Auxin and Root Gravitropism: The State of Our Knowledge

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1 Introduction

During the past 10 years, increasing emphasis has been placed on the study of the involvement of hormones and calcium in growth and gravitropic response of roots. The establishment of gradients of calcium ions across the tip of roots appears to be essential for the initiation of asymmetric growth associated with the gravitropic response [7, 8, 10] and may be the signal transducer which links the root cap-associated sensor of gravitational orientation [9] and the hormonal control of asymmetric growth, which occurs during gravicurvature (GC).

2 Hormonal Involvement in Root Gravitropism

Indole-3-acetic acid (IAA) and abscisic acid (AbA) are central to the controversy concerning hormonal control of root graviresponse. The Cholodny-Went hypothesis of gravitropism [1, 19] proposes that GC of roots results from gravity-induced lateral transport of auxin on the lower side of horizontal roots. The most widely accepted and studied alternate hypothesis of GC is the "root cap inhibitor" model, which substitutes AbA for IAA as the inhibitory hormone-affecting growth on the lower surface of horizontal roots [20]. The role of AbA as the root cap inhibitor has been discounted by the work of numerous workers [4, 12, 17, 18]. The role of IAA as the hormone involved in GC is supported by the work of several workers [2, 3, 11].

3 Interactions of Auxin and Ethylene

Two patterns of gravitropic response have been noted for roots of *Zea mays*. The type I gravitropic response, which occurs in about 30% of the roots examined, is characterized by an initial upward curvature followed by downward bending of the roots (Fig. 1). In these roots, complete (90°) curvature does not occur. Type II gravitropic response, which occurs in about 70% of the roots examined, is characterized by downward bending without an initial upward curvature (Fig. 2). These roots over-

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Plant Growth Substances 1985
(ed. by M. Bopp)

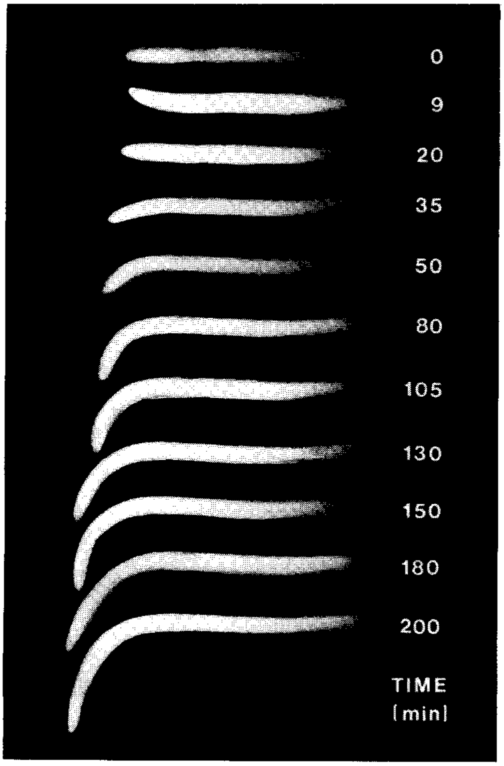

Fig. 1

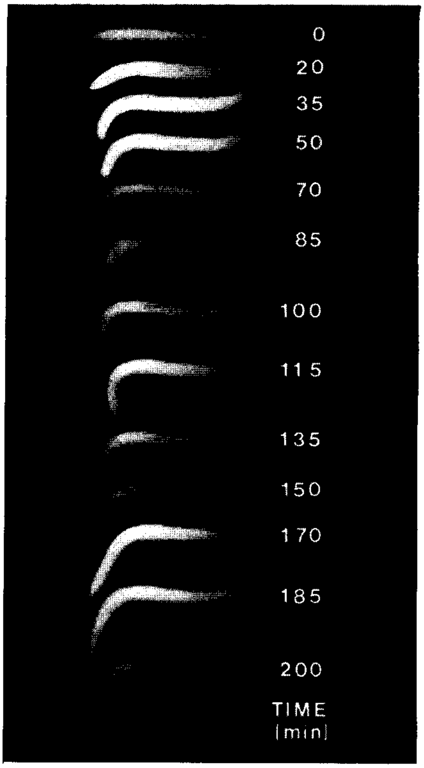

Fig. 2

Fig. 1. Kinetics of type I curvature of intact primary roots of maize. The type I gravitropic response is characterized by an initial upward curvature evident 9 min after the root is placed horizontally. Significant downward curvature is apparent after 35 min (T.J. Mulkey and M.L. Evans)

Fig. 2. Kinetics of type II curvature of intact primary roots of maize. The type II gravitropic response is characterized by significant downward curvature within the first 20 min and an overshoot of 90° (85 min). This is followed by an oscillatory readjustment of the angle of curvature (T.J. Mulkey and M.L. Evans)

shoot 90° curvature and undergo an oscillatory search for vertical orientation. These two types of response have been reported by Hild and Hertel [6] for maize coleoptiles. They suggest that the differences in patterns of GC results from varying sensitivity of the tissue to auxin. Thus, type I roots would be less sensitive to auxin and the initial downward flux of auxin promotes growth in the lower hemisphere of the root and initiate upward curvature. Subsequent accumulation of auxin inhibits growth of the lower hemisphere of the root and induces downward curvature. Conversely, type II roots are more sensitive to auxin and the initial movement of auxin to the lower portion of the root immediately inhibits growth in the lower hemisphere of the root.

