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Suppression of Asymmetric Acid Efflux and Gravitropism in Maize Roots Treated with Auxin Transport Inhibitors or Sodium Orthovanadate

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Abstract. In gravitropically stimulated roots of maize (*Zea mays* L., hybrid WF9 × 38MS), there is more acid efflux on the rapidly growing upper side than on the slowly growing lower side. Since the Cholodny/Went hypothesis of gravitropism states that gravitropic curvature results from lateral redistribution of auxin, we examined the effects of auxin transport inhibitors on the development of acid efflux asymmetry and curvature in gravistimulated roots. All the transport inhibitors tested prevented both gravitropism and the development of asymmetric acid efflux in gravistimulated roots. The results indicate that auxin redistribution may cause the asymmetry of acid efflux, a finding consistent with the Cholodny/Went hypothesis of gravitropism. As further evidence that auxin-induced acid efflux asymmetry may mediate gravitropic curvature, we found that sodium orthovanadate, an inhibitor of auxin-induced H^+ efflux, prevented both gravitropism and the development of asymmetric acid efflux in gravistimulated roots.

Earlier work from this laboratory showed that asymmetric acid efflux occurs in gravitropically responding roots and shoots (Mulkey and Evans 1981; Mulkey et al. 1981). In both cases there is more H^+ efflux on the most rapidly growing side of the gravi-responding organ; i.e., in roots more H^+ efflux occurs on the top, while in shoots more H^+ efflux occurs on the bottom. Since acid pH

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stimulates cell elongation in both roots and shoots (Edwards and Scott 1974; Rayle and Cleland 1977), it is possible that this asymmetric acid efflux mediates the asymmetric growth that causes gravitropism. Further evidence that this may be the case was recently reported by Wright and Rayle (1982), who showed that neutral buffers can prevent gravitropism in a variety of hypocotyls and coleoptiles.

According to the Cholodny/Went hypothesis, gravitropism is mediated by lateral redistribution of auxin toward the lower side of horizontal shoots and roots (Went and Thimann 1937) with the elevated level of auxin promoting growth on the lower side of shoots but inhibiting growth on the lower side of roots. This model of gravitropism is supported by reports that inhibitors of auxin transport, such as naphthylphthalamic acid (NPA), 2,3,5-triiodobenzoic acid (TIBA), DPX-1840, and morphactins, inhibit gravitropism (Gaither 1975; Gaither and Abeles 1975).

These observations raise the question of the relationship between the asymmetric H^+ efflux associated with gravitropism and the apparent requirement for lateral redistribution of auxin in gravitropism. Does asymmetric acid efflux occur independently of auxin redistribution? If so, asymmetric acid efflux should occur even in gravistimulated roots treated with auxin transport inhibitors. Is asymmetric acid efflux linked to asymmetric auxin distribution? If so, auxin transport inhibitors should prevent the development of asymmetric acid efflux as well as gravitropism. The possibility that gravity-induced auxin redistribution might cause the asymmetry in H^+ efflux is suggested by studies showing that auxin stimulates acid efflux from shoots (Rayle and Cleland 1977) and inhibits acid efflux from roots (Evans et al. 1980). In order to test the idea that lateral redistribution of auxin causes the asymmetry of H^+ efflux, we examined the effects of a variety of auxin transport inhibitors as well as vanadate on the development of asymmetric acid efflux in gravistimulated roots of maize. A preliminary report of these findings has been published (Mulkey and Evans 1982). We have recently learned that Wright and Rayle (in press) have tested the effects of vanadate plus a variety of antiauxins and inhibitors of auxin action on asymmetric acid efflux and growth patterns during gravitropism in shoots. Their results are consistent with ours in showing an apparent dependence of the development of asymmetric acid efflux on auxin redistribution.

Materials and Methods

The experiments were performed using 3-day-old seedlings of maize (*Zea mays* L., hybrid WF9 × 38MS; Customaize, Momence, Illinois, USA) germinated and grown as described by Mulkey et al. (1981). Patterns of acid efflux during gravitropism were observed using a modification of the method of Weisenseel et al. (1979) described by Mulkey and Evans (1981). Briefly, the seedling was placed on a 4-mm-thick plate of 0.6% agar containing the pH indicator dye, bromocresol purple (0.71 mM). The pH of the agar-dye mixture was adjusted to 5.0 before pouring the plates. The primary root was pressed gently into the agar so that about half of the cylindrical root was imbedded. The plate was then mounted vertically with the root perpendicular to the direction of gravity. At the initial pH of 5.0, the agar dye is a dull orange. In regions where H^+ efflux from the root occurs, the pH of the medium increases, causing the indicator dye adjacent to the root to become yellow. In regions where H^+ uptake by the root occurs, the pH of the medium increases, causing