Plant Physiol. (1987) 84, 841–846
0032-0889/87/84/0841/06/$01.00/0

An Electric Current Associated with Gravity Sensing in Maize Roots[1]

Received for publication November 18, 1986 and in revised form February 27, 1987

THOMAS BJÖRKMAN*[2] AND A. CARL LEOPOLD
Boyce Thompson Institute for Plant Research, Cornell University, Ithaca, New York 14853-1801

ABSTRACT

The study of gravisensing would be greatly enhanced if physiological events associated with gravity sensing could be detected separately from subsequent growth processes. This report presents a means to discriminate sensing from the growth processes. By using a vibrating probe, we have found an electric current generated by the gravity sensing region of the root cap of maize (*Zea mays* cv Merit) in response to gravistimulation. On the upper surface of the root cap, the change from the endogenous current has a density of 0.55 microampere per square centimeter away from gravity. The onset of the current shift has a characteristic lag of three to four minutes after gravistimulation, which corresponds to the presentation time for gravity sensing in this tissue. A description of the current provides some information about the sensing mechanism, as well as being a valuable means to detect gravity sensing independently of differential growth.

How the physical action of gravity brings about physiological responses is a mystery of long standing. The analysis of gravity sensing has been difficult because this phenomenon has been detectable only by observing differential growth, a much later step in gravitropism. It has thus been impossible to investigate gravitropism in an isolated sensing tissue because the isolated sensor yields no growth response. If we are to understand the sensing mechanism it will be necessary to detect sensing in the sequence leading to curvature at a point preceding the growth processes.

It has been difficult to assess gravity sensing by measuring changes in the concentration of potential signaling substances such as calcium or growth regulators. Gravity sensing regions are usually only small groups of cells, so the changes in concentration of various substances will be subtle against a large background level. Chemical analysis of the upper and lower halves of the whole tissue can easily miss important changes in movement of relevant compounds. Radiolabeling experiments alleviate the problem of background, but detectable changes require long observation periods, giving poor time resolution. This lack of sensitivity has made it difficult to know whether chemical redistributions are primary responses to gravity sensing.

Electrophysiology provides an alternative to chemical means of detecting gravity-sensing processes. It can be used to detect physiological changes with much higher resolution and sensitivity than most chemical methods. There is also a physiological basis for expecting an appropriate electrophysiological signal: some of the earliest events reported in gravity sensing have been electrical, occurring in less than 1 min (3, 30, 33). By making measurements at different accelerations and different temperatures, Johnsson (14) could identify a component of the lag time dependent on temperature (a chemical reaction) and one dependent on acceleration (physical sedimentation). The relationship of these two components suggests that the reactions causing electrical polarization begin when sedimentation has advanced to a given degree, leading to lateral transport of an ionic chemical signal or to a bioelectric signal. Caution must be used when interpreting such electrical events because they may be due to other parts of the gravitropic response or be purely physical effects on the measuring apparatus induced by repositioning. In maize coleoptiles, a transverse polarization develops after 11 to 15 min, much longer than the presentation time: Grahm (9) and Woodcock and Wilkins (37) interpreted the polarization as a consequence of auxin transport. Also, certain instantaneous electrical events are artifacts due only to physical shifting of the apparatus when it is turned (6, 38). Such physical artifacts characteristically begin within seconds of gravistimulation. This possibility is important to consider when evaluating reports of very rapid or immediate responses to gravistimulation.

A study by Behrens *et al.* (3) of the bioelectric current around *Lepidium* root tips suggested that there is a change in the current pattern around the root tip following gravistimulation. This important contribution set the stage for the work reported here. There are, however, limitations on the conclusions which can be drawn from their study for two reasons. First, they used a vibrating probe which was not turned when the root was rotated 90°. Possible conclusions are limited because the current measurements in one vector give no information about the other. Second, the presentation time of *Lepidium* roots is only 7 s (15), and great difficulties would be encountered in attempting to establish a correlation with electrical events over such a brief time.

However, Behrens *et al.* (4) observed that the acropetal current at the root cap had increased between 1 and 7 min after gravistimulation. This observation indicates that changes do occur near the sensing cells after gravistimulation. In this work we have tried to overcome each of these limitations in the hope of confirming and extending their conclusions.

The maize root cap has three important features which make it particularly valuable for studying gravity sensing. First, the sensing region is several millimeters removed from the growing region, so changes in growth-related processes will not confound detection of sensing-related events. Second, the presentation time is relatively long, 3 (AK La Favre, AC Leopold, unpublished data) to 4 (25) min, so that physical artifacts resulting from repositioning the equipment to effect gravistimulation can be separated from the physiological response. Finally, the kinetics

[1] Supported by NASA grant NAG-W3; training in the use of the vibrating probe was supported by NIH grant P41RR01395-SSS to L. F. Jaffe.

