

# Induction of Curvature in Maize Roots by Calcium or by Thigmostimulation<sup>1</sup>

## Role of the Postmitotic Isodiametric Growth Zone

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### ABSTRACT

We examined the response of primary roots of maize (*Zea mays* L. cv Merit) to unilateral application of calcium with particular attention to the site of application, the dependence on growth rate, and possible contributions of thigmotropic stimulation during application. Unilateral application of agar to the root cap induced negative curvature whether or not the agar contained calcium. This apparent thigmotropic response was enhanced by including calcium in the agar. Curvature away from objects applied unilaterally to the extreme root tip occurred both in intact and detipped roots. When agar containing calcium chloride was applied to one side of the postmitotic isodiametric growth zone (a region between the apical meristem and the elongation zone), the root curved toward the side of application. This response could not be induced by plain agar. We conclude that curvature away from calcium applied to the root tip results from a thigmotropic response to stimulation during application. In contrast, curvature toward calcium applied to the postmitotic isodiametric growth zone results from direct calcium-induced inhibition of growth.

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In earlier work, we reported that asymmetric application of Ca near the tips of primary roots of maize causes curvature toward the Ca (17). We also found that immersion of roots in Ca-containing solution causes transient inhibition of elongation (8). Based on these observations, we suggested that curvature toward Ca results from inhibition of root growth by Ca (10).

Takahashi et al. (24) reported effects of Ca opposite to ours. They found that application of Ca to the cap stimulated elongation and that unilateral application induced negative curvature by accelerating elongation on the side to which Ca was applied. We also observed curvature away from Ca in some of our experiments (11).

Ca has been implicated as a mediator of root gravitropism (2, 17) and may also play a role in the modification of gravitropic behavior by light (18, 21, 24). In view of the apparent importance of Ca in root gravitropism, we re-examined the phenomenon of Ca-induced curvature with special attention to (a) kinetics, (b) dependence on the site of

application, (c) localized changes in growth rate accompanying the curvature, and (d) the possible induction of curvature by mechanical stimulation during Ca application.

### MATERIALS AND METHODS

#### Plant Material

Caryopses of maize (*Zea mays* L. cv Merit; Asgrow Seeds, Vineland, NJ) were soaked in tap water overnight and planted between wet paper towels on an opaque plastic tray. A second tray was applied on top and the two trays, forming a sandwich holding the caryopses, were taped together. The trays were held vertically in a pan with the paper towels along the lower end of the tray contacting standing water in the pan. The trays were kept under fluorescent lights (Sylvania cool-white, approximately  $5 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ). Seedlings were used when the primary roots were 2 to 3 cm long (about 3 d after soaking).

#### Application of Materials to the Root Tip

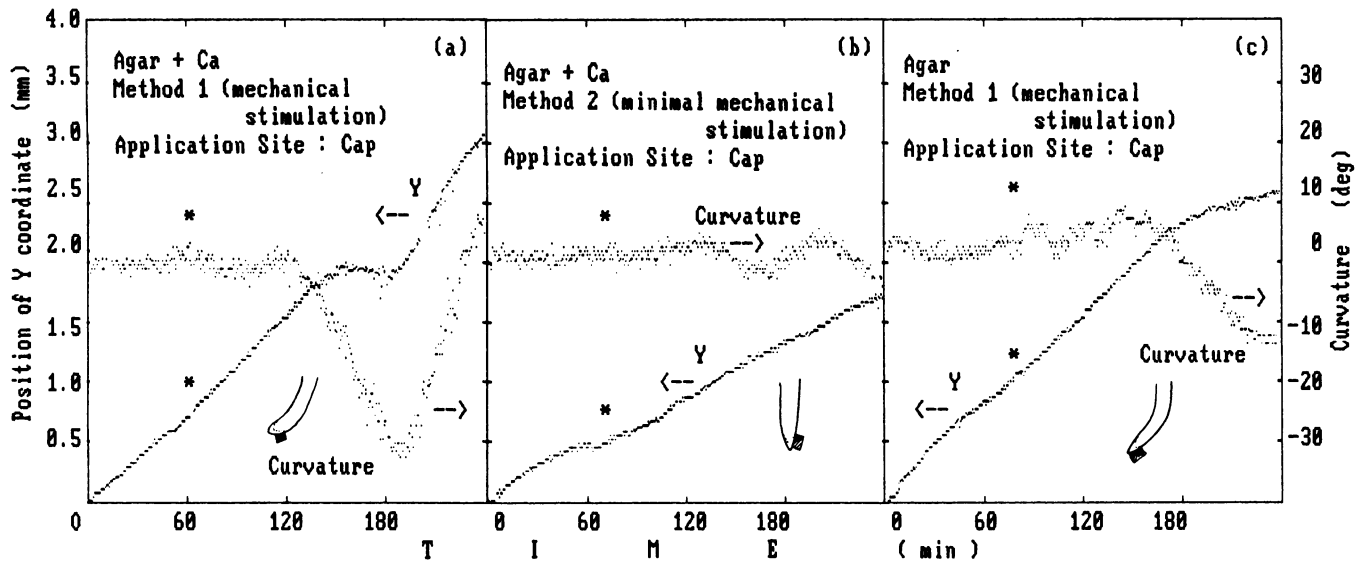
Ca was applied as a small (0.6 mm cube) agar block containing 20 mM  $\text{CaCl}_2$  plus 5 mM Mes/Tris buffer, pH 7. One of two methods was used. In method 1, the agar was attached to the tip of a forceps and the forceps was rubbed along the side of the root to slide the agar onto the root surface. This resulted in mechanical stimulation of the root. In method 2, the flat surface of the agar block was gently brought into contact with the root and the forceps was withdrawn, leaving the agar on the root surface. This resulted in minimal mechanical stimulation of the root.

