

Comparative Effectiveness of Metal Ions in Inducing Curvature of Primary Roots of *Zea mays*¹

Received for publication March 10, 1987 and in revised form November 9, 1987

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ABSTRACT

We used five cultivars of *Zea mays* (Bear Hybrid WF9 * 38MS, B73 * Missouri 17, Yellow Dent, Merit, and Great Lakes Hybrid 422) to reinvestigate the specificity of metal ions for inducing root curvature. Of 17 cations tested, 6 (Al^{3+} , Ba^{2+} , Ca^{2+} , Cd^{2+} , Cu^{2+} , Zn^{2+}) induced curvature. Roots curved away from Al^{3+} , Ba^{2+} , and Cd^{2+} . Roots curved away from low (0.1 millimolar) concentrations of Cu^{2+} but toward higher (1–5 millimolar) concentrations. Roots initially curved away from Zn^{2+} but the direction of the subsequent curvature was unpredictable. In most cases, roots of all cultivars curved towards calcium. However, in some tests there was no response to calcium or even (especially in the cultivars Merit and B73 * Missouri 17) substantial curvature away from calcium. The results indicate that the induction of root curvature is not specific for calcium. The results are discussed relative to the possible role of calmodulin as a mediator of ion-induced root curvature.

MATERIAL AND METHODS

Seeds of maize (*Zea mays* L., cvs B73 * Missouri 17, Merit, Yellow Dent, Bear Hybrid WF9 * 38MS, and Great Lakes Hybrid 422) were soaked in distilled water and germinated on paper towels wetted with distilled water. The growing conditions were as described previously (11). Seedlings were used when the primary roots were between 2 and 3 cm long (*i.e.* about 3 d after imbibition).

Application of Cations. The cations tested in this study were: Al^{3+} , Ba^{2+} , Ca^{2+} , Cd^{2+} , Co^{2+} , Cu^{2+} , Fe^{3+} , Hg^{2+} , K^+ , La^{3+} , Li^+ , Mg^{2+} , Mn^{2+} , Na^+ , Ni^{2+} , Pb^{2+} , and Zn^{2+} . Sheets of agar (25 · 25 · 1.5 mm³, 1.5%, Difco Laboratories) were soaked overnight in solutions of the chloride salts of these cations plus 5 mM Mes/Tris buffer (pH 6). Since solutions of ZnCl_2 and AlCl_3 are acidic and precipitate at neutral pH, solutions of ZnCl_2 and AlCl_3 were buffered at pH 5.5 and 4.5, respectively. The agar sheets were cut into cubes (1.5 mm)³ using a cutting device consisting of a series of razor blades mounted 1.5 mm apart. Groups of five seedlings were mounted vertically in Petri dishes (9 × 2 cm) by attaching the grain with caulking compound to the back of the dish. An agar block containing the cation to be tested was applied to one side of the root tip and an agar block containing buffer (5 mM Mes/Tris) at the same pH as the cation-containing block was applied to the opposite side of the root tip. Plain agar blocks or agar blocks of different pH were used as controls. Moist filter papers were placed in the lids of the Petri dishes, and the dishes were placed in closed plastic trays and oriented so that the roots were in a vertical position. The trays were kept at room temperature in fluorescent laboratory lighting. The roots grew at an average rate of 15 to 20 $\mu\text{m}/\text{min}$.

Measurements and Evaluation. In order to record curvature, photographs of the treated roots were taken 2.5 and 5 h after applying the agar blocks. The agar blocks remained at the caps of intact roots, whereas with decapped roots in some cases the agar blocks moved slightly away from the tip as a result of root growth during the experiment. These agar blocks were repositioned after 2.5 h. The negatives were enlarged to 4 times the size of the original subject and curvature of the roots was measured using a protractor. Each experiment involved 10 to 30 roots.