[2] Present address: Department of Botany KB-15, University of Washington, Seattle, WA 98195.

of amyloplast sedimentation (25), and many physiological (8, 23, 32) and cytological (19, 25) characteristics of the maize root cap have been extensively described.

In the maize root, gravity is sensed in the central columella of the root cap (*cf.* 11). The central columella is not directly accessible, being surrounded by secreting cells. However, activities characteristic of the secreting cells alone can be measured at the tip of the root cap where that is the only cell type. If one measures a response adjacent to the columella, but none at the tip of the cap, it can then be attributed to the columella cells. Any growth responses would be in the elongating zone, about 2 mm behind the root cap. Curvature is first detectable about 30 min after gravistimulation, so any response associated with altered growth rate would be expected to have a lag time considerably longer than the presentation time of 4 min.

The development of the vibrating probe has permitted great advances in the study of cell and tissue polarity (12). This device measures voltage gradients in the medium surrounding a cell or tissue; the gradients are expressed as the current density passing through the conductive medium (for derivation, see Scheffey *et al.* [29]). The vibrating probe has been used to show that transcellular and transembryonic currents are closely linked to developmental processes, especially to the establishment of axes of polarity (*cf.* 22).

A change in the current density will reflect a change in the magnitude or direction of ion pumping in the tissue. If that change is due to gravity sensing, it should be observable only at the sensing region, and should appear coincidently with the presentation time.

A change in the current density may be brought about by a change in the amount of proton pumping. A change in the pH around the tissue could reflect altered proton pumping. The proton component of the net current may be assessed using pH-sensitive dyes.

A method for detecting gravity sensing independently of the transmission of the sensing signal to the elongating zone and independently of asymmetric growth will be a novel tool for elucidating the components of the sensing mechanism in plant statocytes.

MATERIALS AND METHODS

Plants. Three-d-old seedlings of maize (*Zea mays* cv Merit; a gift from Asgrow, Kalamazoo, MI) were used when the radicles were 25 to 35 mm long.

Vibrating Probe. The seedling was held in a Plexiglas chamber and manipulated by a stainless steel cannula inserted into the endosperm. The cannula was not in contact with any part of the embryo, thereby precluding extraneous currents due to wounding. Near the bottom of the chamber were holes for insertion of the probe and a calibration electrode. The top was sealed so that solution would not drain out through these holes. The chamber and the vibrating probe were mounted on a rotatable plate (Newport Corp., Fountain Valley, CA) so that the root cap was at the center of rotation. On the plate were microtranslation stages (Newport) to position the seedling and the probe in three dimensions. When gravistimulation was effected by turning the plate 90°, the seedling, the chamber, and the probe all turned together. Seedlings were viewed through a stereomicroscope at 50-fold magnification.

The suspending buffer was 0.1 mM $CaCl_2$, 0.1 mM $MgCl_2$, 0.1 mM KCl, and 1 mM morpholinoethanesulfonic acid adjusted to pH 6.0 with KOH. The resistivity of this medium was 16 kOhm cm^{-1}. The medium had enough ions to satisfy the root's ion requirement and to stabilize the solution pH, yet it had a low ionic strength to give a high resistivity necessary for a maximum signal-to-noise ratio for the measurements.

The electronic equipment for the vibrating probe was designed and built by Dr. Carl Scheffey and Mr. Al Shipley of the National Vibrating Probe Facility, Marine Biological Laboratory, Woods Hole, MA. It consisted of a preamplifier, an oscillator, and a phase-lock amplifier. An excellent introduction to the vibrating probe is available (27). The oscillator provided a sine wave which stimulated the piezoelectric crystal driving the probe as well as serving as the phase source for the phase-lock amplifier. The phase-lock amplifier compared the signal from the probe with the driving sine wave. This signal was time averaged, with a time constant of 0.1 or 2 s. A potential difference between the two extremes of vibration of 1 μV produced a DC output of 5 mV.

The probes were manufactured in the laboratory as described by Jaffe and Nuccitelli (12). Insulated stainless steel microelectrodes (model SS3003; Micro Probe Inc., Gaithersburg, MD) were electroplated with gold until a sphere 10 μm in diameter had formed; then the probe tip was plated with platinum to a diameter of 20 μm. This was followed by several high-current bursts, which make a more porous platinum deposition, until the probe tip had a diameter of approximately 25 μm and a capacitance of 2 to 10 nF in the suspending buffer. Probes with a capacitance less than 1 nF were prone to artifactual signals and were replated or discarded.