We used small (0.6 mm cube) blocks to study the dependence of the response on the site of application. We were particularly interested in the role of the cells between the apical meristem and the elongation zone. Baluška et al. (1) described this region as a zone in which division has ceased but expansion is still nearly isodiametric. They refer to this as the PIG<sup>2</sup> zone. The PIG zone begins approximately 1.0 to 1.4 mm behind the apex of the root proper and extends back to approximately 2.5 to 3.0 mm behind the apex. We examined the effect of Ca applied to the cap, the PIG zone, and

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<sup>2</sup> Abbreviation: PIG zone, postmitotic isodiametric growth zone; ADAPT, Automated Degree and Position Tracer software; SECANT, Surface Extension and Curvature Analysis Technique software.



**Figure 1.** Induction of negative curvature by mechanical stimulation. a, Response to application (\*) of agar containing  $\text{CaCl}_2$  (20 mM) to the right-hand side of the root cap. Agar applied using method 1 (mechanical stimulation). b, Response to application (\*) of agar containing  $\text{CaCl}_2$  (20 mM) to the right-hand side of the root cap. Agar applied using method 2 (minimal mechanical stimulation). c, Response to application (\*) of plain agar to the right-hand side of the root cap. Agar was applied using method 1 (no effort to avoid mechanical stimulation). In this figure, as well as in Figures 2, 3, and 5, "Y" indicates y coordinate of root tip position as read along the left-hand axis and "Curvature" indicates the angle of curvature as read along the right-hand axis. The arrows adjacent to each plot point to the corresponding axis for that plot. The root diagram in each figure illustrates the shape of the root at the point of maximum curvature.

the elongation zone. To account for possible thigmotropic stimulation during manipulations, we applied plain agar to the root using both method 1 (mechanical stimulation) and method 2 (minimal mechanical stimulation). We also examined the effects of unilateral application of a small piece of sandpaper.

#### Measurement of Growth and Curvature

Seedlings were mounted inside one of two types of chambers. For some experiments, the seedlings were inside a Plexiglas chamber ( $40 \times 35 \times 50$  cm [length, width, height]) with an observation port for a television camera. The chamber contained a misting device and a fan to maintain uniform humidity at 100% (Modus Model 210 Air Moisture Measurement Meter, Modus Inc., Exeter, NH). For some experiments, the seedlings were mounted inside plastic Petri dishes containing wet Kimwipe paper.

Growth and curvature were measured using the system described earlier (13, 15). The root was observed using a Panasonic model WV-1500 television camera fitted with a 16-mm lens. Output was directed (a) to a high-resolution cathode ray tube monitor (Burle TC-1910A, Lancaster, PA), (b) to a time-lapse video recorder (Burle TC-3930), and (c) to a video digitizer (Video Van Gogh, Tecmar, Inc., Cleveland, OH) in an IBM PC.

