots. (After Hasenstein and Evans 1988.)

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