The probes were calibrated by passing a known current through a metal electrode similar to the vibrating probe, but with a diameter of <10 μm. The signal amplitude was measured at different distances (50–250 μm) from the current source and a calibration coefficient calculated. The noise level was approximately 0.01 μA cm^{-2}. Artifacts were avoided by taking the extensive precautions required with this sensitive instrument (28). Most runs were unusable because sloughing cells or secreted mucilage moved too close to the probe tip during the time course, because the root could not be kept in position as the endosperm weakened, because the capacitance of the probe tip declined below a satisfactory value, or because unexplained electronic interference arose. Each of these difficulties prevented calculation of current densities for the full time course.

The current densities adjacent to the root were measured as time courses, each of which was repeated at least three times. The time courses were calculated as deviations from the initial current. The mean current, with standard deviation, was calculated at each time point of replicate runs.

A current-generating, but gravity insensitive, control was used to evaluate physical artifacts associated with turning the apparatus. Large wound currents rendered decapped roots unsuitable. Therefore, a 1000 μm diameter platinum wire was used as a surrogate root. It was insulated along its length except for a 4000 μm section, 1500 μm behind the tip of the wire, which was coated with platinum black. This configuration produced a predictable current pattern in the middle of the platinum black band. With the vibrating probe positioned 100 μm from the surface of the wire and the current being passed through the wire measured, the current density at the center of probe vibration could be calculated. With the actual current held constant, changes in the apparent current measured with the vibrating probe indicated changes in the calibration coefficient. The apparent current density remained constant before turning. On turning, the reference (zero current) value often shifted, occasionally taking up to 1 min to stabilize. The calibration coefficient also changed on some runs. After correcting for changes in the reference and calibration, a pronounced dip in the current sometimes occurred during the first minute. This physical artifact is reflected immediately after gravistimulation in some graphs, either as a large standard deviation or as a rise or drop in the current density. Because this aberrant physical phenomenon could not be corrected for, and also because it may take up to 1 min to realign the root with the probe, changes observed in the current density within seconds of gravistimulation could not be ascribed phys-

iological significance.

Nonphysiological currents and surface charges being interpreted as currents were discounted by measuring dead roots, killed by immersion in 8% glutaraldehyde for 1 h. These produced no current and the current remained zero on turning.

Proton fluxes around the root tip were measured in agar containing bromocresol purple as described by Mulkey *et al.* (21). Plates were poured with 1% agar, 2 mM bromocresol purple, 0.1 mM $CaCl_2$, 0.1 mM $MgCl_2$, 0.1 mM KCl (pH 5.7); pH changes of as little as 0.2 units were obvious. Seedlings were pressed into the agar and held vertically for 10 min to establish a color pattern before the plates were rotated. A small amount of water was released from the agar around the seedling, presumably due to the hydrolytic activity in the root cell walls. In vertical seedlings this water collected as a droplet at the root cap and confounded all color gradients, both by mixing the colors and by acting as a lens. The vertical controls were therefore completely uninformative; color profiles at later time points had to be compared with the profile existing 2 min after gravistimulation. The color became more intense the longer the root was on the agar.

RESULTS

Initial Current Distribution. Before currents associated with gravity sensing could be identified, the initial current distribution had to be established. The current was measured 100 μm from the maize root surface. Closer approaches were sometimes possible, but mucilage on the surface of the root cap would often have caused serious artifacts. Moving the root along its axis allowed measurements from the tip to 3000 μm from the tip, which is in the elongating zone (1, 34). The initial current pattern was assumed to be radially symmetric.

All measurements were of the current moving perpendicular to the root axis. Longitudinal (3, 36) and internal (2) currents occur as well, currents occur as well (3, 36), but the transverse signal induced by gravity sensing is of interest here. Although the currents in and out of the seedling must balance, there is no reason to expect the sum of the currents in the measured region to equal zero. The measured region constitutes less than 10% of the surface of the root and only the transverse component. At the cap apex Behrens *et al.* (3) found a large longitudinal influx.

The endogenous transverse currents had a consistent profile (Fig. 1), but the magnitude of the current density varied from root to root. At the tip of the cap, the current density varied among roots from 1.5 μA cm^{-2} inward to 1.5 μA cm^{-2} outward, but was steady for individual roots. The current density became more outward further back along the root cap, with the transition from inward to outward occurring at a point between 0 and 700 μm behind the tip of the cap. The maximum outward current coincided with the root meristem, about 1000 μm behind the tip of the cap. The current density decreased over the distance between 1000 and 3000 μm from the tip of the cap, and was always outward.

This current profile can be qualitatively compared to the profile of proton flux as revealed by the color of the pH-sensitive dye bromocresol purple around the tip of seedlings in agar. There was no color change around the root cap; a purple (basic) zone formed around the root meristem and a yellow (acidic) zone around the elongating zone. The distribution of proton fluxes around the tip is shown diagrammatically in Figure 2. It was clearly different from that of the net current.