Growth and curvature were recorded and displayed using custom software called Automated Degree and Position Tracer (ADAPT) (13), which finds the longitudinal axis of the root near the tip and calculates the angle relative to vertical. The program also records the  $x, y$  position of the root tip as a function of time, thus allowing determination of root exten-

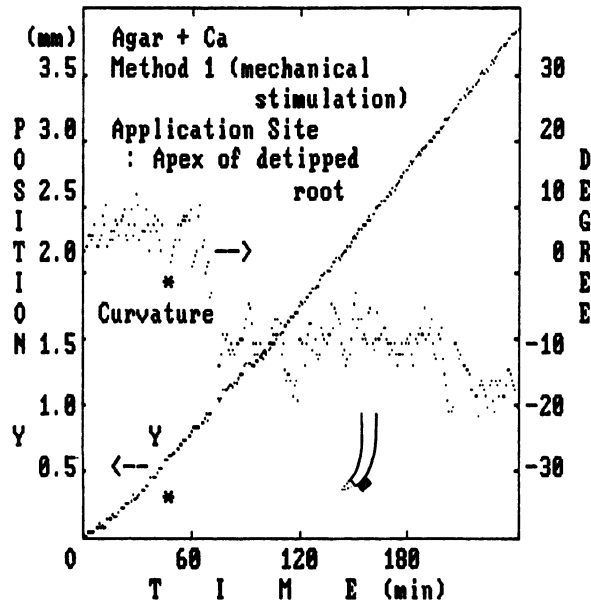
sion. For measurements of localized growth rates, glass beads (approximately 0.25 mm diameter) stained black with India ink were applied along the root surface and their displacement was recorded using SECANT (15). The velocity of movement of each bead relative to the root tip was determined from slopes of individual bead position graphs, and these velocities were plotted versus bead position to obtain velocity-position curves. Relative growth rate ( $\% \cdot \text{h}^{-1}$ ) (5, 6) was determined from the slopes of the velocity-position curves and plotted against position relative to the root tip.

Each experiment was repeated three to seven times, and the curves shown are from representative experiments with an individual seedling. Curvature away from or toward the stimulus is designated as negative or positive, respectively. This is opposite from the designations used earlier (11). Because we are examining thigmotropism in this study, we want to retain the classical designations used for tropic curvatures, i.e. positive curvature as curvature toward the stimulus.

## RESULTS

#### Curvature in Response to Unilateral Application of Substances to the Root Cap

Figure 1a shows curvature induced by application of agar containing Ca to one side of the root cap using method 1 and avoiding contact with the PIG zone. The seedlings were mounted either in a moist Petri dish or in the misting chamber with a reduced rate of misting to maintain the RH slightly less than 100%. The roots either showed weak negative curvature (Fig. 1a) or failed to curve. There was a lag of about



**Figure 2.** Response of detipped roots to unilateral application of Ca. The apical portion of the root tip was excised at the root cap junction 3 h prior to unilateral application of agar containing 20 mM  $\text{CaCl}_2$  to one side of the tip. The agar was applied (\*) using method 1 (mechanical stimulation). The root diagram in this figure illustrates the shape of the root 3 h after application of the agar/ $\text{CaCl}_2$ .

1 h prior to curvature, and the maximum curvature varied from 10 to 30°. After maximum curvature, the root often straightened, approaching the vertical (Fig. 1a), which presumably is a gravitropic correction. When agar containing Ca was applied using method 2 (minimal mechanical stimulation), no curvature was induced (Fig. 1b).

Application of plain agar to one side of the cap using method 1 induced negative curvature (Fig. 1c). Although the timing of curvature was similar to that in response to agar containing Ca, the curvature was somewhat smaller. When these experiments were done in a misting chamber at satu-

ration water vapor, unilateral application of agar with or without Ca failed to induce curvature for either method of application.

#### Curvature in Response to Unilateral Application of Substances Near the Cut End of Detipped Roots

To examine the importance of the cap to the response to unilateral stimulation we surgically removed the cap at least 3 h prior to stimulation. The cap was removed by making a cut at the root cap junction. Application (method 1) of agar containing 20 mM  $\text{CaCl}_2$  to one side of the cut end of a detipped root caused negative curvature (Fig. 2). In these experiments, the agar block did not contact the PIG zone. Plain agar also induced negative curvature, although the curvature was somewhat weaker than that observed in response to agar containing Ca (data not shown).