RESULTS

Applying agar blocks at pH 4.5 to one side and pH 6 to the opposite side of the root cap failed to induce curvature (data not shown). Co^{2+} , Fe^{3+} , Hg^{2+} , K^+ , Li^+ , Mg^{2+} , Mn^{2+} , Na^+ , Ni^{2+} , and Pb^{2+} had little or no ability to induce curvature (Table I). Some curvature away from Hg^{2+} was induced in Missouri seedlings, while roots curved away from Pb^{2+} in all five cultivars. These ions appeared to be toxic since the root tips became ne-

There is increasing interest in the potential role of cation redistribution in shoot and root gravitropism. This is especially true for calcium since this divalent cation is redistributed rapidly in shoots (1, 5, 13) and roots (3, 6, 9, 10) undergoing gravicurvature. Evidence for gravity-induced calcium redistribution in shoots was provided as early as 1959 when Bode (2) reported redistribution of calcium toward the upper side of gravistimulated sunflower hypocotyls. Interest in the potential role of calcium in gravitropism was renewed in 1983 when Lee *et al.* (7) showed that applying a calcium chelator to the root cap causes the primary root of maize to become nonresponsive to gravity. They also found that graviresponsiveness could be restored by replacing the chelator with calcium. As further evidence that calcium might be involved in the graviresponse of roots they reported that unilateral application of calcium to caps of vertically oriented roots causes the roots to curve toward the applied calcium. Since this effect could not be mimicked by manganese or magnesium, the response appeared to be specific for calcium. These observations led to the suggestions that calcium plays an important role in gravitropism, and that calmodulin may be involved in transduction of the gravitropic signal toward the site of the gravitropic growth response. To test more thoroughly the specificity of the response, we examined the effects of ion gradients on root curvature using a variety of cultivars and cations.

¹Supported by National Aeronautics and Space Administration Grants NAGW-297 and NAGW-734 and by National Science Foundation Grants PCM 8305775 and DMB 8608673.

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Table I. Curvature of Maize Roots 2.5 h after Applying Agar Blocks Containing Various Chloride Salts to One Side of Cap of Vertically Oriented Primary Roots

Cation (5 mM)	Curvature ^a				Observations
	Missouri	Merit	Yellow Dent	Bear Hybrid	
Co ²⁺	0	0	0	0	
Fe ³⁺	0	0	0	0	
Hg ²⁺	+	0	0	0	Tips killed after 10 h
K ⁺	0	0	0	0	
La ³⁺	-	0	0	0	Strong growth inhibition
Li ⁺	0	0	0	0	
Mg ²⁺	0	0	0	0	
Mn ²⁺	0	0	0	0	Induction of root hairs
Na ⁺	0	0	0	0	
Ni ²⁺	0	0	0	0	Induction of root hairs
Pb ²⁺	+	+	+	+	Tips killed after 10 h

^a + Indicates curvature away from agar block containing the cation, on average less than 20 degrees. - Indicates curvature toward agar block containing the cation. 0 = No significant curvature.

Table II. Curvature Induced by Applying Agar Blocks Equilibrated with Chloride Salts of Various Cations to One Side of Root Tip, Elongation Zone (EZ), or Decapped Tip (-Cap) of Vertically Oriented Primary Roots of Maize, var Merit

Cation Concentration	mM	Curvature					
		2.5 h			5 h		
		-Cap	EZ	Tip	-Cap	EZ	Tip
		degree ± SE ^a					
Al ³⁺	1	2 ± 3	-3 ± 1	5 ± 2	2 ± 3	-3 ± 2	5 ± 2
Al ³⁺	5	16 ± 4	-7 ± 1	92 ± 10	10 ± 4	-5 ± 1	160 ± 22
Ba ²⁺	1	5 ± 3	0 ± 1	-1 ± 3	4 ± 3	-4 ± 2	-4 ± 2
Ba ²⁺	5	3 ± 2	-2 ± 1	2 ± 1	4 ± 2	-2 ± 1	-2 ± 1
Ca ²⁺	10	-6 ± 2	0 ± 2	-2 ± 2	-7 ± 2	-1 ± 1	9 ± 6
Ca ²⁺	20	-9 ± 3	-2 ± 1	28 ± 6	3 ± 6	-2 ± 2	-3 ± 5
Cd ²⁺	1	-1 ± 3	-15 ± 3	11 ± 3	-33 ± 6	-32 ± 8	26 ± 10
Cd ²⁺	5	-9 ± 3	-21 ± 4	19 ± 6	-44 ± 6	-29 ± 6	12 ± 12
Cu ²⁺	0.1	6 ± 2	-20 ± 4	32 ± 9	-27 ± 6	-38 ± 2	42 ± 11
Cu ²⁺	1	-5 ± 2	-27 ± 4	1 ± 3	-55 ± 4	-37 ± 5	-23 ± 9
Zn ²⁺	1	-3 ± 3	-4 ± 2	5 ± 3	-3 ± 2	-5 ± 4	30 ± 11
Zn ²⁺	5	1 ± 3	1 ± 3	15 ± 5	9 ± 5	1 ± 1	17 ± 9