Response to Gravistimulation. The current density was recorded during and after gravistimulation at the three loci of interest: the columella, the tip of the root cap, and the elongating zone.

All time courses were calibrated before and after the run. The final calibration was done with the apparatus still turned. The zero point was determined regularly during the time course.

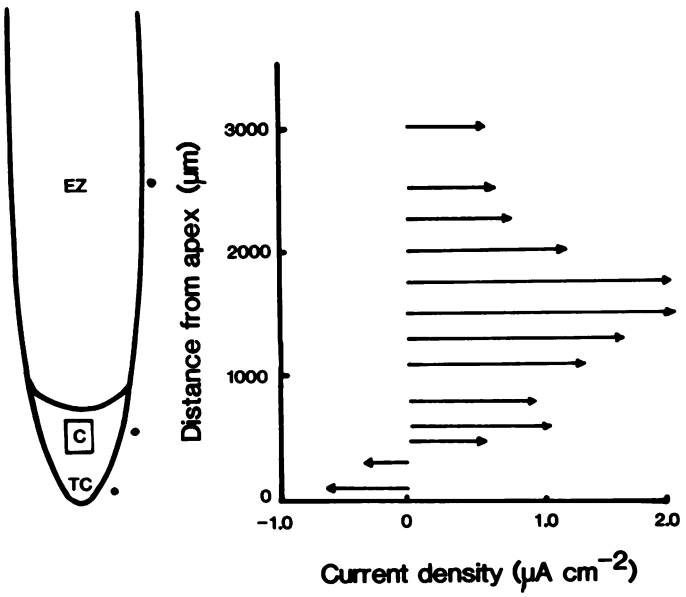

FIG. 1. Profile of endogenous current density. Arrows indicate the magnitude of the lateral current density at each position along the root axis for a representative root. The boxed area in the root cap indicates the columella (statenchyma). The dots on the right of the root indicate the measuring positions referred to as tip of cap (TC), columella (C), and elongating zone (EZ).

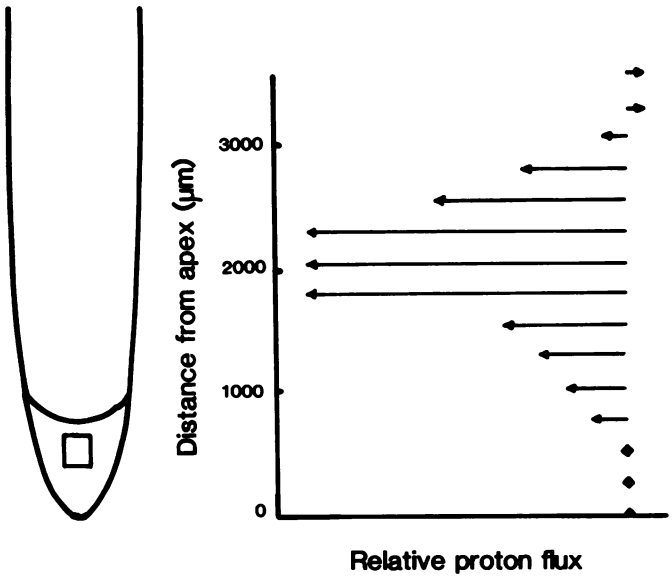

FIG. 2. Profile of the endogenous proton flux. Relative proton flux at the root surface estimated from color changes in bromocresol purple.

These precautions allowed compensation for most artifacts produced by a wire current source. Physical effects of turning the apparatus caused some changes in the signal which could not be compensated for, as described in "Materials and Methods." These sporadic artifacts caused a change in the apparent current density immediately after turning. Therefore, it is most appropriate to compare changes following gravistimulation with the values at 1 min.

When the maize root was gravistimulated, the outward current on the upper side of the cap, lateral to the columella, increased abruptly 4 min after gravistimulation (Fig. 3). The onset of the current shift was always distinct, beginning 3.6 ± 0.6 (±SD; n = 6) min after gravistimulation. The current took 3.0 ± 1.2 (n = 5) min to reach a new steady level which was 0.55 ± 0.21 (n =

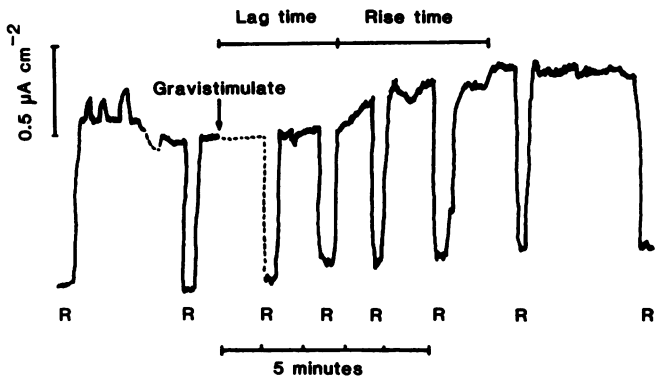

FIG. 3. Sample trace of current density at upper side of columella. R indicates when the probe was moved away from the root surface to a reference location where the current density was zero. Dotted lines indicate when the probe was being realigned.