#### Curvature in Response to Unilateral Application of Substances to the PIG Zone or Elongation Zone

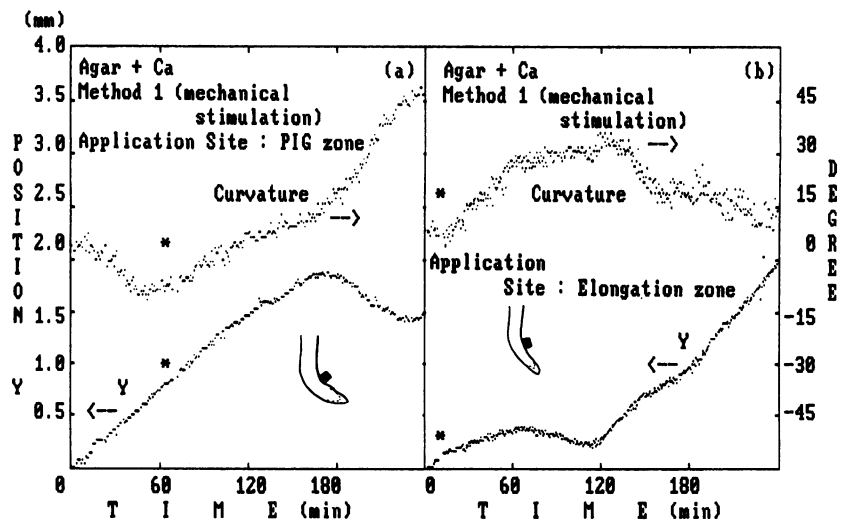
Unilateral application of Ca to the PIG zone caused strong positive curvature (Fig. 3a). This occurred for either method of application and under conditions of either saturating water vapor content or reduced RH. Application of plain agar to the PIG zone using either method induced no curvature.

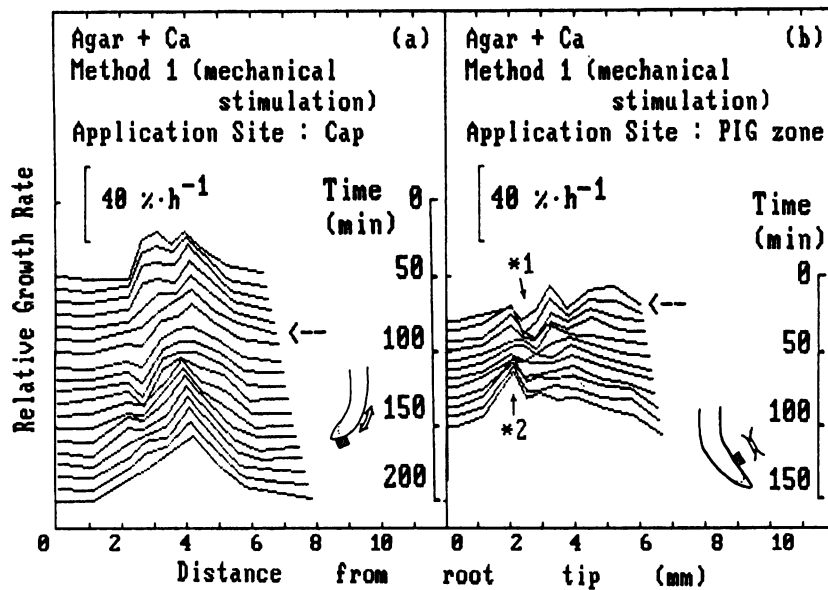
Unilateral application of Ca to the elongation zone caused weak positive curvature (Fig. 3b) independent of the method of application. Curvature was observed at either low or high RH.

#### Pattern of Growth Rate Adjustment upon Unilateral Application of $\text{CaCl}_2$ to the Root Cap or the PIG Zone

Figure 4a shows the change in the relative growth rate pattern in roots responding to Ca application to the root cap. Negative curvature was accompanied by a general acceleration of elongation and encroachment of the elongation zone toward the tip on the stimulated side. A similar pattern was observed in response to plain agar. Figure 4b shows the

**Figure 3.** Induction of curvature toward Ca applied to the PIG zone or elongation zone. At the asterisk, agar containing 20 mM  $\text{CaCl}_2$  was applied to the right-hand side of the root either at the PIG zone (a) or at the elongation zone (b). Curvature is stronger when Ca is applied to the PIG zone than when it is applied to the elongation zone.