^a - Indicates curvature toward side of application, + indicates curvature away from side of application.

crotic after 10 h. La³⁺ treatment either did not induce curvature or, when curvature occurred, it was toward the La³⁺. Neither Mn²⁺ nor Ni²⁺ induced root curvature, but these cations as well as Ca²⁺ and to a lesser extent La³⁺ induced formation of root hairs (data not shown).

Al³⁺, Ba²⁺, Ca²⁺, Cd²⁺, Cu²⁺, and Zn²⁺ induced significant curvature when applied unilaterally to the caps of vertically oriented roots. However, the ability of these cations to induce curvature varied among the cultivars tested (Tables II-VI).

Roots curved away from Al³⁺ when unilaterally applied to an intact tip. Complete loops were formed in the Merit and Missouri seedlings. The ability of Al³⁺ to induce curvature was dramatically reduced when the root cap was removed prior to unilateral application of Al³⁺. Applying Al³⁺ to the elongating zone of intact roots usually induced curvature towards the Al³⁺ source, but the curvature was weak compared to the curvature away from Al³⁺ applied unilaterally to intact tips.

Applying Ba²⁺ unilaterally to the root cap caused strong curvature away from the cation in the Missouri and Bear Hybrid seedlings (Tables III and V) but was relatively ineffective in the Merit and Yellow Dent seedlings (Tables II and IV). Ba²⁺ was more effective at 1 mM than at 5 mM, and the maximum curvature

was reached after about 2.5 h. Curvature in response to unilateral application of Ba²⁺ to tips of decapped roots was much weaker than that observed in intact roots. Applying Ba²⁺ to the elongating zone did not induce curvature in any of the cultivars.

The effect of Ca²⁺ on root curvature depended on the cultivar and the presence or absence of the root cap (Tables II-V). In most cases applying calcium to one side of the tip of an intact root caused curvature toward the calcium source. This was especially true in the Bear Hybrid and Yellow Dent seedlings. Curvature toward calcium was weaker in the Missouri and Merit seedlings. In some experiments the roots either did not respond to calcium or curved away from the calcium source. Curvature of roots of Great Lakes Hybrid 422 toward unilateral application of Ca²⁺ to the tip was concentration dependent (Table VI). Applying Ca²⁺ to the elongating zone had little effect on curvature in the Merit seedlings. In Bear Hybrid and Yellow Dent seedlings, applying Ca²⁺ to the elongating zone induced curvature toward the cation source but the curvature was weaker than that induced by unilateral application of Ca²⁺ to the tip. In Missouri seedlings, applying Ca²⁺ to one side of the elongating zone induced substantial curvature toward the cation.

Application of Cd²⁺ in concentrations of 1 or 5 mM to one

Table III. Curvature Induced by Applying Agar Blocks Equilibrated with Chloride Salts of Various Cations to One Side of Root Tip, Elongation Zone (EZ), or Decapped Tip (-Cap) of Vertically Oriented Primary Roots of Maize, var Missouri