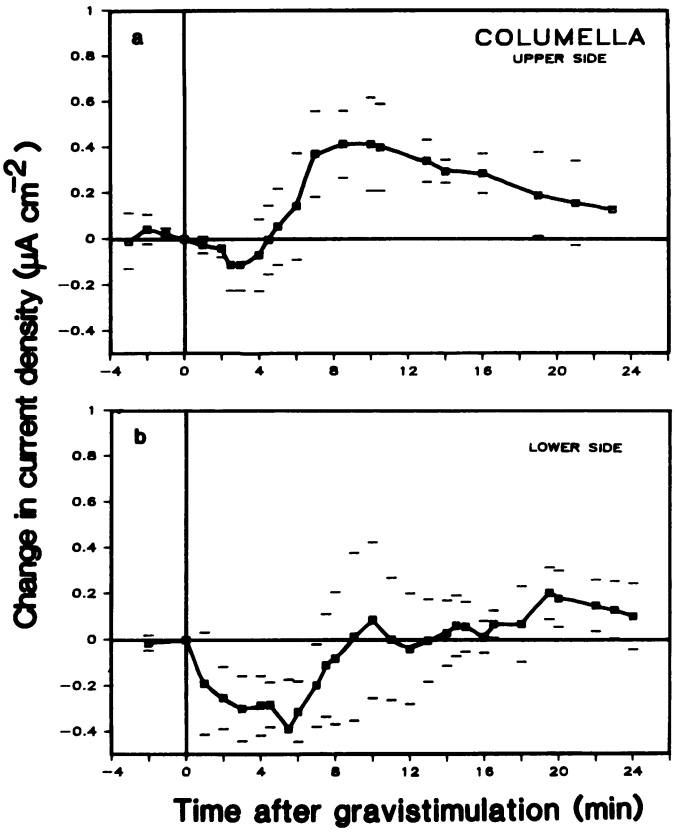

FIG. 4. Time course of current density measured adjacent to the columella (500 μm behind the cap apex). a, Measurement made on upper side of horizontal root; b, measurement made on lower side of horizontal root. Bars indicate the standard deviation of four replicate runs in each orientation.

5) μA cm^{-2} higher (Fig. 4a).

On the lower side changes in the current density following gravistimulation were not consistent among runs. A possible increase in the outward current began 7.0 ± 1.7 (n = 4) min after gravistimulation but it was not distinct as was the increase on the upper side (Fig. 4b). Because the response on the lower side was inconsistent and later than the presentation time, it was considered a poor indicator of gravity sensing.

When similar measurements were made at the tip of the root cap, which has secreting cells but not sensing cells, the current did not change (Fig. 5). The current measured at the elongating zone, where differential growth occurs, also remained constant

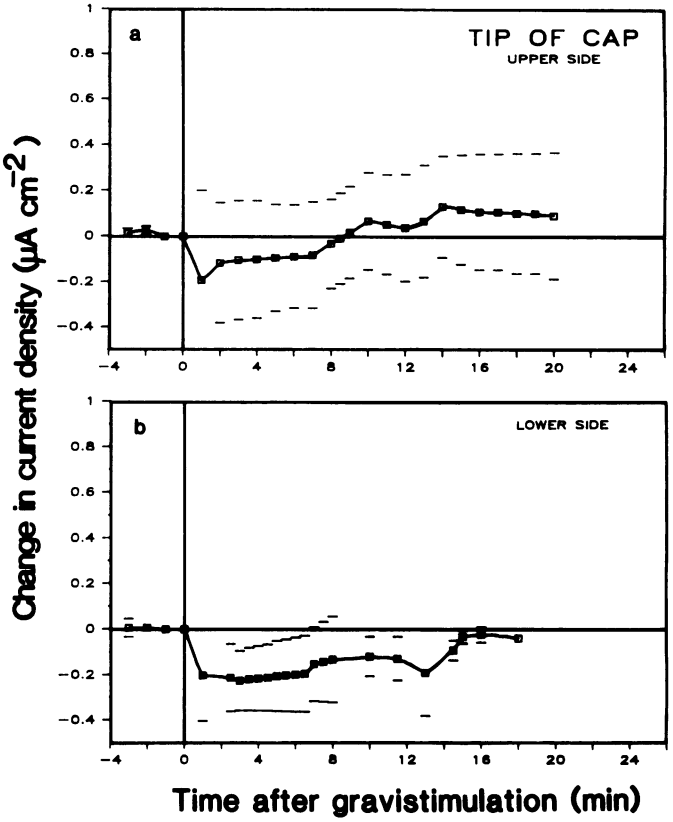

FIG. 5. Time course of current density measured adjacent to the tip of the root cap (100 μm behind the cap apex). a, Measurement made on upper side of horizontal root; b, measurement made on lower side of horizontal root. Bars indicate standard deviation of three replicate runs in each orientation.

for at least 20 min, both on the upper and lower sides of the root (Fig. 6).