**Figure 4.** Time-dependent change in relative growth rate distribution along the right-hand side of a root after applying agar containing  $\text{CaCl}_2$  (20 mM) to the right-hand side of the cap (a) or the PIG zone (b). Agar applied by method 1 (mechanical stimulation). Each individual curve shows relative growth rate (zero at intercept with the left axis = extreme root tip) as a function of position (as read from the x axis) along the root for a particular time interval during the experiment where zero time represents the initiation of the experiment. The intercept of each curve with the left axis, when extended to the time scale at the right, indicates the shape of the curve that were taken from 20 min before to 20 min after the midpoint). Thus, the upper curves in each set represent growth rate distribution curves from early in the experiment, whereas the lower curves represent data from later in the experiment. The uppermost curve in panel a, for example, corresponds to growth rate distribution as determined by data collected from 30 to 70 min after the beginning of the experiment (midpoint = 50 min = intercept of left portion of curve when extended to time scale). The lowermost curve corresponds to growth rate distribution as determined by data collected from 180 to 220 min after the beginning of the experiment (midpoint = 200 min = intercept of left portion of curve when extended to time scale). The relative growth rate ( $\% \cdot \text{h}^{-1}$ ) along each curve is determined from the scale above each set of curves (with relative growth rate = zero at left axis intercept). The arrow points to the first curve taken after application of Ca. In panel a, notice the general acceleration of elongation and encroachment of the elongation zone toward the tip following application of the agar block to the right-hand side of the root cap. In panel b, notice the rapid inhibition of elongation when the Ca-containing block was applied to the PIG zone. Growth was suppressed near the distal end of the elongation zone (\*1) and the region of inhibition gradually migrated basipetally, suppressing extension in the peak of the elongation zone. Beginning about 80 min after application of Ca, the relative growth rate within the PIG zone began to recover and subsequently increased to a rate exceeding that prior to application of Ca (\*2). Growth within most of the elongation zone (the zone approximately 2.5 to 7 mm behind the root tip) remained inhibited.

change in the relative growth rate distribution pattern in roots responding to Ca application to the PIG zone. There was immediate growth inhibition in the region of application. This inhibition gradually migrated basipetally, suppressing extension in the elongation zone. After 80 min, elongation within the PIG zone began to recover and subsequently increased to a rate exceeding that prior to treatment. Growth within the elongation zone remained inhibited.

#### Effect of Mechanical Stimulation on Root Growth and Curvature

When we applied a small piece of sandpaper to one side of the cap, the root curved away (Fig. 5). Curvature was accompanied by growth acceleration along the stimulated side in a pattern similar to that shown in Figure 4a. Unilateral application of a solid material to the PIG zone or to the elongation zone induced little or no curvature (data not shown).

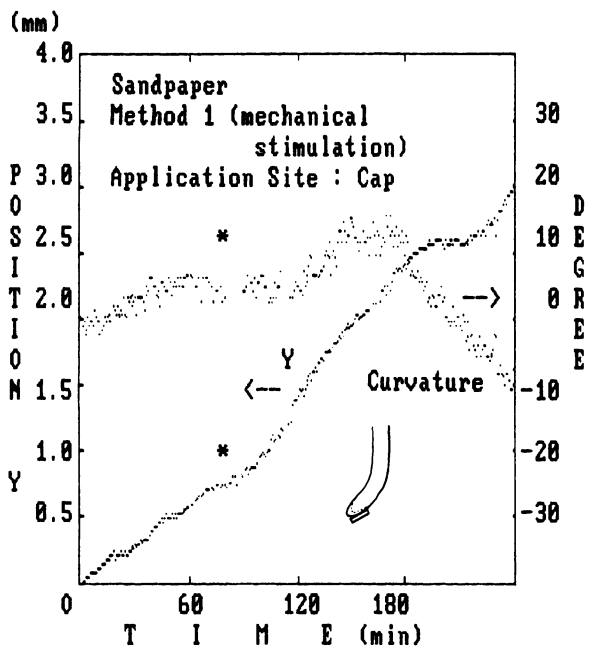
## DISCUSSION

Factors influencing the response of roots to unilateral application of Ca near the apex include (a) the site of application (root cap, PIG zone, elongation zone); (b) mechanical stimulation during application; and (c) RH. In the paragraphs below, we offer our interpretation of these findings with regard to the sensitivity of roots to Ca.