It has been shown that the inhibitory effects of auxin on root growth are correlated with auxin-induced ethylene formation [14]. We have found that application of inhibitors of ethylene (1-canaline, aminoethoxyvinylglycine, silver thiosulphate, aminoethoxyacetic acid) block GC and slight upward curvature of roots occurs. This suggests accumulation of auxin triggers ethylene formation within the lower hemisphere of the root and ethylene inhibits cellular elongation and induces GC. The upward curvature of roots treated with ethylene inhibitors results from auxin-induced promotion of growth in the lower half of the root in the absence of inhibition of growth by ethylene.

4 Interaction of Calcium and Auxin

Calcium movement across tips of roots has been shown to be essential for the induction of GC [7, 8, 10]. Lateral transport of indoleacetic acid is promoted by the presence of a calcium gradient [7]. Inhibitors of IAA transport/activity (triiodobenzoic acid, naphthalpthalmic acid, and morphactins) inhibit GC [11] and inhibit gravity-induced calcium gradient formation across the tip/cap of maize roots [9].

Using a computer-based video image analysis system, we have examined the kinetics of gravicurvature induced by exogenously applied calcium. An examination of growth rates along the upper (Fig. 3) and lower (Fig. 4) surfaces of roots indicates that the rate of elongation and region of elongation are similar between control roots and decapped roots which have 1.5 mm^3 agar blocks containing 1 mM calcium chloride placed asymmetrically at the root tip. High concentrations of calcium (10 mM) significantly altered the elongation rate and position of maximal elongation. As would be expected, the rate of curvature (Fig. 5) is similar between control and decapped, 1 mM $CaCl_2$-treated roots. Since exogenously applied calcium establishes a trans-root

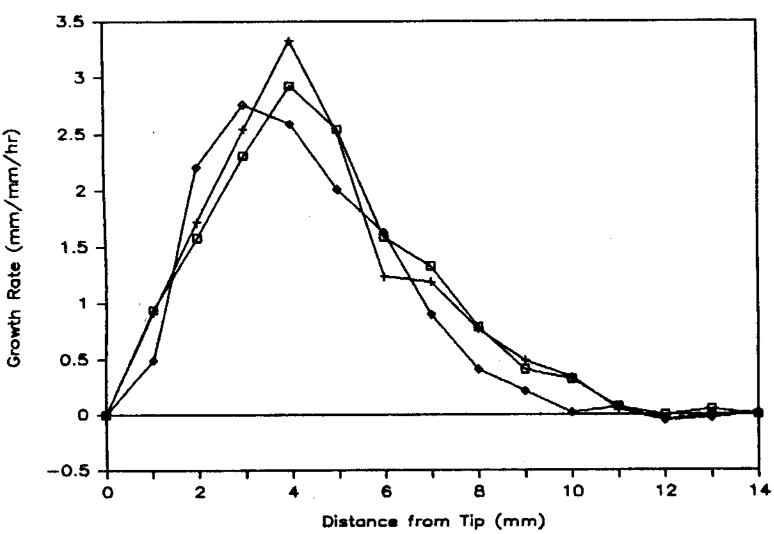

Fig. 3. Elongation rates of regions along the upper surface of maize roots responding to gravity. Comparison of elongation rates of control roots (□) and of decapped roots treated with 1 mM $CaCl_2$ (+) or with 10 mM $CaCl_2$ (◇) asymmetrically applied to the tip in 1.5 mm^3 agar blocks. Growth rates shown are average rates 50 min after exposure to the gravitational/calcium stimulus