In comparison to the net current, the proton flux was not detectably changed as judged by the bromocresol purple color pattern around the cap of roots in agar (Fig. 2).

DISCUSSION

The measurement of electric current densities around maize root tips revealed a change in the current pattern upon gravistimulation in the region of the gravity-sensing columella cells. A distinct increase in outward current appeared on the upper side at about 4 min, coinciding with the presentation time for gravitropism. The net current profile was not similar to the proton flux.

Initial Current Pattern. The current pattern around the root tip is the net result of many different processes which involve differential movement of ions: ion uptake, respiration, electrogenic ion pumps, and so forth. A change in this pattern upon gravistimulation may be the result of modulation of any one of these or it may be caused by induction of ion transport which is specific to gravity sensing. From these experiments it is not possible to distinguish between these possibilities. Therefore, the initial current pattern is only used as a baseline from which changes were measured.

The baseline current pattern was different from those measured by Weisenseel *et al.* (36) in barley and by Behrens *et al.* (3) in *Lepidium*. Those were very similar to each other, with the current density being very small at the tip, with a maximum inward current just proximal to the meristem. The current became smaller further along the elongation zone, finally becom-

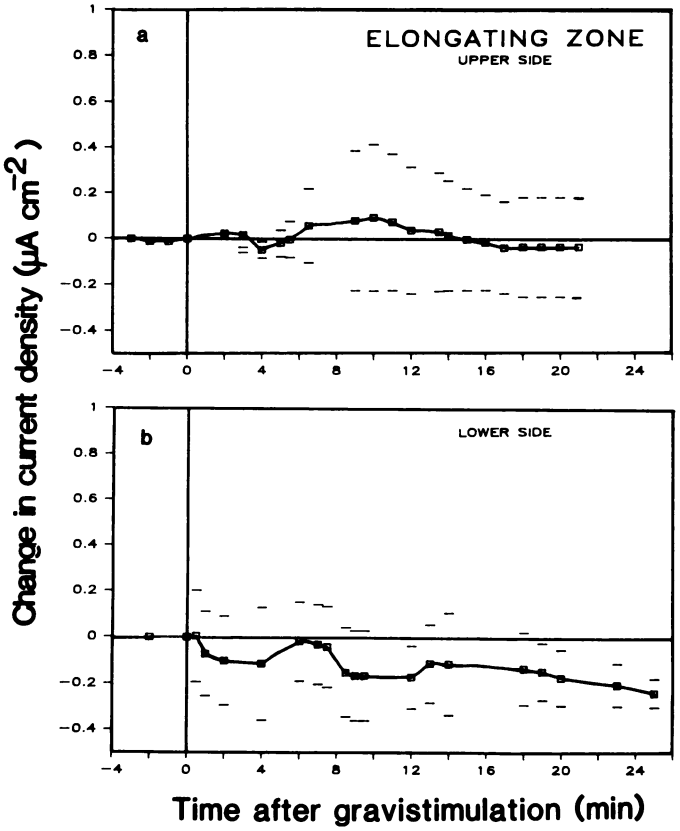

FIG. 6. Time course of current density measured adjacent to the elongating zone (2500 μm behind the cap apex). a, Measurement made on upper side of horizontal root; b, measurement made on lower side of horizontal root. Bars indicate standard deviation of four replicate runs in each orientation.

ing outward. The root-surface potentials measured in *Allium* by Lund and Kenyon (18) would cause outward current at the root cap and inward current at the elongating zone. However, the current pattern at the tip of growing tissues varies a great deal from one species to another. Weisenseel *et al.* (36) noted that the current at the barley root cap also varied from one plant to another. Indeed, in the present study, the transverse current at the root cap was positive in some roots and negative in others, though always more negative closest to the tip of the cap. Even relatively uncomplicated tip-growing tissues, which were all believed to have inward currents at the tip, also show variability (10). The reason for the differences are unknown, but because the entire embryo, including the root, were intact and not in contact with anything, wound currents can be excluded as a source of the difference.