#### Unilateral Ca Application to the Root Cap

Although unilateral application of Ca to the root cap can induce negative curvature (11, 24), this appears to result from mechanical stimulation rather than from a gradient in Ca. Unilateral application of plain agar also induced negative curvature, whereas gentle application of Ca-containing agar failed to induce curvature.

In an earlier study, we reported that mechanical stimulation of the root tip caused rapid acceleration of elongation (14).



**Figure 5.** Negative curvature induced by unilateral contact of a solid material with the root cap. A piece of sandpaper was applied to the right-hand side of the cap at the asterisk.

This is consistent with (a) the observation that unilateral mechanical stimulation induces negative curvature, (b) the finding that curvature away from agar results from enhanced elongation along the side of application, and (c) the data of Takahashi et al. (24) showing that application of Ca-containing agar to the root tip accelerates elongation. Our suggestion that curvature away from agar applied at the root tip results from thigmotropism is consistent with the well-established thigmotropic sensitivity of maize roots (4) and with our finding that the application of material other than agar also induced negative curvature. Okada and Shimura (20) reported that roots of *Arabidopsis* growing along an agar surface at an angle develop a wavy form as a result of periodic reversion of rotation of the root tip as it contacts the agar.

If the response to unilateral Ca application at the tip is thigmotropic, as we suggest, how can one explain the dependence on Ca concentration reported by Takahashi et al. (24)? We propose that this is indicative of a Ca dependence of the thigmotropic response. It has been demonstrated that Ca enhances touch-induced changes in gene expression in *Arabidopsis* (3; and J. Braam, personal communication) and that tactile stimulation of leaves causes a rapid elevation of cytoplasmic Ca levels (16). Takahashi et al. (24) reported that symmetric application of Ca to the root tip stimulated growth relative to application of plain agar, but did not compare the growth rate of roots with a plain agar block at the tip to controls with no treatment.

#### Dependence on RH

We did not observe curvature away from material applied to one side of the root cap when the seedling was in water-

saturated air. Takahashi et al. (24) observed "smaller and irregular responses" when the root tips were maintained "excessively wet." Why should thigmotropic curvature be expressed at reduced RH but not at water vapor saturation? As indicated in Figure 4a, negative curvature results from acceleration of elongation along the stimulated side. At water vapor saturation, the growth rate of the roots was 1.7-fold greater than at reduced RH ( $1.14 \pm 0.47 \text{ mm} \times \text{h}^{-1}$  as compared with  $0.66 \pm 0.31 \text{ mm} \times \text{h}^{-1}$ ). Thigmotropic curvature apparently fails to develop under water vapor saturation because curvature depends upon growth acceleration along the stimulated side. Because the root is already growing at the maximum rate, a growth rate differential fails to develop.

Takahashi et al. (24) reported curvature away from Ca-containing agar when the root was at "100% relative humidity" as measured by a humidity sensor. Humidity was maintained with wet filter paper, similar to our experiments using wet Kimwipe paper. Under these conditions, the sensor we used also registered 100%. However, humidity sensors of this type are recognized to be inaccurate at RHs approaching 100%. In the absence of misting, the roots showed signs of water deficit (partial shrinkage of the mucilage, low growth rate) even though the RH sensor registered 100%. An indication that the seedlings were experiencing a water deficit under the conditions used by Takahashi et al. is that the growth rate of the primary roots of the pea mutant (ageotropum) they studied was approximately  $0.45 \text{ mm} \times \text{h}^{-1}$  (24), whereas Takahashi and Suge (23) reported the growth rate to be approximately  $0.8$  to  $0.9 \text{ mm} \times \text{h}^{-1}$  when the RH was maintained at or near 100% using a different method. The growth rates (approximately  $0.23 \text{ mm} \times \text{h}^{-1}$ ) of the primary roots of the maize seedlings studied by Takahashi et al. (24) were similar to the rates we observed for maize seedlings in chambers lined with wet paper (with the RH probe reading 100%). However, we found that, when supplemental misting was added, the growth rate increased to approximately  $1.1 \text{ mm} \times \text{h}^{-1}$ , even though the RH probe continued to read 100%. For RHs near 100%, change in growth rate is apparently a more reliable qualitative indicator of change in humidity than is the output from this type of commercially available humidity detector.