Cation Concentration	mM	Curvature					
		2.5 h			5 H		
		- Cap	EZ	Tip	- Cap	EZ	Tip
		<i>degree ± SE^a</i>					
Al ³⁺	1	8 ± 4	1 ± 1	8 ± 6	7 ± 7	-2 ± 1	32 ± 10
Al ³⁺	5	19 ± 5	-4 ± 1	79 ± 7	23 ± 5	-20 ± 2	224 ± 16
Ba ²⁺	1	20 ± 2	-5 ± 4	86 ± 7	-7 ± 3	4 ± 3	81 ± 19
Ba ²⁺	5	11 ± 7	-4 ± 1	12 ± 4	-4 ± 3	-3 ± 3	17 ± 7
Ca ²⁺	10	-8 ± 2	-14 ± 2	1 ± 2	-12 ± 2	-15 ± 2	-6 ± 8
Ca ²⁺	20	-4 ± 2	-22 ± 4	0 ± 2	-17 ± 4	-23 ± 4	-1 ± 3
Cd ²⁺	1	-5 ± 2	-13 ± 3	6 ± 2	-12 ± 5	-53 ± 5	14 ± 3
Cd ²⁺	5	6 ± 1	-21 ± 4	12 ± 2	-19 ± 4	-39 ± 16	-4 ± 3
Cu ²⁺	0.1	14 ± 4	-29 ± 3	40 ± 4	1 ± 7	-61 ± 4	28 ± 4
Cu ²⁺	1	14 ± 2	-40 ± 1	5 ± 3	-64 ± 4	-67 ± 5	1 ± 2
Zn ²⁺	1	12 ± 4	-3 ± 2	9 ± 3	19 ± 13	-7 ± 4	11 ± 2
Zn ²⁺	5	8 ± 3	-15 ± 4	17 ± 7	17 ± 8	-28 ± 4	37 ± 16

^a - Indicates curvature toward side of application, + indicates curvature away from side of application.

Table IV. Curvature Induced by Applying Agar Blocks Equilibrated with Chloride Salts of Various Cations to One Side of Root Tip, Elongation Zone (EZ), or Decapped Tip (-Cap) of Vertically Oriented Primary Roots of Maize, var Yellow Dent

Cation Concentration	mM	Curvature					
		2.5 h			5 h		
		- Cap	-EZ	Tip	- Cap	EZ	Tip
		<i>degree ± SE^a</i>					
Al ³⁺	1	5 ± 3	2 ± 2	4 ± 2	3 ± 2	4 ± 2	4 ± 2
Al ³⁺	5	21 ± 3	1 ± 1	73 ± 9	24 ± 5	4 ± 1	140 ± 31
Ba ²⁺	1	-3 ± 2	-2 ± 2	13 ± 3	6 ± 4	-3 ± 5	14 ± 2
Ba ²⁺	5	4 ± 3	-1 ± 1	2 ± 2	-4 ± 1	3 ± 2	0 ± 1
Ca ²⁺	10	-17 ± 4	-4 ± 3	-15 ± 6	-46 ± 7	-12 ± 3	-51 ± 10
Ca ²⁺	20	-24 ± 6	-9 ± 4	-26 ± 9	-58 ± 9	-13 ± 4	-52 ± 11
Cd ²⁺	1	-7 ± 2	-18 ± 7	13 ± 3	-47 ± 16	-38 ± 12	21 ± 8
Cd ²⁺	5	-13 ± 4	-30 ± 9	23 ± 3	-50 ± 10	-40 ± 13	20 ± 8
Cu ²⁺	0.1	-12 ± 5	-22 ± 7	24 ± 9	-40 ± 8	-39 ± 11	52 ± 13
Cu ²⁺	1	-22 ± 8	-39 ± 10	-27 ± 9	-40 ± 13	-53 ± 16	-44 ± 7
Zn ²⁺	1	4 ± 2	2 ± 2	8 ± 1	5 ± 2	10 ± 3	19 ± 4
Zn ²⁺	5	-3 ± 3	-2 ± 1	20 ± 9	13 ± 2	-10 ± 4	27 ± 11

^a - Indicates curvature toward side of application, + indicates curvature away from side of application.

side of an intact root-tip induced strong curvature away from the cation source in all four cultivars (Tables II-V). Applying Cd²⁺ either to one side of the elongating zone or to one side of the tip of decapped roots consistently induced curvature towards the cadmium-containing agar block.