The proton distribution patterns around the maize root, as detected by the color of bromocresol purple in agar, were similar to those published by Weisenseel *et al.* (36) for barley, and by Mulkey and Evans (20) for maize. The baseline current around the cap appeared to involve a minimal flux of protons. At the root meristem, the pronounced influx of protons contrasted with the large efflux of positive charge. The elongating zone was acidic, as expected from acid growth. The lack of correlation between the net current and the proton flux indicates that the baseline current was not primarily a consequence of proton flux as it apparently is in barley (36).

Effect of Gravistimulation. The shift in the current pattern around the root tip after gravistimulation is important because it is coincident, spatially and temporally, with gravity sensing. It appeared only adjacent to the gravity sensing region—the columella. Because the current density remained constant at the tip of the cap, distal to the columella, the current shift did not arise from the secreting cells, and may therefore be ascribed to the cells of the central columella. The current shift also began after 3 to 4 min, coincident with the presentation time. Direct consequences of sensing would be expected to occur promptly after the presentation time. The current shift observed on gravistimulation is at the time and location where a gravisensing-induced event should occur.

The current on the lower side of the columella region was affected by gravistimulation as well, but the shifts were not as distinct nor as repeatable as were those on the upper side. It is difficult to make a general conclusion about the change on the lower side.

There are several ways in which the current shift may be related to the primary sensing event. If specific ion carriers in the plasma membrane are activated by the sedimentation of amyloplasts, a current such as the one observed would result. The current would be a reflection of the movement of those ions. For example, the downward calcium flux induced by gravistimulation is of similar magnitude (16). Small differential potentials across individual cells, as seen by Etherton and Dedolph (7), would act as batteries in series to produce a large potential difference, and current, across the tissue (24).

A current could also be generated if cells depolarized, as observed by Behrens *et al.* (4), because of inhibition of the electrogenic proton pump in the plasma membrane. There was no detectable change in the pH profile around the root cap in the first 30 min; an exchange of as little as 2×10^{-13} mol of protons should have been obvious (a change from orange [pH 5.7] to yellow [pH 5.5] in a 0.5 mm wide band along the root cap). That amount of proton flux would cause a current of 0.05 $\mu A\ cm^{-2}$ for 20 min; the observed current, being 10 times that large, would have been easily observable were it a proton flux. The lack of a pH change around the root cap is evidence against the information-carrying currents being generated by regulation of the proton pump.

There are other possible mechanisms by which a current may arise as a secondary result of gravity sensing. Most schemes for the establishment of a physiological asymmetry involve the translocation of ions, and the current may be only the nonspecific return current resulting from the primary signaling process.

Bioelectric currents do cause the establishment of polarity in some organisms (5, 13, 17, 26, 31, 35). While the current observed in the maize root cap may indicate establishment of a change in polarity, care must be taken not to draw unwarranted conclusions about a possible causal role of the current in establishing a physiological signal.

This paper has presented evidence for an electrophysiological response which is associated with gravity sensing, but which precedes growth-related processes. The ability to determine whether sensing is occurring, even if curvature is prevented, should permit the discrimination of events involved in sensing from those events involved in the differential growth part of gravitropism.

Acknowledgments—We would like to thank Dr. L. F. Jaffe, Dr. C. Scheffey, and A. Shipley of the National Vibrating Probe Facility, Marine Biological Laboratory, Woods Hole, MA, for training in the use of the vibrating probe and for loan of the equipment.

LITERATURE CITED

1. BARLOW PW, EL RATHFINDER 1985 Distribution and redistribution of extension growth along vertical and horizontal gravireacting maize roots. Planta 165: 134–141
2. BEHRENS HM, D GRADMANN 1985 Electrical properties of the vertically growing root tip of *Lepidium sativum* L. Planta 163: 453–462
3. BEHRENS HM, MH WEISENSEEL, A SIEVERS 1982 Rapid changes in the pattern of electric current around the root tip of Lepidium sativum L. following gravistimulation. Plant Physiol 70: 1079–1083
4. BEHRENS HM, D GRADMANN, A SIEVERS 1985 Membrane-potential responses