#### Role of the Root Cap

In earlier reports, we noted that both positive (presumably resulting from contact with the PIG zone) and negative (presumably resulting from mechanical stimulation of the tip) curvature occurred in decapped roots when Ca was unilaterally applied near the tip (11, 17). In the present study, we found that agar with or without Ca induced negative curvature when applied to one side of the cut end of a detipped root. This indicates that the thigmotropic response does not require the cap, an observation consistent with our earlier finding that mechanical stimulation of the tip enhances growth in both intact and decapped roots (14). Takahashi et al. (24) reported that unilateral application of Ca to the cut end of detipped roots of Alaska or Ageotropum peas caused slight positive curvature. This contrasts with our finding of negative curvature in maize roots. Although this may be a

species difference, it seems more likely that the absence of negative curvature in the pea experiments may have been because the stimulus was applied during the period of growth acceleration that follows detipping (see below). We waited at least 3 h after detipping before using the roots.

Alternatively, the failure to obtain negative curvature may have resulted from reduced mechanical stimulation during application or from contact with or diffusion of Ca toward the PIG zone. It is reasonable to expect more stimulation of the PIG zone in detipped roots because the stimulus is applied closer to the PIG zone.

In agreement with the data of Pilet (22), we observed transient stimulation of elongation upon detipping followed by a return to the control rate (or somewhat less) within 3 h (data not shown). However, our observation that mechanical stimulation enhances growth indicates that growth acceleration upon detipping may result from the mechanical stimulation of detipping rather than from the absence of the root cap as a source of growth inhibitor, as has been suggested (22).

### Unilateral Ca Application to the PIG Zone

Curvature induction by unilateral Ca application to the PIG zone appears to be a true Ca response. Curvature toward Ca applied to the PIG zone occurred consistently and developed whether the roots were maintained under partial water deficit or at true 100% RH. Also, curvature could not be induced by application of plain agar or by mechanical stimulation. Curvature resulted from inhibition of elongation along the side of application, an observation consistent with reports that Ca is a strong inhibitor of root elongation (9). In our earlier studies, we used agar blocks large enough to contact the PIG zone and observed curvature toward the side of application. The curvature away from Ca reported by Takahashi et al. (24) and by Hasenstein et al. (11) apparently resulted from thigmotropic stimulation at the root tip.

### Importance of the PIG Zone in the Sensory Responses of Roots

Our finding that the PIG zone is the primary region of sensitivity to Ca adds to the evidence that the PIG zone plays a special role in the sensory responses of roots. Selective activation and deactivation of elongation in the PIG zone is important in gravitropism (7, 15), and this zone also appears to participate in gravity-induced electrophysiological responses (12). Cells of the PIG zone also account for the ability of roots to adapt to inhibitory levels of auxin (7, 8).

Cells of the PIG zone may play a key role in the response mechanism of roots, whereas more apical cells (root cap and cells at the apex of the root proper) play the major role in stimulus perception. Björkman and Cleland (2) examined apoplastic Ca gradients at the tips of decapped maize roots. In roots decapped long enough to regain gravitropic sensitivity (but prior to regeneration of a cap), gravistimulation induced a gradient in apoplastic Ca activity at the tip. No gradient formed in roots stimulated shortly after decapping, i.e. prior to regaining gravity-responsiveness. This indicates that activities associated with perception may be localized

near the root tip and that a signal moves to the responding cells behind the tip. It has been observed (25) that gravitropic curvature is more rapid than would be expected if signal transmission occurs by auxin transport from the cap to the elongation zone. However, if the PIG zone is the major region of response (15), the kinetics of curvature may be compatible with the idea of signal transmission by auxin transport because the PIG zone is close to the tip.

A further indication that the PIG zone is a key region of response to stimuli perceived by apical cells is provided by Meuwly and Pilet (19), who examined curvature in maize roots in response to localized application of IAA. They found that gradients of IAA at various positions along the apical 2-mm induced curvature in a region 3.5 to 4 mm from the root tip.

We conclude that curvature away from material applied to the root cap results from negative thigmotropism, whereas curvature toward calcium applied to the PIG zone results from calcium-induced inhibition of elongation. It appears that the PIG zone is particularly important in the response of roots to environmental stimuli.

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