Applying 0.1 mM Cu²⁺ to one side of an intact root tip induced curvature away from the cation source in all five cultivars (Tables II-V). At 1 mM Cu²⁺ caused strong curvature toward the cation in Merit, Yellow Dent, and Bear Hybrid seedlings but had little effect on curvature in the Missouri seedlings. However, roots of Missouri seedlings responded to 5 mM Cu²⁺ by curving strongly toward the cation (data not shown). Within 5 h after applying 5 mM Cu²⁺ the root tip became brown and the root stopped growing. Roots curved toward Cu²⁺ when applied to the elongating zone in all cultivars and at all concentrations tested.

Responses of roots to unilateral application of Zn²⁺ were unlike those for any of the other cations tested. Applying Zn²⁺ to one side of the root cap initially induced curvature away from the cation (Tables II-V). However, the direction of subsequent curvature was unpredictable. Indeed, these roots often curved out of the plane of the initial curvature (data not shown). Ap-

plication of Zn²⁺ (5 mM) to decapped roots of Merit seedlings had little effect except for slight curvature away from the cation after 5 h. In the Missouri, Yellow Dent, and Bear Hybrid cultivars, applying Zn²⁺ to the decapped tip induced significant curvature away from the cation. Applying Zn²⁺ to the elongating zone of the Merit cultivar had little effect. Unilateral application of Zn²⁺ to the elongating zone induced curvature toward the cation in the Missouri, Yellow Dent, and Bear Hybrid seedlings.

DISCUSSION

Our data indicate that, in addition to calcium, there are at least five cations capable of inducing curvature when applied unilaterally to the tips of intact roots and that the direction of curvature depends upon the cation applied. Since application of a pH gradient across the root tip does not induce curvature, the curvature in response to Al³⁺ and Zn²⁺, which are acidic in solution, seems attributable to the cations rather than to the acidity of agar blocks containing these cations. Also, the action of the chloride salts of these cations must be attributed to the cation rather than to chloride because most of the chloride salts

Table V. Curvature Induced by Applying Agar Blocks Equilibrated with Chloride Salts of Various Cations to One Side of Root Tip, Elongation Zone (EZ), or Decapped Tip (-Cap) of Vertically Oriented Primary Roots of Maize, var Bear Hybrid

Cation Concentration	mM	Curvature					
		2.5 h			5 h		
		-Cap	EZ	Tip	-Cap	EZ	Tip
		degrees ± SE ^a					
Al ³⁺	1	9 ± 3	-3 ± 1	11 ± 6	15 ± 4	0 ± 1	30 ± 7
Al ³⁺	5	20 ± 6	-3 ± 1	60 ± 14	38 ± 7	-8 ± 4	200 ± 21
Ba ²⁺	1	9 ± 2	-3 ± 2	27 ± 3	2 ± 2	-1 ± 1	71 ± 9
Ba ²⁺	5	15 ± 6	2 ± 2	-2 ± 1	1 ± 1	-10 ± 4	-46 ± 9
Ca ²⁺	10	8 ± 4	-12 ± 6	-20 ± 7	42 ± 8	-4 ± 2	13 ± 3
Ca ²⁺	20	-7 ± 5	-9 ± 3	-30 ± 8	-37 ± 10	-9 ± 2	-39 ± 4
Cd ²⁺	1	-1 ± 1	-20 ± 3	8 ± 1	-23 ± 4	-49 ± 7	17 ± 5
Cd ²⁺	5	-1 ± 1	-29 ± 2	8 ± 3	-30 ± 7	-36 ± 5	3 ± 1
Cu ²⁺	0.1	-5 ± 3	-19 ± 5	19 ± 3	-32 ± 7	-50 ± 7	26 ± 5
Cu ²⁺	1	-7 ± 3	-30 ± 7	-22 ± 8	-93 ± 11	-60 ± 9	-43 ± 6
Zn ²⁺	1	9 ± 4	-1 ± 1	13 ± 7	17 ± 3	3 ± 3	9 ± 3
Zn ²⁺	5	2 ± 2	-10 ± 6	20 ± 3	18 ± 2	-19 ± 5	41 ± 6

^a - Indicates curvature toward side of application, + indicates curvature away from side of application.