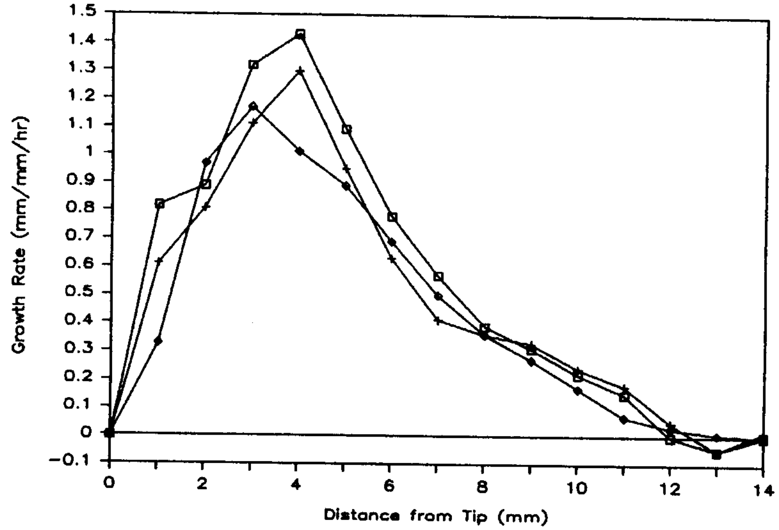

Fig. 4. Elongation rates of regions along the lower surface of maize roots responding to gravity. Comparison of elongation rates of control roots (□) and of decapped roots treated with 1 mM $CaCl_2$ (+) or with 10 mM $CaCl_2$ (◇) asymmetrically applied to the tip in 1.5 mm^3 agar blocks. Growth rates shown are average rates 50 min after exposure to the gravitational/calcium stimulus

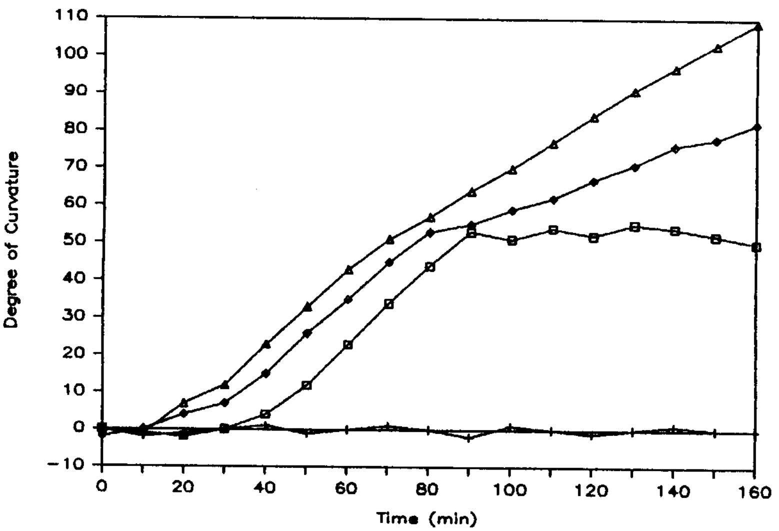

Fig. 5. Kinetics of gravicurvature of maize roots. The angle of gravicurvature is shown for decapped roots (+), for control roots (□), and for decapped roots treated with 1 mM $CaCl_2$ (◇) or with 10 mM $CaCl_2$ (△) asymmetrically applied to the tip in 1.5 mm^3 agar blocks

calcium gradient more quickly than the normal gradient develops, curvature is initiated earlier in the calcium-treated, decapped roots. Another notable difference is that exogenous calcium maintains the trans-root calcium gradient and prolongs curvature of the roots past vertical orientation. A definite and unexplained decrease in the rate of curvature occurs as the root tip passes through vertical orientation with respect to the gravitational stimulus.

Another calcium/auxin interaction has been suggested by Raghothama et al. [16]. These workers found that inhibitors of calmodulin activity (phenothiazine and napthalene sulfonamide drugs) accentuate auxin activity in *Avena* coleoptiles. In roots of *Zea mays*, we have found no promotion of growth by auxin (10^{-10} M to 10^{-6} M) in roots pretreated with phenothiazine drugs (Stelazine and chlorpromazine) or napthalene sulfonamide drugs (W5, W7, W13). This difference in effect of calmodulin inhibitors on auxin-induced growth may be another difference in the response of roots to auxin [14] compared to the response of stems to auxin.

Other calcium antagonists do effect root growth and GC. Hasenstein and Evans [5] have reported promotion of root elongation by auxin in maize roots treated with calcium chelators. Lee et al. [8] have shown that calcium chelators inhibit GC. We have shown that pharmacologic calcium entry blockers (verapamil, diltiazem, nifedipine, cinnarizine) promote growth of maize roots [15], but inhibit GC [13]. These data suggest an interaction of calcium with auxin in roots which is not modulated by calmodulin or dependent on inhibition of root elongation by calcium antagonists.

5 Conclusions

The role of plant hormones in relation to root elongation and more specifically, asymmetric elongation associated with gravicurvature, has been discussed. The evidence presented supports a role for auxin in modulating asymmetric growth, which results in gravicurvature. The inhibition of cellular elongation along the lower hemisphere of a horizontally-oriented root appears to be due to auxin-induced ethylene. Inhibitors of auxin action and of ethylene synthesis/action block gravicurvature. Calcium ions are involved with the transduction of the signal between the sensor at the root cap and the elongation zone. Within the elongation zone, calcium affects both the lateral transport and the growth-promoting activity of auxin.

Acknowledgments. This work was funded in part by an Indiana State University Grant-in-Aid of Research to T.J.M., a Sigma Xi Grant-in-Aid of Research to M.A.V., and NSF/ASPP Travel Grants to T.J.M. and to M.A.V.

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