following gravistimulation in roots of Lepidium sativum L. Planta 163: 463–472
5. BERRY LJ, RC HOYT 1943 Polarization and stimulation of the onion root by direct current. Plant Physiol 18: 372–396
6. BRAUNER L 1926 Ueber das geoelectrische Phänomen. Kolloidchem Beih 23: 143–152
7. ETHERTON B, RR DEDOLPH 1972 Gravity and intracellular differences in membrane potentials of plant cells. Plant Physiol 49: 1019–1020
8. FELDMAN LJ 1981 Light-induced inhibitors from intact and cultured caps of *Zea* roots. Planta 153: 471–475
9. GRAHM L 1964 Measurements of geoelectric potential and auxin-induced potentials in coleoptiles with a refined vibrating electrode technique. Physiol Plant 17: 231–261
10. HAROLD FM 1986 Transcellular currents in tipgrowing organisms: where are they taking us? *In* R Nuccitelli, ed, Ionic Currents in Development. A. R. Liss, New York, pp 359–366
11. JACKSON MB, PW BARLOW 1981 Root geotropism and the role of growth regulators from the cap: a reexamination. Plant Cell Environ 4: 107–123
12. JAFFE LF, R NUCCITELLI 1974 An ultrasensitive vibrating probe for measuring steady extracellular currents. J Cell Biol 63: 614–628
13. JAFFE LF, R NUCCITELLI 1977 Electrical controls of development. Annu Rev Biophys Bioeng 6: 445–476
14. JOHNSSON A 1965 Investigations into the reciprocity rule by means of geotropic and geoelectric measurements. Physiol Plant 18: 945–966
15. LARSEN P 1969 The optimum angle of geotropic stimulation and its relation to the starch statolith hypothesis. Physiol Plant 22: 469–488
16. LEE JS, TJ MULKEY, ML EVANS 1983 Gravity-induced polar transport of calcium across root tips of maize. Plant Physiol 73: 874–876
17. LUND EJ 1923 Electric control of organic polarity in the egg of *Fucus*. Bot Gaz 76: 288–301
18. LUND EJ, WA KENYON 1927 Relation between continuous bio-electric currents and cell respiration. I. Electric correlation potentials in growing root tips. J Exp Zool 48: 333–357
19. MCNITT RE, J SHEN-MILLER 1975 Organelle distributions in geotropism of corn roots. Plant Physiol 56: S-51
20. MULKEY TJ, ML EVANS 1981 Geotropism in corn roots: evidence for its mediation by differential acid efflux. Science 212: 70–71
21. MULKEY TJ, KM KUZMANOFF, ML EVANS 1981 The agar-dye method for visualizing acid efflux patterns during tropistic curvatures. What's New Plant Physiol 12: 9–12
22. NUCCITELLI R (ed) 1986 Ionic Currents in Development. Alan R. Liss, New York
23. PILET PE 1975 The role of the cap in the geotropism of roots exposed to light. Z Pflanzenphysiol 89: 411–426
24. ROSENE HF 1935 Proof of the principle of summation of cell E.M.F.'s. Plant Physiol 10: 209–224
25. SACK FD, MM SUYEMOTO, AC LEOPOLD 1985 Amyloplast sedimentation kinetics in gravistimulated maize roots. Planta 165: 295–300
26. SAUNDERS MJ 1986 Correlation of electrical current influx with nuclear position and division in *Funaria* caulonema tip cells. Protoplasma 132: 32–37
27. SCHEFFEY C 1986 Electric fields and the vibrating probe, for the uninitiated. *In* R Nuccitelli, ed, Ionic Currents in Development. A. R. Liss, New York, pp xxv–xxxvii
28. SCHEFFEY C 1986 Pitfalls of the vibrating probe technique, and what to do about them. *In* R Nuccitelli, ed, Ionic Currents in Development. Alan R. Liss, New York, pp 3–12
29. SCHEFFEY C, JK FOSKETT, TE MACHEN 1983 Localization of ionic pathways in the teleost opercular membrane by extracellular recording with a vibrating probe. J Membr Biol 75: 193–203
30. SCHRANK AR 1945 Changes in electrical polarity in the *Avena* coleoptile as an antecedent to hormone action in geotropic response. Plant Physiol 20: 133–136
31. SCHRANK AR 1948 Electrical and curvature responses of the *Avena* coleoptile to transversely applied direct current. Plant Physiol 23: 188–200
32. SCHWARTZ H, HAW SCHNEIDER 1985 Light-mediated growth inhibition of maize roots. J Plant Physiol 119: 281–284
33. TANADA T, C VINTEN-JOHANSEN 1980 Gravity induces fast electrical field changes in soybean hypocotyls. Plant Cell Environ 3: 127–130
34. VERSEL JM, PE PILET 1986 Distribution of growth and proton efflux in gravireactive roots of maize (*Zea mays* L.). Planta 167: 26–29
35. WEISENSEEL MH, RM KICHENER 1981 Ionic currents as control mechanisms in cytomorphogenesis. Cell Biol Monogr 8: 379–399
36. WEISENSEEL MH, A DORN, LF JAFFE 1975 Natural H^+ currents traverse growing roots and root hairs of barley (*Hordeum vulgare* L.). Plant Physiol 64: 512–518
37. WOODCOCK AER, MB WILKINS 1969 The geoelectric effect in plant shoots. I. The characteristics of the effect. J Exp Bot 20: 156–169
38. WOODCOCK AER, MB WILKINS 1969 The geoelectric effect in plant shoots. II. Sensitivity of concentration chain electrodes to reorientation. J Exp Bot 20: 687–697