Table VI. Curvature Induced by Applying Agar Blocks Equilibrated with Various CaCl₂ Concentrations for 4.5 h to One Side of Intact Root Tip of Vertically Oriented Primary Roots of Maize, var Great Lakes Hybrid 422

Cation	Concentration	Curvature
	mM	degrees ± SE ^a
Ca ²⁺	1	-18 ± 2
Ca ²⁺	10	-24 ± 3
Ca ²⁺	50	-33 ± 2

^a - Indicates curvature toward side of application.

tested were ineffective. Although the mean curvature induced by some of the ions was small, the curvature of individual roots was often large. In some cases, the direction of curvature was inconsistent, *i.e.* the roots curved toward or away from the ion source. In other cases there was little or no curvature.

It was reported in a previous study (7) that primary roots of maize curve toward calcium applied unilaterally across the tip. In the present paper we show that, in some cases, roots curve away from rather than toward applied calcium, and that there are at least five cations other than calcium that can induce root curvature. How do these results relate to the earlier studies and to the potential involvement of calmodulin in the response to calcium?

The observation that roots sometimes curve away from calcium applied at the tip does not necessarily contradict the proposed role of calcium accumulation at the bottom of root caps as a mediator of positive gravitropism. When primary roots of maize are oriented horizontally a certain fraction of them initially curves upward (4). This variation in the direction of the initial response has been attributed to natural variation in root tissue sensitivity to whatever factor ultimately controls the differential growth leading to curvature. If calcium gradients induce curvature by somehow inducing unilateral redistribution of this same factor, one would expect a certain amount of 'wrong way curvature' for calcium responses just as in normal gravitropism. Both upward curvature after gravistimulation and curvature away from applied Ca²⁺ indicate that establishment of a calcium gradient across the root tip may be but one step in a sequence of events which leads to differential growth or graviresponse. The curvature away from the high side of the Ca²⁺ gradient indicates that the 'calcium-

signal' (uneven Ca²⁺ distribution) can be modulated by other factors.

There are several possible explanations of the effects of ion gradients on root curvature. One possibility is that the ions directly inhibit (possibly by toxic effects) or promote growth on the side to which they are applied. Although toxic effects have been observed (Table I), the dramatic response of roots to applied ion gradients is unlikely to result from ion toxicity since: (a) The cations are ineffective or much less effective when applied directly to the elongating region; (b) the effects are rapid, making it unlikely that curvature results from changes in meristematic cells which are ultimately transmitted to the elongating zone; (c) in most cases curvature is away from ions likely to be toxic at high concentrations; growth inhibition on the side of application would be expected to cause curvature toward the point of application; (d) auxin transport inhibitors prevent ion-induced curvature indicating an indirect effect of the ions on growth patterns through modification of auxin distribution patterns; (e) when the ion containing agar blocks were removed the roots immediately reoriented themselves vertically; if the effects of the ions were due to their toxicity, one would not expect the effects to be eliminated simply by removing the ion gradient.

It has been suggested (6) that the effect of Ca²⁺ on curvature may be mediated by calmodulin. This suggestion was based, in part, on early tests (7) showing that the induction of curvature by Ca²⁺ could not be mimicked by Mg²⁺ or Mn²⁺. We confirmed the earlier observation that Mg²⁺ and Mn²⁺ do not induce curvature, but we found a variety of other cations also capable of inducing curvature. If calmodulin mediates ion induced curvature then metal ions that induce curvature should also interact with calmodulin. It has recently been reported that several metal ions can bind to calmodulin (8, 12). Some of these ions bind to calmodulin at a site different from the calcium binding site, thereby changing the conformation of calmodulin and altering its affinity for calmodulin-binding drugs and perhaps for target proteins as well. Aluminum binds to calmodulin with high affinity and inhibits its activation by calcium (12). Thus, the observation that aluminum and calcium have opposite effects on root curvature is consistent with the possibility of calmodulin mediating ion-induced curvature.

Treatment of maize roots with auxin transport inhibitors such as 2,3,5-triiodobenzoic acid or naphthylphthalamic acid prevents curvature in response to unilateral application of either Al³⁺ or

Ca²⁺ to the cap (data not shown). This indicates that the effect of these ions (whether mediated by calmodulin or some other factor) may ultimately be expressed as an effect on auxin distribution. This possibility is being investigated and will be the subject of a later report.

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